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AN IMPACT OF ENVIRONMENT ON SEGREGATION RATIO OF QUALITATIVE TRAITS IN MAIZE

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The significant influence of environment was found on the segregation ratio in a dihybrid inheritance in maize. Two possible causes are proposed for this segregation distortion: 1) environmental influence (selection) prior forming the gametes or/and 2) different preferential pairing in different environments. Further studies, however, on other self or cross-pollinated plant species, and with different traits are needed to better understand this phenomena.

Key words: environment, maize, segregation distortion, qualitative traits

INTRODUCTION

Since re-discover of MENDELIAN (1865) work in 1900, made independently by VON TCHERMAK, CORRENS and DE VRIES, genetic theory and practice was mostly based on two basic Mendelian laws: 1) Random segregation of alleles in parents during formation of gametes, and 2) Free recombination of gametes during fertilization leading to formation of the zygotes of next generation.

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Few modes of inheritance of so-called qualitative traits (whose inheritance is influenced by small number of major-genes, and not influenced by the environment) were found according to this laws, and their rules were given by the particular segregation ratios of the phenotypes in F2 and BC progenies of the appropriate parental crosses.

Segregation distortion skews the genotypic frequencies from their Mendelian expectations. Such a distortion in maize was first reported by MANGELSDORF and JONES (1926), based on the linkage of gametophyte factor *Gal* and the *Su* allele for starchy endosperm. They found that pollination with *Gal* or *gal* pollen separately led to normal genotypic ratios, but pollination with a mixture of the two, because of the faster growth of a pollen-tube carrying *Gal* allele led to an excess of the genotypes with the linked *Su* allele. *Ga* genes of incompatibility were also reported by DEMEREC (1929) and SCHWARTZ (1950). Career of the *Ga* gene can pollinate any other corn, but can be pollinated only by a carrier of the same dominant allele. Allele *Gal-S* shows partial domination (NELSON, 1952).

Further evidence of the segregation distortion in maize was given by BURNHAM (1936), RHOADES (1942), LONGLEY (1945), HELENTJARIS *et al.* (1986), WENDEL *et al.* (1987), RASHID and PETERSON (1992), GARDINER *et al.* (1993), and by LU *et al.* (2002). The latest mentioned authors, comparing four mapping populations of maize, found 18 consistent chromosomal regions on ten maize chromosomes associated with segregation distortion, designated as segregation distortion regions (SDRs). Only three out of 18 SDRs detected were close to the location of five known gametophytic factors, and the authors stated that this gametophytic factors may not be the only genetic reason for segregation distortion.

Among nine genetically-enzymatic systems for phosphorous-sugary metabolic cycle in *Drosophyla melanogaster*, within 400 individuals in a population, MARINKOVIC *et al.* (1987) found also complete distortion from the Mendelian law. With this nine systems, theoretically about 78.000 different genotypes are possible, with an expectation, according to the second Mendelian law, that every of the 400 analysed individuals be different, i.e. unique. But among 400 individuals, only 160 genotypes were found, some of which were repeated even more than 20 times. The investigators concluded that frequent genotypes serve for the maintenance of the population, while the rare ones are usefull for the survival if the population undergone the extreme environmental conditions. Also, such a reduction of the possible genotypes is realized already during meiosis, so there is selection even before formation of gametes (MARINKOVIC, 1997).

A little evidence is present on the impact of the environment on the segregation ratio of different traits in maize. While staying in Africa, working in the winter nurcery, the author noticed that there is complete difference in the phenotype of maize inbred lines in Zemun Polje in comparison to Zambia conditions. Also, in quantitative genetic studies (VANCETOVIC and DRINIC, 1993; VANCETOVIC, 1995), additive and dominance genetic variance were different in varying environments. To study such phenomena, we have chosen a known

segregation ratio (dihybrid mode of inheritance) of two traits in maize, and studied it in the F₂ population of a cross, produced in different environments.

MATERIAL AND METHOD

For this investigation, two homozygous genotypes were chosen. Their genetic constitution was a₂a₂Su₁Su₁ (yellow kernel with normal endosperm) and su₁su₁AACCRR. Both genotypes had, in homozygous state, *in* factor, causing the blue color of the aleurone layer of the former genotype, that was also with sugary endosperm. Endosperm is the triploid tissue that has nutrients for the germ, while aleurone is a thin layer under the pericarp, which is diploid in nature. In the season of 2001 we crossed the two, and obtained the heterozygous F₁ genotype of genetic constitution Aa₂Su₁su₁, phenotypically with blue kernel and normal endosperm. Expected ratio of phenotype segregation in F₂ generation of this cross, by Mendelian law, as for the classical dyhybrid inheritance is: 9 (A_Su₁_, blue, normal endosperm kernel) : 3 (A_su₁su₁, blue, sugary kernel) : 3 (a₂a₂Su₁_, yellow, normal endosperm kernel) : 1 (a₂a₂su₁su₁, yellow, sugary kernel).

