EPISTASIS IN THREE-WAY CROSSES INVOLVING EARLY AND LATE INBRED LINES OF MAIZE

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ABSTRACT

Three single hybrids were crossed with 12 early and late (flint and dent) inbred lines. The three-way and single crosses were compared for the influence of epistasis on grain yield. The inbred lines with the same growing season used as female and male parents were involved in significant epistatic effects. Depiste the fact that both flint and dent types of inbreds were included in the present study, the obtained epistatic deviations were comparable in frequency with other studies with only dent inbred lines. The use of single crosses as parents for three-way crosses was found to cause under estimation of the positive and overestimation of the negative epistatic deviations. The group of three-way hybrids with late parental lines recorded the lowest number of three-way crosses with epistatic deviations from the predicted performances.

Key words: epistatic deviation, maize observed yield, predicted yield.

INTRODUCTION

Soon after Shull and East (1908) developed single crosses between the inbred lines of maize, a major problem arose, that of finding an efficient method to produce hybrid seeds.

Consequently, in 1918, Jones suggested the alternative of using double crosses, and in 1932 Jenkins came with the idea of elaborating formulae of double crosses and three-way crosses, on the prediction basis (Hallauer and Miranda, 1981). By the end of the 1970, in the USA, single crosses were cultivated on very large areas (Duvick, 1984). Therefore, a natural question arises: is it necessary to develop hybrid formulae for double or three-way cross hybrids ?

The answer is that, within regions with restricted thermic resources, it could be more useful to cultivate double cross and three-way cross hybrids owing to the following reasons:

- the yield ability of very early and early inbred lines is relatively reduced and the seed production from the hybridization plots is not economical or the cost of the seed is prohibitive;
- a higher adaptability of double crosses and three-way crosses for the large diversity of climatic and soil conditions from these regions;
- three-way cross and double cross hybrids have, in most cases, larger seeds, assuring an early vigor to the plant (Beil, 1975; Schnell, 1975; Gupta and Kovacs, 1976; Schnell and Singh, 1978; Nemeth, 1981; Melchinger et al., 1986; Cãbulea, 1987; Haº, 1992).

It is well-known that for developing three-way cross and double cross hybrids, the prediction of formulae is frequently used, based on the value of single cross hybrids possible to obtain between the component parental lines. In most cases the observed yields of three-way crosses and double crosses, deviate from the prediction.

Many authors who approached this problem (Bauman et al., 1959; Sprague et al., 1962; Otsuka et al., 1972; Stuber, 1973; Schnell and Singh, 1978; Melchinger et al., 1986) consider that the differences recorded between prediction and double and three-way crosses are due to the epistatic effects.

Recent reports have pointed out the importance of epistasis of dominant x dominant and additive x dominant type in expressing heterosis in maize, besides dominance and superdominance (Goodnight, 1999; Miranda Filho, 1999).

The aim of the present paper is to demonstrate the existence of epistatic effects within the group of inbred lines with which we have worked to obtain hybrids adapted to restricted thermic potential regions and to study the role of the epistatic deviations in predicting the formulae of three-way crosses and the possibility to identify some methods of restricting the

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epistatic deviations with negative effect upon the yield ability.

MATERIALS AND METHODS

The evidence of the epistatic effects was proved with the method of average generations analysis (Gamble, 1962).

Higher densities (70,000 plants/ha and 80,000 plants/ha) were used to emphasize the epistatic interactions (Martin and Hallauer, 1977).

To develop single crosses and three-way crosses, three inbred lines RT 223, RT 291 and W 182B (with middle growing season) and the single crosses RT 223 x W 128B, RT 223 x RT 291 and W 182B x RT 291 were used as maternal forms and three groups of inbred lines (very early, middle-early and late) as male parent forms.

The necessary hybrid seed was produced with these lines for a simultaneous trial (within the same experimental system) of the corresponding single crosses and three-way crosses. The single and three-way crosses according to the above model were distributed in four comparative trials, at three experimental densities (50,000 plants/ha, 70,000 plants/ha and 90,000 plants/ha).

Each trial included 18 genotypes, 9 single crosses and 9 three-way crosses, obtained by crossing the inbred lines and the maternal crosses, with other three inbred lines (as male parent) diversified concerning the growing season (early, middle and late).

The differences between the predicted yield and the observed yield for the three-way crosses were pointed out with the orthogonal comparisons among the groups of hybrids, and the deviations in three-way crosses were calculated with the formula suggested by Schnell and Singh (1978):

$$E_{(A\,x\,C)} = \frac{SC_{A\,x\,C} + SC_{B\,x\,C}}{2} - TWC_{(A\,x\,B)\,x\,C}$$

were $E_{(A\,x\,B)\,x\,C}$ = epistatic deviation of the three-way cross as compared to the prediction obtained on the basis of non-parental single crosses.

The effects of specific combining ability in three-way crosses (owing to the interaction among the male inbred line and the segregating gametes of the maternal single cross) were calculated as a yield deviation of the three-way crosses obtained from the regression observed yield depending on predicted yield.

Effects SCA (in TWC) = $\hat{y} - y_{TWC}$.

RESULTS AND DISCUSSIONS

The study of the genic effects involved in the yield ability control, performed with the average generation analysis, at densities of 40,000 and 80,000 plants/ha (Table 1) emphasized the preponderance of dominance effects in yield heredity, but also pointed out the epistatic effects, especially at densities of 80,000 plants/ha.

