

THE MODE OF INHERITANCE OF GRAIN YIELD IN TWO SINGLE-CROSS MAIZE (*ZEA MAYS* L.) HYBRIDS

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ABSTRACT

Efficacy of maize breeding program based on maize grain and choice of breeding method depend on effects of genes included in expression of this trait. The objective of this study was to determine genetic parameters for grain yield using generation mean analysis (GMA) in two maize single-cross hybrids with one parent in common. Dominance gene effects were the most important in the inheritance of the grain yield. Significant values of two-gene epistasis were obtained. Interaction between dominant genes was in most instances of duplicate type, and was associated to a smaller effect of dominant genes. Less importance was estimated for epistatic effects between additive genes and additive and dominant genes which varied a large degree depending on the hybrid under consideration and on the environment. Higher values obtained for the interaction with the environment of the dominant in comparison to additive genes showed that it is not possible to predict with greater confidence the performances of the grain yield in both hybrids, so that successful estimation of the value of each inbred line can be derived only based on its performance in the particular hybrid combination.

Key words: maize, grain yield, inheritance, epistasis.

INTRODUCTION

One of the best genetic models for discovering the existence and estimation of epistasis is Generation Mean Analysis (GMA) (Hayman, 1958 and 1960; Jinks and Jones, 1958; Mather and Jinks, 1971). Using GMA with two parents, specific information for particular pairs of lines is gained, i.e. the information about relative importance of non-additive genetic effects (dominance and epistasis), which is important for proper choice of the breeding method in order to obtain new lines of maize with high yield potential. The purpose of our investigation was to evaluate the mode of inheritance of the genes for maize grain yield, based on the values of parents and their offspring after crossing. The additive, dominant and epistatic gene effects were determined, based on the analysis of fourteen generations of two investigated hybrids, by implementing the GMA analysis.

MATERIAL AND METHODS

For this study two single-cross hybrids with one parent in common were chosen. These two hybrids are different from each other in yield and some other traits: ZPLB 735 x B 432 and ZPLB 735 x ZPLB 439. From each hybrid 14 generations-families were analyzed (P_1 , P_2 , F_1 , F_2 , BC_1 , BC_2 , BC_1 self, BC_2 self, $BC_1 \times P_1$, $BC_1 \times P_2$, $BC_2 \times P_1$, $BC_2 \times P_2$, $BC_1 \times F_1$ and $BC_2 \times F_1$). Comparative trials were conducted in 2006 and 2007 in two locations (Zemun Polje and Indjija, Serbia).

The experimental design was a randomized complete block with seven replications, and plant density was 71,400 plants ha⁻¹. Yield plot surface was 2.8 m². Row length was 4 m, space between rows 0.7 m, and between hills in the row 0.4 m, with two plants per hill. F_2 generations were sown in two rows, parental lines in three, and all other generations in one row per replication.

Results of the trial were analyzed by the ANOVA, fixed model (Hadživuković, 1991).

Estimation of genetic effects for grain yield was done based on the generation mean analysis of the crosses of two parents. Using the means of 14 generations and reciprocal values (W), with inclusion of additive-dominant and interaction model it was possible to obtain estimated values for the following genetic effects (Hayman, 1960):

- mean [m]
- additive effect of the genes [d]
- dominant effect of the genes [h]
- two-gene epistasis effects:
 - additive x additive [i]
 - additive x dominant [j]
 - dominant x dominant [l]
- three-gene epistasis effects:
 - additive x additive x additive [i/aaa]
 - additive x additive x dominant [j/aad]
 - additive x dominant x dominant [j/add]
 - dominant x dominant x dominant [l/ddd]

The first step in the GMA analysis is the estimation of the basic (additive and dominant) gene effects using the additive-dominant model with three parameters. Based on that model, the following values are estimated: average [m], additive gene effect [d] and the dominance effect of genes [h] (Gamble, 1962).

Using the system of equations based on the values of the parameters [m], [d] and [h] from the additive-dominant model, mean values of the each generation (\bar{x}) and reciprocal values, over the system of equations, three equations for the information matrices are obtained.