In the winter nursery in Zambia in the season of 2001/2002 we did the selfing of the F₁, as well as in 2002 in Moldavia, Kazahstan, Ukraine and in Zemun Polje, Serbia in four planting dates, two weeks each after another. We counted the produced seed of F₂s for each phenotypic class, and each selfed plant separately (except for Zambia's seed, were counting was done for seven selfed plants all-together). The observed ratios of segregation were tested for deviation from their expected values with a χ^2 goodness-of-fit test, for each selfed plant separately (except for Zambia), and for the whole population (sum over selfed plants). Also, test of the consistency among the segregation ratios between separate selfed plants in the population was done (according to COCHRAN, 1954; FISHER, 1958; YULE and KENDALL, 1958).

RESULTS AND DISCUSSION

In Tables 1-8 are shown the results for different environments. Since chosen traits are qualitative in nature, no environmental influence on the expression of the genes is expected, as well as segregation distortion in any of the environments. However, only in one of the eight investigated environments clear expected segregation ratio was observed (in Moldavia). In all other environments segregation distortion was observed, most obvious in Kazahstan and Zambia. Even in the same location of Zemun Polje, within different planting dates, different results were obtained.

Table 1. Segregation ratio obtained in Zambia in the season of 2001/2002, summing over seven selfed plants, and compared to the expected ratio

A_Su1_	A_su1su1	a2a2Su1_	a2a2su1su1	DF	χ^2	signif. ^A
1227	377	615	217	3	111.26656	**

^A – significance of χ^2 in comparison with the expected ratio of 9:3:3:1

** - statistically significant at 0.01 probability level

Table 2. Segregation ratio obtained in Ukraine in the season of 2002, for each selfed plant and summing over all plants, and compared to the expected ratio

Plant	A_Su1_	A_su1su1	a2a2Su1_	a2a2su1su1	DF	χ^2	signif. ^A
1	276	76	63	31	3	8.6487	*
2	247	61	60	20	3	8.664	*
3	280	76	95	30	3	2.8179	ns
4	197	29	25	6	3	44.122	**
5	118	32	29	15	3	3.424	ns
6	164	42	60	18	3	3.3489	ns
7	137	45	35	11	3	2.86	ns
8	64	11	26	4	3	7.27	ns
Sum of χ^2					24	81.1555	**
S. of plants	1483	372	393	135	3	35.4738	**
Consistency					21	62.9944	**
% ns plants							62.5

^A – significance of χ^2 in comparison with the expected ratio of 9:3:3:1

*,** - statistically significant at 0.05 and 0.01 probability level, respectively

ns – statistically non-significant

This segregation distortion was, however, not observed in all of the individual plant progenies in the particular environments, but in the sum of the progenies it was clarified. In Zemun Polje, in all planting dates, in some of the plant progenies an absence of the a_2a_2 genotype was observed, indicating probably absence of the allele in the progeny, so the summary results were given for all the progenies and separately for progenies with exclusion of those without of a_2a_2 genotypes. No matter of that, even with exclusion of these progenies, expected ratio of segregation was observed only for the second planting date in Zemun Polje. Very low consistency of different plant progenies within F2 generations was observed in almost all environments (it was insignificant only in the fourth planting date in Zemun Polje). Also, different % of plant progenies showed expected ratio of segregation in different environments (from 10% in Kazakhstan to 80% for the first planting date in Zemun Polje).

Table 3. Segregation ratio obtained in Moldavia in the season of 2002, for each selfed plant and summing over all plants, and compared to the expected ratio

Plant	A_Su1_	A_su1su1	a2a2Su1_	a2a2su1su1	DF	χ^2	signif. ^A
1	202	52	78	19	3	5.654	ns
2	40	24	14	4	3	6.0216	ns
3	94	20	28	10	3	3.415	ns
4	174	66	51	19	3	1.948	ns
5	121	30	42	20	3	5.95	ns
6	47	18	14	5	3	0.529	ns
7	105	26	45	15	3	5.886	ns
8	139	54	32	17	3	5.875	ns
9	31	8	12	2	3	1.373	ns
10	173	45	65	21	3	3.883	ns
11	60	26	29	4	3	4.9215	ns
12	133	48	40	13	3	0.925	ns
13	97	30	34	12	3	0.3898	ns
14	167	52	47	16	3	1.259	ns
Sum of χ^2					42	48.0299	ns
S. of plants	1583	499	531	177	3	1.3889	ns
Consistency					39	46.641	ns
% ns plants							100

^A – significance of χ^2 in comparison with the expected ratio of 9:3:3:1 ns – statistically non-significant