For a number of seven pairs of inbred lines, involving crossings among the whole range of inbred lines compatible with less favourable climatic conditions from the central and northern areas of Romania, the average generations analysis showed in all cases the importance of the dominance effects (Table 2), but also evidenced a strong implication of the epistatic interactions of d x d, a x a and a x d type.

The high value of the epistatic interactions d x d type comparable in some situations with the value of the intraallelic interactions (Sv 952 x S 54, DBe 16 x RT 9, W 401 x RF 175) should be noticed.

From both tables one can observe that the contribution of additive effects is reduced, this aspect being critically remarked also by Hallauer and Miranda Filho (1981) who spotlighted this deficiency of the average generation

Table 1. Estimates of six genetic effects in yielding capacity

Crosses	Densities	Genetic effects						h[1)]
		m	a	d	aa	ad	dd	
RT 10 x W 182 B	40,000 pl/ha	131.45***	16.48**	169.86***	45.16**	45.82***	-11.60^{0}	113.10
FE x DME	80,000 pl/ha	76.82***	-1.40	38.96***	-17.12^{00}	8.42*	80.66***	136.78
Fv 120 x PI 187	40,000 pl/ha	109.91***	-10.24	214.34***	96.20***	-13.06^{00}	-2.40	115.74
ME x FL	80,000 pl/ha	66.48***	-0.78	56.52****	5.96	1.34	67.12***	117.64
PI 187 x A 344	40,000 pl/ha	131.65***	-1.10	174.84***	34.24*	-3.66	-35.80^{00}	104.80
FL x DE	80,000 pl/ha	70.13***	17.94***	105.84***	32.00**	26.82***	28.44**	102.28

1) h – heterotic effects; h = d + dd – aa (Moreno Gonzales and Dudley, 1981)
F – flint; D – dent; E – early; ME – medium early; L – late

Table 2. Estimates of six genetic effects in yielding capacity (70,000 pl/ha)

Crosses	Genetic effects						h[1)]
	m	a	d	aa	ad	dd	
Fv 7 x W 375 B FE x DL	104.84***	-20.94^{000}	146.13***	39.72***	-1.48	-17.46^{000}	88.77
W 401 x RF 175 DE x DL	106.77***	-37.94^{000}	150.68***	55.84***	-27.46^{000}	-90.84^{000}	4.00
CO 125 R x RT 384 a DE x DL	102.53***	16.96***	113.80***	19.20*	8.26**	-27.48^{00}	67.12
SV 952 x S 54 DME x DE	100.70***	-6.30	86.20***	-1.32	4.10	60.48***	148.00
DBe 16 x RT 9 FE x FE	92.52***	7.50	45.10****	-23.36^{0}	0.60	90.12***	158.58
RT 223 x RT 365 DME x FL	108.40**	-10.84^{000}	147.91***	52.40***	4.92	-29.37^{000}	66.14
Lo 3 Berg. x RT 251 FL x FME	98.23***	-5.91	15.73***	-2.20	-11.48^{00}	30.21***	48.14

1) h. – heterotic effects; h = d + dd – aa (Moreno Gonzales and Dudley, 1981)
F – flint; D – dent; E – early; ME – medium early; L – late

Table 3. Analyses of variance for yielding capacity (Orthogonal analyses in relation with maternal – female parent)

Sources	fd	Mean square (s^2) for trial 1	Mean square (s^2) for trial 2	Mean square (s^2) for trial 3	Mean square (s^2) for trial 4
Large plots	5				
Densities	2	1046.16	724.96**	839.90**	678.63
Reps	1				
Error (a)	2	102.81	11.71	20.17	24.27
Small plots	107				
Hybrids	17	437.49**	1223.42**	1090.28**	419.30**
Comparisons among SC obtained with female parent RT 223	(2)	727.69**	979.03**	238.29**	536.00**
Comparisons among SC obtained with female parent RT 291	(2)	501.19**	2332.75**	794.52**	253.07**
Comparisons among SC obtained with female parent W 182 B	(2)	391.50**	2280.32**	1749.99**	230.50**
Comparisons among TWC obtained with female parent RT 223 x W 182 B	(2)	174.05**	869.12**	2545.02**	1335.99**
Comparisons among TWC obtained with female parent RT 223 x RT 291	(2)	387.02**	1157.38**	1464.54**	725.09**
Comparisons among TWC obtained with female parent W 182 B x RT 291	(2)	379.25**	1288.52**	1355.65**	131.83
Comparisons among groups of hybrids with the same female parents	(5)	463.01**	596.76**	439.74**	140.64
Comparison among groups of SC	[(2)]	597.53**	34.41	754.91**	53.06
Comparison among groups of TWC	[(2)]	305.60**	1371.81**	268.47**	215.23*
Comparison SC - TWC	[(1)]	508.73**	172.01	151.04	165.02
Densities x Hybrids (D x H)	34	89.33**	133.97	76.92	78.03
Error (b)	51	50.56	184.54	75.32	64.44

analysis.

In order to find out the differences between single crosses and three-way crosses, obtained with the same male inbred line, they were distributed in four trials.

The results of analysis of variance as well as the orthogonal analysis are presented in tables 3 and 4. For yield ability, in all four trials, the differences between the tested hybrids were statistically assured. Taking into consi-deration this aspect, we passed on to the orthogonal analysis of variances.

We can notice (Table 3) the comparisons between single crosses and three-way crosses (comparisons SC-TWC), statistically significant only in the case of trial 1. For the other trials, the variance of the three-way crosses, obtained with the same maternal forms, appears significant for all four comparative trials, while for the single crosses, the variance is significant only in the case of two out of the four trials. These statistic data show a higher variability of the three-way crosses, and the presence of some additional genetic mechanisms, probably epistatic, which determined such results.