Making information and summing matrices

$$J \times M = S$$

where: J – information matrices; M – parameter value; S – summing matrices.

Estimated values of parameters were derived by inversion of information matrices.

$$M = J^{-1} \times S$$

Standard errors for [m], [d] and [h] ($SE_{[m]}$, $SE_{[d]}$ and $SE_{[h]}$) were calculated from the square root of diagonal values of the inverse matrices J^{-1} .

Testing of the parameters mentioned was done through t-test. Number of degrees of freedom was determined as the product of the number of replications minus one and the number of generations which are involved in calculation of a given parameter.

Based on the additive-dominant model, estimated values for the additive and dominant effects of genes can be derived, while presence or absence of epistasis is determined by testing the adequacy of the additive-dominant model by:

- individual tests (Scaling-tests: A, B, C, X, Y, Z, Z');
- mutual test (χ^2 -test; Cavalli, 1952).

Statistical significance of the mutual χ^2 -test and significance of any of the individual tests indicates that the additive-dominant model is not adequate, meaning that epistatic gene effects are significant in expression of the trait examined (two- or three-gene epistasis). For fourteen generations seven individual tests could be formed. Values of individual tests and their standard errors were calculated applying the following formulas:

$$A = 2BC_1 - P_1 - F_1$$

$$B = 2BC_2 - P_2 - F_1$$

$$C = 4F_2 - 2F_1 - P_1 - P_2$$

$$X = 0.5(P_1 - P_2) - (BC_1 \times P_1 + BC_1 \times P_2) + (BC_2 \times P_1 + BC_2 \times P_2)$$

$$Y = F_1 - 0.5(P_1 + P_2) + (BC_1 \times P_1 - BC_1 \times P_2) - (BC_2 \times P_1 - BC_2 \times P_2)$$

$$Z = (BC_1 - BC_2) - 2(BC_1 \times F_1 - BC_2 \times F_1)$$

$$Z' = (BC_1 - BC_2) - 2(BC_{1s} - BC_{2s})$$

$$SE_A = \sqrt{V_A} \quad V_A = 4V_{BC1} + V_{P1} + V_{F1}$$

$$SE_B = \sqrt{V_B} \quad V_B = 4V_{BC2} + V_{P2} + V_{F1}$$

$$SE_C = \sqrt{V_C} \quad V_C = 16V_{F2} + 4V_{F1} + V_{P1} + V_{P2}$$

$$SE_X = \sqrt{V_X} \quad V_X = 0.25(V_{P1} + V_{P2}) + V_{BC1 \times P1} + V_{BC1 \times P2} + V_{BC2 \times P1} + V_{BC2 \times P2}$$

$$SE_Y = \sqrt{V_Y} \quad V_Y = V_{F1} + 0.25(V_{P1} + V_{P2}) + V_{BC1 \times P1} + V_{BC1 \times P2} + V_{BC2 \times P1} + V_{BC2 \times P2}$$

$$SE_Z = \sqrt{V_Z} \quad V_Z = V_{BC1} + V_{BC2} + 4(V_{BC1 \times F1} + V_{BC2 \times F1})$$

$$SE_{Z'} = \sqrt{V_{Z'}} \quad V_{Z'} = V_{BC1} + V_{BC2} + 4(V_{BC1s} + V_{BC2s})$$

Significance of the individual tests was checked by t-test. Obtained significant values of tA, tB and tC indicate existence of two-gene epistasis. In the case of the significance of some of the other tests, apart from the three mentioned, three-gene epistasis is considered present.

Adequacy of the additive-dominant model could be also tested by χ^2 -test, comparing the experimental mean values of the generations with expected mean values. Expected mean values are given through estimated values of [m], [d], [h] and parameters from the additive-dominant model.

The differences between calculated experimental values and expected values of the generations are squared and multiplied by W reciprocal value. Sum of the obtained values over generations is the value of χ^2 -test. The degrees of freedom for the mutual test are derived from the difference between the number of the generations and number of the estimated gene effects. Based on the significant χ^2 -value it is confirmed that additive-dominant model is not adequate, which is in accordance with the results of individual tests.