Table 4. Segregation ratio obtained in Kazakhstan in the season of 2002, for each selfed plant and summing over all plants, and compared to the expected ratio

Plant	A_Su1_	A_su1su1	a2a2Su1_	a2a2su1su1	DF	χ^2	signif. ^A
1	93	3	37	2	3	33.809	**
2	42	5	9	5	3	6.234	ns
3	124	83	36	4	3	41.439	**
4	276	99	7	1	3	107.792	**
5	163	33	7	0	3	59.577	**
6	63	20	1	0	3	25.46	**
7	93	28	8	0	3	25.25	**
8	147	57	11	0	3	47.276	**
9	179	1	1	0	3	133.765	**
10	52	22	2	0	3	21.497	**
Sum of χ^2					30	502.099	**
S. of plants	1232	351	119	12	3	289.066	**
Consistency					27	213.033	**
% ns plants							10

^A – significance of χ^2 in comparison with the expected ratio of 9:3:3:1

** - statistically significant at 0.01 probability level ns – statistically non-significant

Table 5. Segregation ratio obtained in Zemun Polje, the first planting date, in the season of 2002, for each selfed plant and summing over all plants, and compared to the expected ratio

Plant	A_Su1_	A_su1su1	a2a2Su1_	a2a2su1su1	DF	χ^2	signif. ^A
1	145	44	46	9	3	3.067	ns
2	210	45	66	21	3	7.38	ns
3	122	32	36	13	3	1.6195	Ns
4	165	52	56	28	3	4.949	ns
5	152	37	33	18	3	7.363	Ns
6	213	100	34	34	3	35.408	**
7	237	59	85	19	3	6.827	Ns
8	152	39	46	10	3	4.3	Ns
9	126	56	38	16	3	4.4519	Ns
10	170	64	52	29	3	5.954	Ns
11	184	52	62	13	3	3.518	Ns
12	126	49	36	17	3	2.5497	Ns
13	177	206	0	0	3	353.348	**
14	98	26	38	7	3	3.571	ns
15	86	7	19	3	3	19.6	**
Sum of χ^2					45	463.906	**
S. of plants	2363	868	647	237	3	34.756	**
Consistency					42	429.15	**
% ns plants							80
Sum of χ^2							
without					42	110.558	**
plant 13							
Sum of pl.							
without	2186	662	647	237	3	9.658	**
plant 13							
Consistency							
without					39	100.9	**
plant 13							

^A – significance of χ^2 in comparison with the expected ratio of 9:3:3:1

** - statistically significant at 0.01 probability level

ns – statistically non-significant

Table 6. Segregation ratio obtained in Zemun Polje, the second planting date, in the season of 2002, for each selfed plant and summing over all plants, and compared to the expected ratio

Plant	A_Su1_	A_su1su1	a2a2Su1_	a2a2su1su1	DF	χ^2	signif. ^A
1	154	283	0	0	3	636.92	**
2	232	345	0	0	3	689.009	**
3	19	26	0	0	3	49.38	**
4	121	18	45	9	3		**
5	155	84	45	29	3	21.182	**
6	143	69	53	17	3	6.479	ns
7	204	51	44	31	3	14.113	**
8	136	31	31	14	3	6.247	ns
9	107	32	40	9	3	1.598	ns
10	80	30	24	15	3	4.354	ns
Sum of χ^2					30	1447.77	**
S. of plants	1351	969	282	124	3	547.198	**
Consistency					27	900.572	**
% ns plants							40
Sum of χ^2							
without pl.					21	67.462	**
1,2 and 3							
Sum of pl.							
without pl.	946	315	282	124	3	6.849	ns
1,2 and 3							
Consistency							
without pl.					18	60.613	**
1,2 and 3							

^A – significance of χ^2 in comparison with the expected ratio of 9:3:3:1

** - statistically significant at 0.01 probability level

ns – statistically non-significant

Table 7. Segregation ratio obtained in Zemun Polje, the third planting date, in the season of 2002, for each selfed plant and summing over all plants, and compared to the expected ratio

Plant	A_Su1_	A_su1su1	a2a2Su1_	a2a2su1su1	DF	χ^2	signif. ^A
1	171	52	54	15	3	1.0045	ns
2	209	49	49	21	3	8.347	*
3	158	218	0	0	3	416.132	**
4	114	50	34	12	3	3.841	ns
5	69	37	17	15	3	13.497	**
6	141	20	58	4	3	26.662	**
7	70	14	20	5	3	3.75	ns
8	82	30	26	13	3	1.736	ns
9	138	25	49	9	3	11.08	*
10	146	52	32	14	3	5.647	ns
11	49	13	11	2	3	3.388	ns
12	134	54	44	26	3	7.95	*
13	39	10	13	2	3	1.667	ns
14	54	18	6	7	3	7.8	ns
15	61	16	13	4	3	3.21	ns
16	21	10	9	0	3	3.733	ns
Sum of χ^2					48	519.445	**
S. of plants	1656	668	435	149	3	56.079	**
Consistency					45	463.366	**
% ns plants							62.5
Sum of χ^2							
without					45	103.313	**
plant 3							
Sum of pl.							
without	1498	450	435	149	3	8.978	**
plant 3							
Consistency							
without					42	94.335	**
plant 3							