Table 4 presents the orthogonal analysis of variances in relation with the growing season of the male parent.

For all the analysed cases concerning early and late male parent lines, the differences between single crosses and the corresponding three-way crosses were statistically non-significant.

The fact that in the case of the comparisons "SC-TWC with middle early male parent lines", in all four analysed trials, the variance has statistically significant values, points out the existence of some differences between three-way crosses and single crosses, on the basis of which the predictions were made.

Table 4. Analyses of variance for yielding capacity (Orthogonal analyses in relation with male parent)

Sources	fd	Mean square (s^2) for trial 1	Mean square (s^2) for trial 2	Mean square (s^2) for trial 3	Mean square (s^2) for trial 4
Large plots	5				
Densities	2	1046.16	724.96**	839.90**	678.63
Reps	1				
Error (a)	2	102.81	11.71	20.17	24.27
Small plots	107				
Hybrids	17	437.49**	1223.42**	1090.28**	419.30**
Comparisons among groups of hybrids with the same male parent	(2)	762.21**	7880.02**	6970.28**	2386.00**
Comparisons among hybrids with male parent – very early inbred line	(5)	304.93**	219.75	129.53	150.13
Comparisons among SC with very early male parent	[(2)]	619.50**	179.28	163.94	68.15
Comparisons among TWC with very early male parent	[(2)]	78.98	364.15	123.77	288.98**
Comparisons among SC-TWC with very early male parent	[(1)]	127.69	11.90	72.25	36.40
Comparisons among hybrids with male parent – late inbred line	(5)	536.64**	503.85**	419.52	141.50
Comparisons among SC with late male parent	[(2)]	828.90**	269.30**	62.29	13.62
Comparisons among TWC with late male parent	[(2)]	182.79*	768.45**	305.80**	200.02
Comparisons among SC-TWC with late male parent	[(1)]	659.63**	443.80**	1355.47**	282.27*
Comparisons among hybrids with male parent – middle early inbred line	(5)	341.05**	283.39	369.66**	178.95*
Comparisons among SC with middle early male parent	[(2)]	541.68**	253.81	895.46**	186.92
Comparisons among TWC with middle early male parent	[(2)]	308.78**	441.67	4.42	260.31
Comparisons among SC-TWC with middle early male parent	[(1)]	4.34	26.01	48.53	0.34
Densities x Hybrids (D x H)	34	89.33	133.97	79.62	78.03
Error (b)	51	50.56	184.57	75.32	63.44

For the aim of our work we are especially interested in the comparisons:

"SC-TWC with male parent – very early lines";

"SC-TWC with male parent – middle early lines";

"SC-TWC with male parent – late lines".

The mentioned aspects could confirm that the incidence of the epistatic effects could be more frequent and more intense within the crossings of less diversified parents. The following tables (5, 6, 7) present, related to the growing season for the male parent lines, the observed and predicted yields of the three-way crosses.

Table 5. Grain yield (q/ha) predicted and observed in three-way crosses (TWC) obtained with very early male parental inbreds and estimates for epistatic deviations

TWC	Non parental SC yield average (predicted for TWC), q/ha	Observed yield in TWC q/ha	Differences between predicted and observed yields (epistatic deviations)	Effects of specific combining ability in TWC (SCA)
(RT 223 x W 182 B) x Fv 7	95.7	97.9	-2.2	-3.7
(W 182B x RT 291) x Fv 7	97.6	91.5	+6.1	+3.9
(RT 223 x RT 291) x Fv 7	105.3	97.8	+7.5	+2.4
Hybrid average with male parent Fv 7	99.5	95.7	+3.8	
LSD 5%			8.3	
(RT 223 x W 182 B) x Rc 7-47	87.5	69.3	+18.2*	+13.9
(W 182B x RT 291) x Rc 7-47	83.8	79.4	+4.4	+0.3
(RT 223 x RT 291) x Rc 7-47	79.0	84.6	-5.6	-9.5
Hybrid average with male parent Rc 7-47	83.4	77.8	+5.7	
LSD 5%			15.7	
(RT 223 x W 182 B) x Sv 952	89.0	92.6	-3.6	-7.5
(W 182B x RT 291) x Sv 952	94.1	99.4	-5.3	-8.2
(RT 223 x RT 291) x Sv 952	90.9	92.3	-1.4	-5.0
Hybrid average with male parent Sv 952	91.3	94.8	-3.4	
LSD 5%			10.1	
(RT 223 x W 182 B) x Bucovina 66	97.2	89.1	+8.1*	+5.8
(W 182B x RT 291) x Bucovina 66	98.0	97.5	+0.5	-1.4
(RT 223 x RT 291) x Bucovina 66	100.5	102.8	-2.3	-3.0
Hybrid average with male parent Bucovina 66	98.6	96.5	+2.1	
LSD 5%			8.1	

Table 6. Grain yield (q/ha) predicted and observed in three-way crosses (TWC) obtained with middle early male parental inbreds and estimates for epistatic deviations

