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Inheritance of matroclinal haploidy in diallel crosses

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Gynogenesis is an apomictic pathway of reproduction when a new organism arises from an unpollinated egg cell and is called a matroclinal haploid. First S.S.Chase (Genetics 34: 328-332, 1949) has founded matroclinal haploidy in maize. E.H.Coe (Am Nat 93:381-382, 1959) and J.L.Kermicle (Sci 166:1422-1424, 1969) created marker lines those permitted taking as pollinators to identify haploids in populations and to stimulate to some extent the ability to produce haploids. Now in maize breeding practice matroclinal haploids after diploidyization are widely used for rapid production of homozygous lines.

The investigation of genetic control of matroclinal haploidy is actual both for the characterization of apomixis in flowering plants and for the forecast of the structures of synthetic populations which could become the initial material for selection of new lines. Inheritable peculiarities of this phenomenon should be taken into consideration also in programs of breeding lines with high ability to haploid production to be used as testers in selection of marker genotypes.

The aim of the given investigation was to analyse the inheritance of the ability to produce matroclinal haploids in maize. Genetic analysis was conducted in the system of full diallel crosses according to B.I.Hayman (Biometrics 16: 369 - 381, 1960). Five lines were included to diallel scheme, DK276-1, DK247, DK293, DK303/427, DK205/710, and their reciprocal hybrids. 25 genotypes in total were organized in 4 repetitions. For production of matroclinal haploids every genotype of diallel scheme was pollinated with pollen of marker genotype Zarodyshevij marker krasnodarskij 1 (ZMK-1). This marker had been selected by

E.R.Zabirova et al. (Kukuruza i sorgo 4: 17-19, 1996). It keeps dominant genes of plumule and endosperm coloration in purple. Seeds after pollination with ZMK-1 of all the genotypes of diallel scheme were harvested and haploids were identified as caryopses with colourless embryos and coloured endosperm. Caryopses with haploid embryos were sown next year into the soil and grown to anthesis to verify their haploid status. “Frequency of matroclinal haploidy” was calculated as the percentage ratio of the amount of caryopses with haploid embryos to the total amount of caryopses with coloured endosperm. According to our observations after pollination of different maize populations with pollen of ZMK-1 grain amount per ear is greatly declined in comparison with free pollination (fig.1). Such a character was named “degree of ear graininess”, calculated as the percentage ratio of average grain amount per ear after pollination with ZMK-1 to grain amount per ear of the same genotype after free pollination, and also analysed in diallel crosses.



Figure 1. Maize ears after pollination with marker genotype ZMK-1 show the declination of grain amount.

The average values of two traits for genotypes of diallel set are shown in table 1.

Table 1. The frequency of matroclinal haploidy and the degree of ear graininess for inbred lines and hybrids of diallel set.

Genotype	Frequency of matroclinal haploidy, % ¹	Degree of ear graininess, % ¹
DK 276-1	6,45±0,73	27,46±2,73
DK 247	7,79±1,23	22,93±4,14
DK 293	8,07±0,77	38,18±3,47
DK 303/427	5,62±0,71	42,60±4,14
DK 205/710	0,59±0,22	50,12±4,39
DK 276-1xDK293	5,05±0,77	17,94±2,79
DK 293xDK276-1	7,00±1,08	28,77±3,07
DK 276-1xDK247	6,27±1,03	22,86±3,61
DK 247xDK276-1	5,67±0,97	33,02±3,53
DK 276-1xDK303/427	5,73±1,04	28,71±3,95
DK 303/427xDK276-1	6,58±1,07	34,79±4,37
DK 276-1xDK205/710	2,36±0,63	13,01±2,63
DK 205/710xDK276-1	3,30±0,95	12,22±2,14
DK 293xDK303/427	7,42±0,76	47,35±7,16
DK 303/427xDK293	7,71±0,77	48,11±5,48
DK 247xDK293	10,68±0,89	33,26±4,94
DK 293xDK247	11,12±3,15	25,17±3,59
DK 293xDK205/710	6,42±0,92	26,13±6,45
DK 205/710xDK293	6,65±0,71	43,56±4,95
DK 247xDK303/427	7,89±0,78	36,98±4,89
DK 303/427xDK247	8,46±0,81	25,23±4,49
DK 247xDK205/710	5,31±0,65	37,64±4,83
DK 205/710xDK247	5,72±0,67	37,15±4,70
DK 303/427xDK205/710	4,51±0,61	42,19±4,43
DK 205/710xDK303/427	6,83±0,74	46,79±4,96
	r*	r _{0,95} **
For all the experiment	0,05	0,40
For hybrids	0,33	0,44

For inbred lines	-0,78	0,90
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¹-data are shown as $X \pm mt_{0,05}^*$ - Coefficient of pair correlation between frequency of matroclinal haploidy and degree of ear grainness, ** - critical value of coefficient of pair correlation at the 0,95 probability level.