^A – significance of χ^2 in comparison with the expected ratio of 9:3:3:1

*,** - statistically significant at 0.05 and 0.01 probability level, respectively

ns – statistically non-significant

Table 8. Segregation ratio obtained in Zemun Polje, the fourth planting date, in the season of 2002, for each selfed plant and summing over all plants, and compared to the expected ratio

Plant	A_Su1_	A_su1su1	a2a2Su1_	a2a2su1su1	DF	χ^2	signif. ^A
1	174	79	53	27	3	8.606	*
2	100	30	49	7	3	8.447	*
3	100	155	0	0	3	317.2	**
4	140	42	48	17	3	0.629	ns
5	183	41	63	18	3	5.994	ns
6	101	31	42	10	3	2.242	ns
7	159	49	47	16	3	0.685	ns
8	173	27	57	14	3	15.196	**
9	139	35	51	11	3	4.21	ns
10	57	14	17	8	3	1.78	ns
11	55	14	15	3	3	2.277	ns
12	30	5	9	3	3	2.135	ns
Sum of χ^2					36	369.401	**
S. of plants	1411	522	451	134	3	9.706	*
Consistency					33	359.695	**
% ns plants							66.7
Sum of χ^2 without plant 3					33	52.201	**
Sum of pl. without plant 3	1311	367	451	134	3	10.949	*
Consistency without plant 3					30	41.252	ns

^A – significance of χ^2 in comparison with the expected ratio of 9:3:3:1

*, ** - statistically significant at 0.05 and 0.01 probability level, respectively

ns – statistically non-significant

DISCUSSION

We consider that segregation distortion in this investigation could emerge from two reasons: 1) environmental influence (selection) before formation of gametes, so their ratio would not be, as theoretically expected, 1(ASu₁):1(Asu₁):1(a₂Su₁):1(a₂su₁), or/and 2) different preferential pairing in different environments (i.e. in some environments some types of gametes would pair more often than it would be expected by chance). An absence of the a₂a₂ genotype in some of the plant progenies in Zemun Polje could be explained by

somatic mutation of the allele prior meiosis, or even, but very improbably, by the preferential pollination during selfing of some plants. For testing the first hypothesis mentioned, we are planning to do the testcrosses (with the double recessive), in different environments, of newly produced the same F_1 . This will show the exact proportion of gametes in the silks of the F_1 (definite number of silks is on the cob), but not in the pollen grains, since potential preferential pairing could occur (much more pollen grains are produced than silks for pollination).

The question arises, if the environment can have such an impact on a relatively simply inherited, qualitative traits, what is in the case of more complex, i.e. quantitative traits, inherited by a larger number of minor genes. Our results also raise some questions considering applied breeding programs. Namely, often F_{1s} between two inbred lines for further selfing (producing of new lines) are made on test locations (breeding nurseries) in target regions for plant production, in Europe and USA for instance, and are sent for selfing for production of F_2s to winter nurseries, with completely different climatic conditions (some of them are in tropical or sub-tropical regions). How much of the genetic variability is skewed by this procedure, and maybe lost for further selection in target regions? In our experiment, one of the largest segregation distortions was observed in the former winter nursery in Zambia.

Further similar investigations on other, self or cross-pollinated plant species, or with different traits in maize could give more information on the environmental influence on inheritance of various traits in plants. One of the possibilities is selfing F_1s in different environments for producing F_2 mapping populations, and comparing data so obtained. This could be done for mapping F_2s of dihaploid lines, since they are, at least theoretically, completely homozygous, so no potential heterozygosity in an inbred line could interfere with obtained results.

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UTICAJ SPOLJAŠNJE SREDINE NA SEGREGACIONI ODNOS KVALITATIVNIH SVOJSTAVA KUKURUZA

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I z v o d

Značajan uticaj spoljašnje sredine na segregacioni odnos je utvrđen kod dihibridnog nasleđivanja kod kukuruza. Dva moguća uzorka segregacione distorzije su: 1) uticaj spoljašnje sredine (selekcija) pre formiranja gameta ili/i 2) različita preferencijalna ukrštanja u različitim sredinama. Dalja istraživanja, na drugim samooplodnim ili stranooplodnim biljnim vrstama i sa različitim svojstvima su potrebna da bi se ovaj fenomen bolje razumeo.

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