TWC	Non parental SC yield average (predicted for TWC), q/ha	Observed yield in TWC q/ha	Differences between predicted and observed yields (epistatic deviations)	Effects of specific combining ability in TWC (SCA)
(RT 223 x W 182 B) x RT 251	96.8	88.7	+8.1	+6.2
(W 182B x RT 291) x RT 251	107.6	96.8	+10.8	+4.8
(RT 223 x RT 291) x RT 251	106.2	99.3	+6.9	+1.5
Hybrid average with male parent RT 251	103.5	94.6	+8.6**	
LSD 5%			8.3	
(RT 223 x W 182 B) x RT 410	104.4	89.1	+15.3	+10.1
(W 182B x RT 291) x RT 410	107.2	100.6	+6.6	+1.3
(RT 223 x RT 291) x RT 410	111.1	11.8	-0.7	-6.1
Hybrid average with male parent RT 410	107.6	100.5	+7.1**	
LSD 5%			15.7	
(RT 223 x W 182 B) x RPI 690	91.5	72.7	+18.8*	+15.4
(W 182B x RT 291) x RPI 690	93.9	85.5	+8.4	+5.4
(RT 223 x RT 291) x RPI 690	92.6	84.6	+8.0	+4.8
Hybrid average with male parent RPI 690	92.7	80.9	+11.7**	
LSD 5%			10.1	
(RT 223 x W 182 B) x W 401	89.7	77.2	+12.5	+6.5
(W 182B x RT 291) x W 401	89.6	88.4	+1.2	-4.8
(RT 223 x RT 291) x W 401	88.4	85.3	+3.1	-3.5
Hybrid average with male parent W 401	89.2	83.6	+5.6*	
LSD 5%			8.1	

Table 7. Grain yield (q/ha) predicted and observed in three-way crosses (TWC) obtained with late male parental inbreds and estimates for epistatic deviations

TWC	Non parental SC yield average (predicted for TWC) q/ha	Observed yield in TWC q/ha	Differences between predicted and observed yields (epistatic deviations)	Effects of specific combining ability in TWC (SCA)
(RT 223 x W 182 B) x RF 211	110.6	98.7	+12.4	+5.3
(W 182B x RT 291) x RF 211	101.4	107.8	-5.8	-9.4
(RT 223 x RT 291) x RF 211	107.9	112.3	-4.4	-10.5
Hybrid average with male parent RF 211	106.6	105.9	+0.7	
LSD 5%			8.3	
(RT 223 x W 182 B) x Mo 17	102.9	91.0	+11.9	+6.8
(W 182B x RT 291) x Mo 17	105.2	107.6	-2.4	-7.6
(RT 223 x RT 291) x Mo 17	98.8	103.2	-4.4	-9.3
Hybrid average with male parent Mo 17	102.3	100.6	+1.7	
LSD 5%			15.7	
(RT 223 x W 182 B) x RT B 329	110.4	113.8	-3.4	-3.1
(W 182B x RT 291) x RT B 329	119.2	115.5	+3.7	+5.8
(RT 223 x RT 291) x RT B 329	107.5	114.7	-7.2	-7.5
Hybrid average with male parent RT B 329	112.4	114.7	-2.3	
LSD 5%			10.1	
(RT 223 x W 182 B) x A 632	105.2	106.8	-1.6	+0.1
(W 182B x RT 291) x A 632	99.6	94.8	+4.8	+4.8
(RT 223 x RT 291) x A 632	101.8	105.5	-3.7	-3.7
Hybrid average with male parent A 632	102.2	102.4	-0.2	
LSD 5%			8.1	

The differences between predicted and observed yield, in three-way crosses may be attributed both to epistatic deviations and to specific interaction effects, due to the additional genic recombinations, which take place in the three-way crosses, as compared to the single crosses, used for prediction.

The data presented in table 5, for very early male parent lines, prove that in their case (Fv-7, Rc 7-47, Bucovina 66) the average of non-parental single crosses, on the basis of which the predictions were made, had been higher than the observed yield in three-way crosses, but in all cases the differences were statistically non-significant.

For the group of early inbred lines, we must notice the value of the hybrids with Sv 952, male parent line for which the epistatic deviations and the effects of specific combining ability, may be appreciated as favourable for the three-way crosses.

The data from table 6, corresponding to the medium-early male parent inbred lines, are relevant for the recorded differences between the predicted and observed yields.

In all four analysed cases, the average of three-way crosses was statistically inferior (in three out of the four cases, it was distinctly significant) as compared to the hybrids for prediction.

Only in one out of the 12 analysed cases (RT 223 x RT 291) x RT 410, the value of the three-way cross was superior to prediction, in all the other cases the differences being in favour of the prediction, with values ranging between 1.2-18.8 q/ha.

For the three-way crosses, obtained with late male parent lines (Table 7), the differences compared to predictions, ranged on the average, for the four comparative trials, between + 1.7 q/ha for the hybrids obtained with Mo 17 and – 2.3 q/ha for the hybrids obtained with the male parent inbred line RT B329.

The reduced epistatic deviations, favourable to three-way crosses, in eight out of the 12 cases, are an illustration of the possibility to find out some combinations of three-way crosses, to which the epistatic effects, considered by many authors responsible for the lower yield of the three-way crosses as compared to predictions (Sprague et al., 1962; Stuber et al., 1973; Schnell, 1975; Schnell and Singh, 1978; Melchinger et al., 1986) be minimized or even used positively.

Relevant concerning the difference between the observed three-way cross yield and the non-parental single cross yield is the graphic presentation of the yield regression as related to the predicted yield (Figure 1).

If for the early and late male parent inbreds, the regression lines were relatively close to the bisector line of the coordinating axes, for the three-way crosses obtained with male parent lines having the same growing season as the maternal inbred lines, the three-way crosses yield regression is inferior to the bisector line, none of the three-way crosses reaching the prediction level.

Our results are in accordance with those of Hallauer and Miranda (1981), Moreno-Gonzales and Dudley (1981) and Melchinger et al. (1986) for North-American and central European inbred lines, to which, in yield heredity, the intraallelic effects are important but the interallelic effects of d x d or d x a type are important as well.