For calculation of the estimated values of parameters for two- or three-gene epistasis, it is necessary to use the interaction model. Estimated parameter values for two-gene epistasis, [i], [j], [l] and three-gene epistasis, [i/aaa], [j/aad], [l/add] and [l/ddd], are calculated through the system of matrices like in the additive-dominant model. Testing of the interaction model is done by χ^2 -test like in additive-dominant model. If the epistatic effect and the basic gene effect have the same sign (+ or -), it is the case of complementary epistasis, and in the opposite case duplicate epistasis is less favorable.

The interaction of additive and dominant gene effects and the environment (two locations, L₁ and L₂) was estimated according to formulas given to Bucio (1966) and Bucio and Hill (1966):

$$T_{(d)} = 1/4[\bar{P}_1(L_1) - \bar{P}_2(L_1) - \bar{P}_1(L_2) + \bar{P}_2(L_2)]$$

$$T_{(h)} = 1/2\bar{F}_1(L_1) - 1/2\bar{F}_1(L_2) - 1/4[\bar{P}_1(L_1) + \bar{P}_2(L_1) - \bar{P}_1(L_2) - \bar{P}_2(L_2)]$$

where $T_{(d)}$ = interaction of additive genes and the environment; $T_{(h)}$ = interaction of dominant genes and the environment.

Standard errors of the interaction of additive and dominant genes with the environment were calculated using the following formulas:

$$SET_{(d)} = \sqrt{T_{(d)}}$$

$$T_{(d)} = 1/16[\bar{P}_1(L_1) + \bar{P}_2(L_1) + \bar{P}_1(L_2) + \bar{P}_2(L_2)]$$

$$SET_{(h)} = \sqrt{T_{(h)}}$$

$$T_{(h)} = 1/4\bar{F}_1(L_1) + 1/4\bar{F}_1(L_2) + 1/16[\bar{P}_1(L_1) + \bar{P}_2(L_1) + \bar{P}_1(L_2) + \bar{P}_2(L_2)]$$

Significance of the interaction of genotype x environment was tested by t-test:

$$t_{(d)} = \frac{T_{(d)}}{SET_{(d)}} \quad t_{(h)} = \frac{T_{(h)}}{SET_{(h)}}$$

The number of degrees of freedom was calculated multiplying the number of replications minus one by the number of generations involved in the calculation of the interaction of basic gene effect and the environment.

RESULTS AND DISCUSSION

The highest grain yield in both locations and years among parents of two hybrids was found in line B 432. Average yield (g plant⁻¹) of this line varied from 59.4 in Indjija 2007 to 68.4 in Zemun Polje 2007. The drought effect, particularly expressed in Zemun Polje 2007, did not have negative influence on the grain yield of that line, which showed its high drought tolerance. The lowest yield in both years was given by the inbred line ZPLB 439, whose yield varied from 42.3 g plant⁻¹ in Zemun Polje 2007 to 56.5 in Zemun Polje 2006. Inbred line ZPLB 735 had the least variation of the average grain yield over environments (Table 1).

Based on the additive-dominant model of the GMA analysis we concluded that dominant gene effects were the most important in the inheritance of grain yield in both hybrids. Highly significant values of the dominant gene effects [h] were several times

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greater than additive [d] gene effects, for which significant values were only detected in Zemun Polje in 2007, for hybrid ZPLB 735 x B 432 and ZPLB 735 x B 432 in both

locations in 2007. Highly significant values of the effects of the means [m] in both years for both investigated hybrids were obtained (Table 2).

Table 1. Mean values of grain yield (g plant⁻¹) of the generations of studied hybrids