In general frequency of matroclinal haploidy in the diallel set fluctuated from 0,59% to 11,12%. Ear grainness after pollination with ZMK-1 compared to free pollination was reduced to 12,22-50,12%. It could be suggested that such declination was connected with the ability of genotype to induce matroclinal haploidy. However, in the given experiment coefficients of pair correlations between the frequency of matroclinal haploidy and the degree of ear grainness in total for the experiment, separately for hybrids and separately for lines were not significant. So, the existence of such a relationship is not confirmed.

In the given diallel set parental forms were presented by inbred lines, multiple allelism is improbable, the data on the irregularity of meiotic chromosome disjunction are absent. For the exclusion of few differences between reciprocal hybrids their mean values were taken to genetic analysis.

For “frequency of matroclinal haploidy” the coefficient of regression Wr/Vr was $b=0,88 \pm 0,11$ ($t_b=7,70$, $t_{1-b}=1,03$, $t_{0,05}=3,20$), for “degree of ear grainness” it was $b = 0,98 \pm 0,14$ ($t_b = 6,83$; $t_{1-b} = 0,16$; $t_{0,05} = 3,20$). The significance of regression coefficients for both traits and their non-significant deviation from 1 testified the absence of the effects of nonallelic interaction and dependent gene distribution in parental forms. Therefore, additive and dominant genetic system determines the manifestation of two characters.

The analysis of variance of a half of diallel table is represented in table 2.

Table 2. The analysis of variance of “frequency of matroclinal haploidy” and “degree of ear grainness” in diallel crosses.

Components of genetic variation	Square sums	Degrees of freedom	Mean square	F _{fact.}	F _{0,01}
“Frequency of matroclinal haploidy”					

<i>a</i>	0,6316	4	0,1579	65,93	4,22
<i>b</i>	0,1690	10	0,0169	7,04	3,17
<i>b</i> ₁	0,0373	1	0,0373	15,56	7,82
<i>b</i> ₂	0,1011	4	0,0253	10,55	4,22
<i>b</i> ₃	0,0306	5	0,0061	2,55	3,90
<i>R</i>	0,0094	3	0,0031	1,31	4,72
<i>Rt</i>	0,0575	24	0,0024		
“Degree of ear graininess”					
<i>a</i>	1,2877	4	0,3219	19,05	4,22
<i>b</i>	2,9134	10	0,2913	17,24	3,17
<i>b</i> ₁	1,5816	1	1,5816	93,58	7,82
<i>b</i> ₂	0,6934	4	0,1734	10,26	4,22
<i>b</i> ₃	0,6384	5	0,1276	7,55	3,90
<i>R</i>	0,0453	3	0,0151	0,89	4,72
<i>Rt</i>	0,4056	24	0,0169		

For both traits the significance of mean squares *a* and *b* testifies the effect of additivity and dominance. The significance of *b*₁ proves that the effects of dominance are mainly concentrated in the same direction. The significance of *b*₂ shows that dominant alleles are not dispersed among lines identically. Mean square *a* includes not only additive variance, but also a part of variance that is connected with dominant effects. Mean square *b*₃ is not significant for “frequency of matroclinal haploidy”, so specific for every cross dominant effects which are not connected with *b*₁ and *b*₂ are not established. Non-significant *R* means weak effect of the environment on the development of the characters.

On the diagram of regression Wr/Vr for “frequency of matroclinal haploidy” the regression line intersects the positive part of axis Wr (fig.2), therefore, the middle degree of dominance for all the loci are incomplete, $H1/D < 1$. Points of inbreds DK276-1, DK247, DK293 and DK303/427 are located nearer to the start of the regression line, they contain mainly dominant alleles (from 75% to 100%), which are responsible for the decrease of “frequency of matroclinal haploidy”. For inbred DK205/710 ratio of dominant and recessive genes reaches the level 25% : 75%.

This inbred includes the biggest portion of recessive alleles, which determine the increasing of matroclinal haploidy.