For the whole balanced set of compared single crosses and three-way crosses, the high deviation amplitude of the three-way crosses compared to the prediction may be attributed to the large range of inbred lines used in the cross-breeding system. The obtention of higher yields with three-way crosses, superior to predictions in a few combinations, where there have been used earlier or later male parent inbred lines than the maternal lines, could be the expression of some positive epistatic deviations produced between maternal lines within parental single crosses and male parental lines.

The reduced frequency of good combinations between maternal single crosses and in-

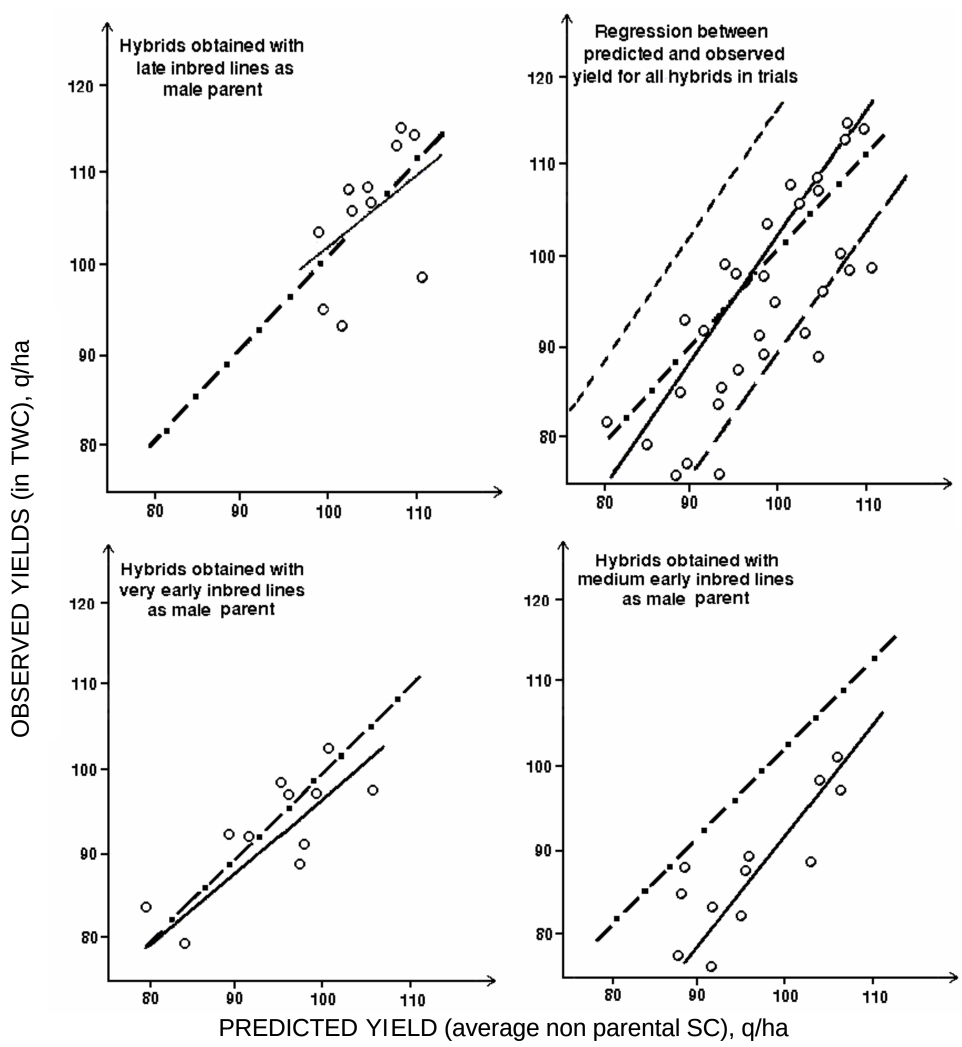

Figure 1 . Regression deviations from bisector line

bred lines with the same vegetation period could be explained by a favourable balance of genes with epistatic actions in single crosses, the balance in three-way crosses being disturbed.

It is obvious anyway, regardless the genetic complications to obtain valuable three-way crosses, the benefits in seed production are important at commercial level. This advantage pleads for an additional creative effort to obtain three-way crosses with more favourable genetic balance.

CONCLUSIONS

The three-way crosses are, with a relative higher frequency, inferior to the single crosses for prediction, when between the parental inbred lines do not exist diversity for the growing season. When the male parent inbred lines were earlier or later than the parental inbred lines of the maternal single crosses, the three-way crosses exhibit yields resembling to predictions with a higher frequency.

The effects of specific combining ability, expressed by yield deviations noticed in three-way crosses as compared to the predictions, generally have the same direction in epistatic deviations and the numerical values are relatively close. The reduction of the differences between three-way crosses and predictions, when the male parent form has a shorter or a longer growing season than the inbred lines of the maternal single cross, is due to the positive epistatic deviations that help realize a new genic balance within the three-way cross.