Year	2006				2007			
	Zemun Polje		Indjija		Zemun Polje		Indjija	
Location	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735
Hybrid	x	x	x	x	x	x	x	x
	B 432	ZPLB 439	B 432	ZPLB 439	B 432	ZPLB 439	B 432	ZPLB 439
Generation								
P ₁	62.4±2.64	62.4±1.37	56.4±2.41	56.4±2.84	59.0±2.28	59.0±2.05	58.5±2.94	58.5±2.63
P ₂	67.4±2.49	56.5±2.64	66.1±3.83	53.5±2.58	68.4±1.66	42.3±2.18	59.4±2.39	54.4±2.55
F ₁	162.3±2.27	124.0±3.21	138.5±3.50	105.8±3.57	153.4±3.11	121.7±1.75	144.1±2.45	118.5±2.45
F ₂	110.3±3.40	101.0±3.95	101.8±4.37	87.6±4.04	88.1±3.77	84.1±3.3	101.4±3.78	89.2±3.32
BC ₁	114.1±3.11	104.2±3.63	101.9±3.54	91.2±3.87	94.7±4.08	92.0±3.76	105.6±3.58	100.8±3.36
BC ₂	109.2±3.23	101.5±3.75	97.8±4.66	86.5±3.73	88.5±3.04	88.9±2.10	102.5±3.56	81.2±2.94
BC ₁ x F ₁	117.0±2.95	104.4±2.82	102.7±3.86	89.3±4.52	93.8±3.74	88.0±3.12	102.1±2.79	92.3±3.24
BC ₂ x F ₁	114.9±2.91	102.0±2.03	94.7±2.90	86.8±4.90	93.0±4.31	78.2±3.10	97.6±3.26	86.8±3.12
BC _{1s}	83.3±2.51	87.8±3.21	77.0±6.09	78.6±3.63	62.8±4.71	62.6±2.12	80.2±3.33	76.4±3.10
BC _{2s}	85.8±2.76	82.9±3.92	73.7±5.34	72.2±4.43	63.7±3.98	60.4±3.73	80.2±2.13	70.4±2.95
BC ₁ x P ₁	90.8±4.81	88.2±4.02	88.3±3.12	77.0±4.71	73.8±3.39	72.9±3.79	87.7±3.75	83.7±3.73
BC ₁ x P ₂	139.4±4.94	120.5±3.16	126.2±4.38	99.2±4.77	125.3±6.74	107.3±3.63	128.5±3.70	110.0±2.99
BC ₂ x P ₁	131.4±4.82	113.9±3.30	117.3±5.68	99.1±3.78	121.5±5.27	104.7±3.70	122.3±4.52	102.9±2.74
BC ₂ x P ₂	84.4±4.81	84.2±3.30	88.6±5.98	83.4±4.15	81.9±3.23	61.9±3.47	85.3±5.68	75.4±3.18
Hybrid mean	105.2	95.2	95.1	83.3	90.6	80.3	96.8	85.7
Average of the location		100.2		89.2		85.4		91.2
Average of the year				94.7				88.3

Table 2. Additive-dominant model of the GMA analysis for grain yield

Year	2006				2007			
	Zemun Polje		Indjija		Zemun Polje		Indjija	
Location	LB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735
Hybrid	x	x	x	x	x	x	x	x
	B 432	ZPLB 439	B 432	ZPLB 439	B 432	ZPLB 439	B 432	ZPLB 439
Gene effects								
[m]	63.15**	63.33**	62.84**	59.35**	58.63**	48.80**	59.21**	58.60**
[d]	0.52	1.37	2.58	1.49	3.13*	6.09**	0.06	5.12**
[h]	98.60**	71.80**	75.67**	53.75**	80.54**	73.62**	85.42**	62.17**
χ ² test	13.120	36.204**	15.994	21.727*	83.672**	32.781**	8.687	22.492*
Scaling tests								
A	-11.320	21.910*	-8.990	20.230*	-44.800**	3.350	1.380	24.590**
B	3.380	22.420*	8.888	13.780	-22.900**	13.760*	8.530	-10.440
C	-13.320	36.830*	7.660	29.130*	-81.540**	-8.350	-0.530	6.870
X	16.860	-7.575	13.480	7.817	0.410	-5.195	9.045	-13.353
Y	1.780	2.535	10.630	13.003	-1.290	-6.145	7.385	8.233
Z	-0.710	-1.970	11.881	-0.420	-4.700	-16.410	6.000	8.540
Z'	-9.970	-7.010	2.485	-8.060	-8.060	-1.294	-5.140	7.560

* P≤5%, ** P≤1%

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Significant and highly significant values of χ^2 -test, and also of individual Scaling-tests, showed the non-adequacy of additive-dominant model, i.e. existence of the epistasis. In the hybrid ZPLB 735 x ZPLB 439, non-allele interaction was found in both locations and years, while this interaction was detected in the hybrid ZPLB 735 x B 432 only in Zemun Polje in 2007. Based on the individual Scaling-tests, it was revealed that in the all instances two-allele epistasis was present (Table 2).