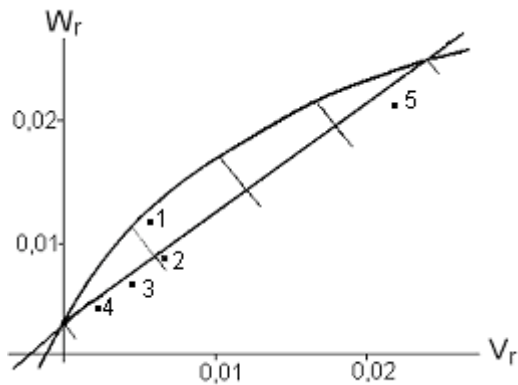


Fig.2. Regression W_r/V_r for “frequency of matroclinal haploidy” in maize (1 – DK276-1, 2 – DK247, 3 – DK293, 4 – DK303/427, 5 – DK205/710).

For “degree of ear graininess” the regression line (fig.3) passes through the negative part of axis W_r , so the superdominance plays the significant role in the manifestation of this character, $H_1/D > 1$. Dominant alleles are responsible for the decreasing, but recessive ones - for the increasing of ear graininess. The distribution of dominant and recessive alleles is located within interval 75%: 25% for inbreds DK293 and DK303/427, for inbred DK276-1 it is near to 50%: 50%. For inbreds DK205/710 and DK247 such distribution approaches 25%: 75%.

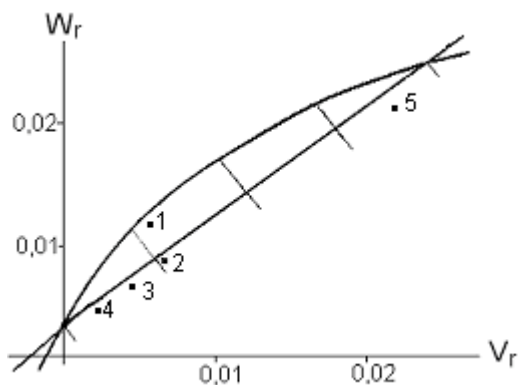


Fig.3. Regression W_r/V_r for “degree of ear graininess” in maize (1 – DK276-1, 2 – DK247, 3 – DK293, 4 – DK303/427, 5 – DK205/710).

The estimates of genetic parameters are represented in table 3.

Table 3. Genetic parameters for “frequency of matroclinal haploidy” and “degree of ear graininess”.

Genetic parameters	“Frequency of matroclinal haploidy”	“Degree of ear graininess”
D	0,03±9,54E-05	0,04±0,0005
H ₁	0,02±0,0003	0,23±0,0012
H ₂	0,01±0,0002	0,20±0,0011
F	0,01±0,0002	0,02±0,0012
E	0,002±3,89E-0,5	0,02±0,0002
H ₁ /D	0,54	5,40
$\sqrt{H_1/D}$	0,73	2,32
$\frac{1}{2} F / \sqrt{D(H_1 - H_2)}$	0,53	0,31
H ₂ /4H ₁	0,18	0,21
Heritability in wide sense	0,85	0,82
Heritability in narrow sense	0,67	0,28

For “frequency of matroclinal haploidy” incomplete dominance takes place ($H_1/D=0,54$), including separate loci ($\sqrt{H_1/D}=0,73$). For “degree of ear graininess” superdominance is shown ($H_1/D=5,4$), in that number in every locus ($\sqrt{H_1/D}=2,3$).

For the studied traits the estimate of $\frac{1}{2} F / \sqrt{D(H_1 - H_2)}$ differs from 1, the level of dominance varies in different loci. $H_1 \neq H_2$, so dominant and recessive alleles are spread irregularly among parental inbreds. Positive estimate of F verifies the exceeding of the amount or effects of dominant alleles over the recessive ones in the given set of lines and hybrids.

For the given characters the high values of heritability in wide sense proves the primary effect of genotypic variance in the development of the characters. The significant value of heritability in narrow sense for “frequency of matroclinal haploidy” (0,67) confirms the significant role of additive gene effects and permits to make favourable prognosis in phenotype selection for high

frequency of matroclinal haploidy. It is important for production of testers, which are necessary in breeding programs of new inducer genotypes. The definite role of dominant effects in the development of “degree of ear graininess” is indicated also by the considerable difference between the heritability in wide sense (0,82) and the heritability in narrow sense (0,28).