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Table 1 . Estimates of six genetic effects in yielding capacity

Crosses	Densities	Genetic effects						h 1)
		m	a	d	aa	ad	dd	
RT 10 x W 182 B	40.000 pl/ha	131.45***	16.48**	169.86***	45.16**	45.82***	-11.60 0	113.10
FE x DME	80.000 pl/ha	76.82***	-1.40	38.96***	-17.12 00	8.42*	80.66***	136.78
Fv 120 x PI 187	40.000 pl/ha	109.91***	-10.24	214.34***	96.20***	-13.06 00	-2.40	1115.74
ME x FL	80.000 pl/ha	66.48***	-0.78	56.52****	5.96	1.34	67.12***	117.64
PI 187 x A 344	40.000 pl/ha	131.65***	-1.10	174.84***	34.24*	-3.66	-35.80 00	104.80
FL x DE	80.000 pl/ha	70.13***	17.94***	105.84***	32.00**	26.82***	28.44**	102.28

1) – h. heterotic effects; h = d + dd – aa (Moreno Gonzales and Dudley, 1981)
F – flint; D – dent; E – early; ME – medium early; K – late

Table 2 . Estimates of six genetic effects in yielding capacity

Crosses	Genetic effects						h 1)
	m	a	d	aa	ad	dd	
Fv 7 x W 375 B FE x DL	104.84***	-20.94 000	146.13***	39.72***	-1.48	-17.46 000	88.77
W 401 x RF 175 DE x DL	106.77***	-37.94 000	150.68***	55.84***	-27.46 000	-90.84 000	4.00
CO 125 R x RT 384 a DE x DL	102.53***	16.96***	113.80***	19.20*	8.26**	-27.48 00	67.12
SV 952 x S 54 DME x DE	100.70***	-6.30	86.20***	-1.32	4.10	60.48***	148.00
DBe 16 x RT 9 FE x FE	92.52***	7.50	45.10****	-23.36 0	0.60	90.12***	158.58
RT 223 x RT 365 DME x FL	108.40**	-10.84 000	147.91***	52.40***	4.92	-29.37 000	66.14
Lo 3 Berg. x RT 251 FL x FME	98.23***	-5.91	15.73***	-2.20	-11.48 00	30.21***	48.14

2) – h. heterotic effects; h = d + dd – aa (Moreno Gonzales and Dudley, 1981)
F – flint; D – dent; E – early; ME – medium early; K – late

Table 3 . Analyses of variance for yielding capacity (Orthogonal analyses in relation with maternal – female parent)

Sources	fd	Mean square (s^2) for trial 1	Mean square (s^2) for trial 2	Mean square (s^2) for trial 3	Mean square (s^2) for trial 4
Large plots	5				
Densities	2	1046.16	724.96**	839.90**	678.63
Reps	1				
Error (a)	2	102.81	11.71	20.17	24.27
Small plots	107				
Hybrids	17	437.49**	1223.42**	1090.28**	419.30**
Comparisons among SC obtained with	(2)	727.69**	979.03**	238.29**	536.00**

female parent RT 223					
Comparisons among SC obtained with female parent RT 291	(2)	501.19**	2332.75**	794.52**	253.07**
Comparisons among SC obtained with female parent W 182 B	(2)	391.50**	2280.32**	1749.99**	230.50**
Comparisons among TWC obtained with female parent RT 223 x W 182 B	(2)	174.05**	869.12**	2545.02**	1335.99**
Comparisons among TWC obtained with female parent RT 223 x RT 291	(2)	387.02**	1157.38**	1464.54**	725.09**
Comparisons among TWC obtained with female parent W 182 B x RT 291	(2)	379.25**	1288.52**	1355.65**	131.83
Comparisons among groups of hybrids with the same female parents	(5)	463.01**	596.76**	439.74**	140.64
Comparison among groups of SC	[(2)]	597.53**	34.41	754.91**	53.06
Comparison among groups of TWC	[(2)]	305.60**	1371.81**	268.47**	215.23*
Comparison SC - TWC	[(1)]	508.73**	172.01	151.04	165.02
Densities x Hybrids (D x H)	34	89.33**	133.97	76.92	78.03
Error (b)	51	50.56	184.54	75.32	64.44

Table 4 . Analyses of variance for yielding capacity (Orthogonal analyses in relation with maternal – male parent)

Sources	fd	Mean square (s^2) for trial 1	Mean square (s^2) for trial 2	Mean square (s^2) for trial 3	Mean square (s^2) for trial 4
Large plots	5				
Densities	2	1046.16	724.96**	839.90**	678.63
Reps	1				
Error (a)	2	102.81	11.71	20.17	24.27
Small plots	107				
Hybrids	17	437.49**	1223.42**	1090.28**	419.30**
Comparisons among groups of hybrids with the same male parent	(2)	762.21**	7880.02**	6970.28**	2386.00**
Comparisons among hybrids with male parent – very early inbred line	(5)	304.93**	219.75	129.53	150.13
Comparisons among SC with very early male parent	[(2)]	619.50**	179.28	163.94	68.15
Comparisons among TWC with very early male parent	[(2)]	78.98	364.15	123.77	288.98**
Comparisons among SC-TWC with very early male parent	[(1)]	127.69	11.90	72.25	36.40
Comparisons among hybrids with male parent – late inbred line	(5)	536.64**	503.85**	419.52	141.50
Comparisons among SC with late male parent	[(2)]	828.90**	269.30**	62.29	13.62
Comparisons among TWC with late male parent	[(2)]	182.79*	768.45**	305.80**	200.02
Comparisons among SC-TWC with late male parent	[(2)]	659.63**	443.80**	1355.47**	282.27*
Comparisons among hybrids with male parent – middle early inbred line	(5)	341.05**	283.39	369.66**	178.95*
Comparisons among SC with middle early male parent	[(2)]	541.68**	253.81	895.46**	186.92
Comparisons among TWC with middle early male parent	[(2)]	308.78**	441.67	4.42	260.31
Comparisons among SC-TWC with middle early male parent	[(2)]	4.34	26.01	48.53	0.34
Densities x Hybrids (D x H)	34	89.33	133.97	79.62	78.03
Error (b)	51	50.56	184.57	75.32	63.44