Using the interaction model of the generation mean analysis with six parameters, higher values of dominant gene effects [h] were obtained in all the cases where epistasis was detected. For hybrid ZPLB 735 x B 432 in Zemun Polje in 2007, beside highly significant value of dominant gene effects [h], highly significant values of additive gene effects [d]

were also obtained. Highly significant values of complementary epistasis between additive genes [i/aa] found for this hybrid points out to the increased significance of additive genes in the inheritance of grain yield. A more favorable type of complementary epistasis was also found between dominant genes [l/dd], although its value was not statistically significant (Table 3).

In hybrid ZPLB 735 x ZPLB 439 higher values of the dominance gene effects [h] were derived in comparison with hybrid ZPLB 735 x B 432. These values were significantly smaller because of the undesirable duplicate epistasis between dominant genes [l/dd], which resulted in lower yields of the hybrid ZPLB 735 x ZPLB 439 in both locations and years, in comparison with hybrid ZPLB 735 x B 432 (Table 3).

Table 3. Interaction model of GMA analysis for grain yield

Year	2006				2007			
	Zemun Polje		Indjija		Zemun Polje		Indjija	
Location	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735	ZPLB 735
Hybrid	x	x	x	x	x	x	x	x
	B 432	ZPLB 439	B 432	ZPLB 439	B 432	ZPLB 439	B 432	ZPLB 439
Gene effect								
[m]	63.15**	58.39**	62.84**	52.12**	31.16**	18.77**	59.21**	46.68**
[d]	0.52	2.62	2.58	1.16	5.02**	8.17*	0.06	1.59
[h]	98.60**	114.50**	75.67**	97.00**	102.83**	148.25**	85.42**	101.08**
[i] aa		1.51		3.79	32.53**	31.38**		10.70
[j] ad		4.88		1.25	-11.39	-7.69		23.85**
[l] dd		-49.01**		-44.80	19.94	-45.17**		-29.74
χ^2 test	13.120	2.181	15.994	7.125	7.556	7.125	8.687	6.487

* P≤5%, ** P≤1%

Significant value of the additive genes effect of the [d] for the hybrid ZPLB 735 x ZPLB 439 was confirmed only in Zemun Polje in 2007, indicating their minor importance in comparison with the dominant genes effects. Non-allele interaction between additive genes [i/aa] was of the complementary type, but significant value was obtained only in Zemun Polje, in 2007.

As far as the epistasis between additive and dominant genes [j/ad] is concerned, there was positive highly significant value in Indjija 2007, while in other instances non-significant values were obtained (Table 3).

The differences between investigated hybrids for grain yield were caused mostly by the differences between dominant gene effects and their non-allele interaction [l/dd].

For both hybrids, the interaction of dominant genes and the environments was more pronounced than the interaction of the additive genes and the environments. Derived values of the interaction of the additive genes and the environments were not statistically significant in the higher yielding hybrid ZPLB 735 x B 432, while for the hybrid ZPLB 735 x ZPLB 439 they were highly significant and significant for the interaction between Zemun

Polje and Indjija in 2007, Zemun Polje 2007 and Indjija 2006 and Zemun Polje in 2006 and 2007 (Table 4).

When values of the interaction of the dominant genes and the environments are compared, it can be stated that they were a little bit higher for hybrid ZPLB 735 x ZPLB 439 than for hybrid ZPLB 735 x B 432. Speaking in absolute terms, based on the results in Table 4, it could be stated that in better yielding hybrid ZPLB 735 x B 432 there was less interaction of the basic gene effects with the environments in comparison with lower yielding hybrid ZPLB 735 x ZPLB 439.