Table 5. Grain yield (q/ha) predicted and observed in three-way crosses (TWC) obtained with very early male parental inbreds and estimates for epistatic deviations

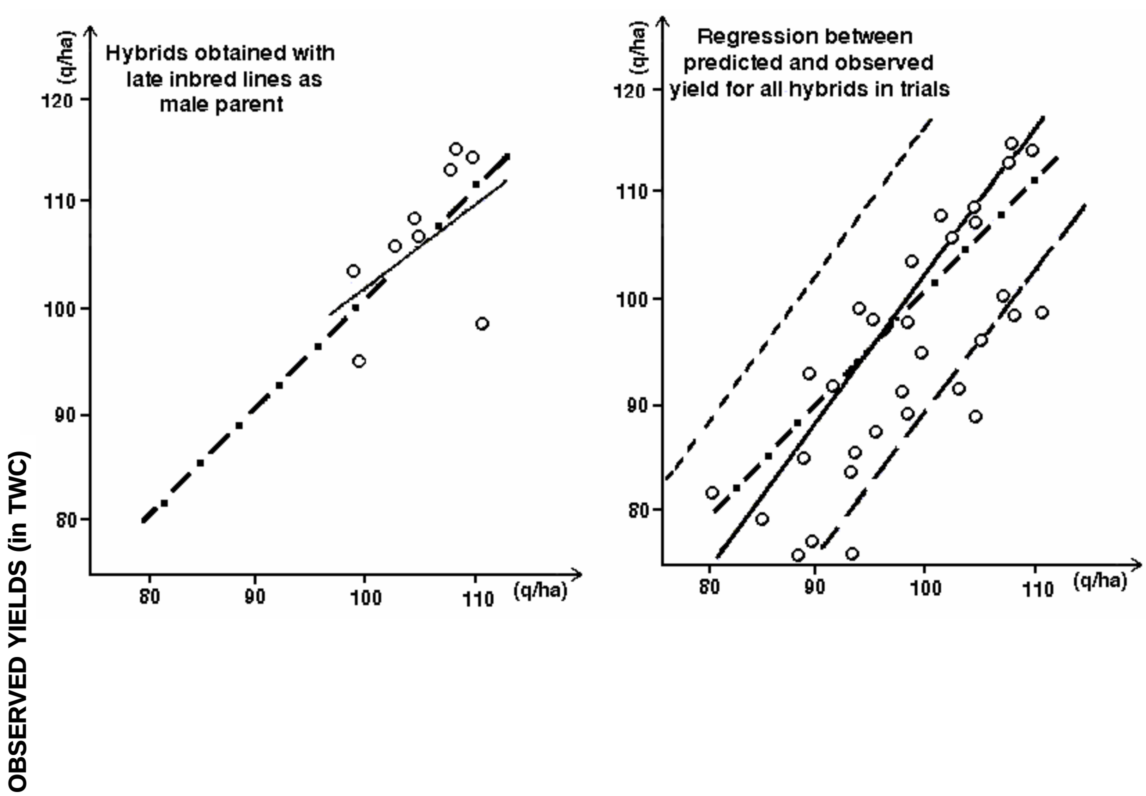
TWC	Non parental SC yield average (predicted for TWC) q/ha	Observed yield in TWC q/ha	Differences between predicted and observed yields (epistatic deviations)	Effects of specific combining ability in TWC (SCA)
(RT 223 x W 182 B) x Fv 7	95.7	97.9	-2.2	-3.7
(W 182B x RT 291) x Fv 7	97.6	91.5	+6.1	+3.9
(RT 223 x RT 291) x Fv 7	105.3	97.8	+7.5	2.4
Hybrid average with male parent Fv 7	99.5	95.7	+3.8	
LSD 5%			8.3	
(RT 223 x W 182 B) x Rc 7-47	87.5	69.3	+18.2*	+13.9
(W 182B x RT 291) x Rc 7-47	83.8	79.4	+4.4	+0.3
(RT 223 x RT 291) x Rc 7-47	79.0	84.6	-5.6	-9.5
Hybrid average with male parent Rc 7-47	83.4	77.8	+5.7	
LSD 5%			15.7	
(RT 223 x W 182 B) x Sv 952	89.0	92.6	-3.6	-7.5
(W 182B x RT 291) x Sv 952	94.1	99.4	-5.3	-8.2
(RT 223 x RT 291) x Sv 952	90.9	92.3	-1.4	-5.0
Hybrid average with male parent Sv 952	91.3	94.8	-3.4	
LSD 5%			10.1	
(RT 223 x W 182 B) x Bucovina 66	97.2	89.1	+8.1*	+5.8
(W 182B x RT 291) x Bucovina 66	98.0	97.5	+0.5	-1.4
(RT 223 x RT 291) x Bucovina 66	100.5	102.8	-2.3	-3.0
Hybrid average with male parent Bucovina 66	98.6	96.5	+2.1	
LSD 5%			8.1	

Table 6. Grain yield (q/ha) predicted and observed in three-way crosses (TWC) obtained with middle early male parental inbreds and estimates for epistatic deviations

TWC	Non parental SC yield average (predicted for TWC) q/ha	Observed yield in TWC q/ha	Differences between predicted and observed yields (epistatic deviations)	Effects of specific combining ability in TWC (SCA)
(RT 223 x W 182 B) x RT 251	96.8	88.7	+8.1	+6.2
(W 182B x RT 291) x RT 251	107.6	96.8	+10.8	+4.8
(RT 223 x RT 291) x RT 251	106.2	99.3	+6.9	+1.5
Hybrid average with male parent RT 251	103.5	94.6	+8.6**	
LSD 5%			8.3	
(RT 223 x W 182 B) x RT 410	104.4	89.1	+15.3	+10.1
(W 182B x RT 291) x RT 410	107.2	100.6	+6.6	+1.3
(RT 223 x RT 291) x RT 410	111.1	11.8	-0.7	-6.1
Hybrid average with male parent RT 410	107.6	100.5	+7.1**	
LSD 5%			15.7	
(RT 223 x W 182 B) x RPI 690	91.5	72.7	+18.8*	+15.4
(W 182B x RT 291) x RPI 690	93.9	85.5	+8.4	+5.4
(RT 223 x RT 291) x RPI 690	92.6	84.6	+8.0	+4.8
Hybrid average with male parent RPI 690	92.7	80.9	+11.7**	
LSD 5%			10.1	
(RT 223 x W 182 B) x W 401	89.7	77.2	+12.5	+6.5
(W 182B x RT 291) x W 401	89.6	88.4	+1.2	-4.8
(RT 223 x RT 291) x W 401	88.4	85.3	+3.1	-3.5
Hybrid average with male parent W 401	89.2	83.6	+5.6*	
LSD 5%			8.1	

Table 7. Grain yield (q/ha) predicted and observed in three-way crosses (TWC) obtained with late male parental inbreds and estimates for epistatic deviations

TWC	Non parental SC yield average (predicted for TWC) q/ha	Observed yield in TWC q/ha	Differences between predicted and observed yields (epistatic deviations)	Effects of specific combining ability in TWC (SCA)
(RT 223 x W 182 B) x RF 211	110.6	98.7	+12.4	+5.3
(W 182B x RT 291) x RF 211	101.4	107.8	-5.8	-9.4
(RT 223 x RT 291) x RF 211	107.9	112.3	-4.4	-10.5
Hybrid average with male parent RF 211	106.6	105.9	+0.7	
LSD 5%			8.3	
(RT 223 x W 182 B) x Mo 17	102.9	91.0	+11.9	+6.8
(W 182B x RT 291) x Mo 17	105.2	107.6	-2.4	-7.6
(RT 223 x RT 291) x Mo 17	98.8	103.2	-4.4	-9.3
Hybrid average with male parent Mo 17	102.3	100.6	+1.7	
LSD 5%			15.7	
(RT 223 x W 182 B) x RT B 329	110.4	113.8	-3.4	-3.1
(W 182B x RT 291) x RT B 329	119.2	115.5	+3.7	+5.8
(RT 223 x RT 291) x RT B 329	107.5	114.7	-7.2	-7.5
Hybrid average with male parent RT B 329	112.4	114.7	-2.3	
LSD 5%			10.1	
(RT 223 x W 182 B) x A 632	105.2	106.8	-1.6	+0.1
(W 182B x RT 291) x A 632	99.6	94.8	+4.8	+4.8
(RT 223 x RT 291) x A 632	101.8	105.5	-3.7	-3.7
Hybrid average with male parent A 632	102.2	102.4	-0.2	
LSD 5%			8.1	



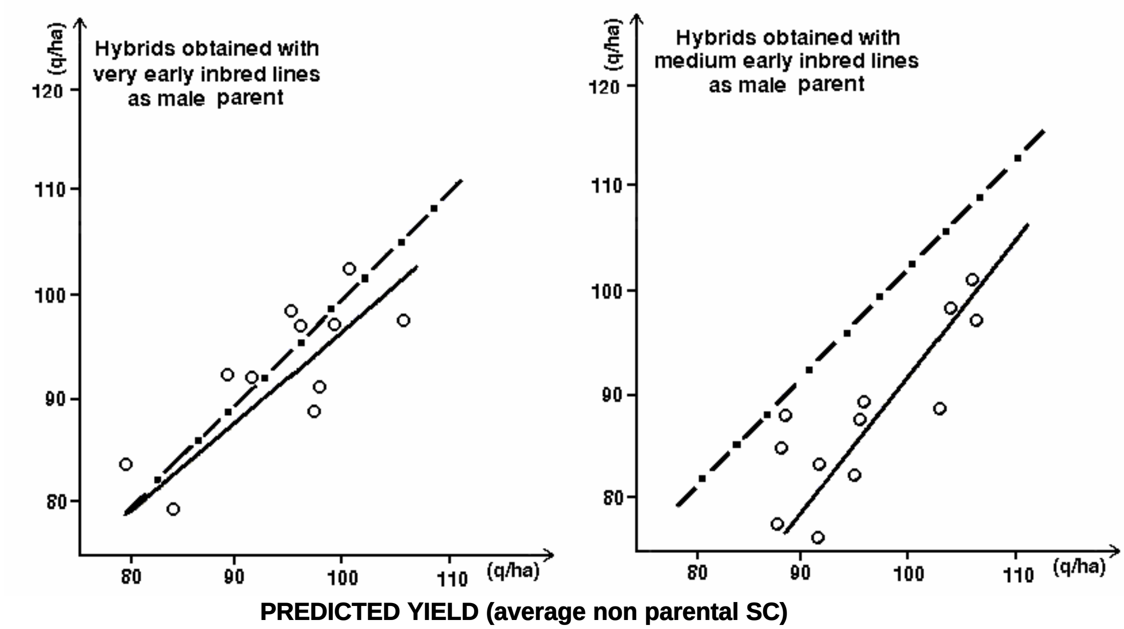


Figure 1. Regression deviations from bisectiar line