Table 4. Interaction of the basic gene effects with the environment

Environment	ZPLB 735 x B 432		ZPLB 735 x ZPLB 439	
	[d] x E	[h] x E	[d] x E	[h] x E
ZP 2006 :	-1.125	3.835	-2.665*	-3.235
ZP 2007				
IN 2006 :	2.182	-3.982	-0.295	-5.635*
IN 2007				
ZP 2006 :	-1.190	10.085**	0.775	6.875**
IN 2006				
ZP 2007 :	2.117	2.267	3.145**	4.475*
IN 2007				
ZP 2006 :	0.993	6.102**	0.480	1.240
IN 2007				
ZP 2007 :	0.065	-6.250*	-3.440**	-10.110**
IN 2006				

* $P \leq 5\%$, ** $P \leq 1\%$

Results of the investigations of many authors, based on the work with previously selected material, point out that dominant gene effects are the most important for the inheritance of grain yield (Ivanovic and Pooni, 1988; Vidal-Martinez et al., 2001, and Azizi et al., 2006). Our results are in accordance with these. Values of dominance gene effects for grain yield in both investigated hybrids were the highest and the most significant.

Epistatic gene effects were of smaller importance than dominance effects, while their importance was far more important than additive gene effects. The importance of epistasis in the inheritance of the grain yield and its components depends largely upon the genetic nature of the investigated material. Sprague and Thomas (1967) demonstrated that, when crossing inbred lines of corn

derived from already selected materials, there is the possibility that these lines possess rare genetic combinations, so that the probability of non-allelic interaction is highly increased.

Based on our results, epistatic gene effects are of more importance in lower yielding hybrid ZPLB 735 x ZPLB 439 in comparison with higher yielding hybrid ZPLB 735 x B 432. In hybrid ZPLB 735 x ZPLB 439, the most important was the two-gene non-allelic interaction between dominant genes which was of duplicate type. This caused a high degree the reduction of the positive effects of dominant genes, leading to smaller yield. A more desirable type of complementary epistasis was found in the hybrid ZPLB 735 x B 432, but only in the location Zemun Polje in 2007. In all other instances, the epistatic gene effect was not found for this hybrid. The duplicate type of epistasis between dominant genes prevailed, and the complementary one in the inheritance of the grain yield was demonstrated also in the investigations of Darrah and Hallauer (1972), Moreno-Gonzales and Dudley (1981), Lamkey et al. (1995). Low positive values of two-gene epistasis between the additive genes were obtained in all instances in both hybrids, so their contribution to the increase of the significance of additive genes was very low. The interaction of additive and dominant genes was highly significant only for the hybrid ZPLB 735 x ZPLB 439, while in the other cases the values obtained were not statistically significant and had negative and positive values.

Using the model of GMA analysis, very small values of additive gene effects were obtained, which points to their small importance in the inheritance of the grain yield in comparison with epistatic and dominant gene effects. Hallauer and Miranda (1981) stated that generation mean analysis is a method not effective enough for the estimation of the additive gene effects and their contribution to the inheritance of the quantitative traits, because estimation of their value depends only on the difference between mean values of the two parents.

In accordance with obtained results, which showed very small importance of additive genes in the inheritance of grain

yield, in the program of selection and breeding of corn it is necessary to choose methods that favors dominant and epistatic gene effects. According to Comstock et al. (1949) the method of reciprocal recurrent selection is the best choice in such case.

CONCLUSIONS

Out of this investigation the following can be concluded:

For grain yield, dominant genes are the most important in the inheritance of the trait while the role of additive genes is much smaller.

Interaction between dominant gene effects was predominantly of duplicate type and was associated to the smaller effect of dominant genes. Smaller importance for epistatic effects between additive genes and additive and dominant genes was observed. Epistatic effects varied to a large degree,

depending on the hybrid under consideration and the environment.

Higher values of interaction with the environment of the dominant in comparison to additive genes showed that it is not possible to predict with higher confidence the grain yield performances, in both hybrids.

Based on the results of this study, in the program of selection and breeding for grain yield in corn it is recommended to use reciprocal recurrent selection as the best method, since it favours dominant and epistatic gene effects.

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