

COMPONENTS OF GENETIC VARIABILITY AND HERITABILITY OF GRAIN YIELD OF SILAGE MAIZE

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The aim of the present study was to evaluate the following parameters for the grain yield of silage maize: variability of inbred lines and their diallel hybrids, superior-parent heterosis and components of genetic variability and heritability on the basis of the diallel set. The two-year four-replicate trial was set up according to the randomised complete-block design at Zemun Polje. It was determined that a genotype, year and their interaction significantly affected variability of this trait. The highest, i.e. the lowest grain yield, on the average for both investigation years, was recorded in the silage maize inbred lines ZPLB402 and ZPLB405, respectively. The analysis of components of genetic variance for grain yield shows that the additive component (D) was lower than the dominant (H_1 and H_2) genetic variance, while a positive component F and the frequency of dominant (u) and recessive (v) genes for this observed trait point to prevalence of dominant genes over recessive ones. Furthermore, this is confirmed by the ratio of dominant to recessive genes in parental genotypes for grain yield ($K_d/K_r > 1$) that is greater than unity in both years of investigation. The estimated value of the average degree of dominance (H_1/D)² exceeds unity, pointing out to superdominance in inheritance of

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this trait in both years of investigation. Results of V_r/W_r regression analysis indicate superdominance in inheritance of grain yield. Moreover, a registered presence of non-allelic interaction points out to the need to study effects of epistasis, as it can have a greater significance in certain hybrids. A greater value of dominant than additive variance resulted in high values of broad-sense heritability for grain yield in both investigation years (98.71%, i.e. 97.19% in 1997, i.e. 1998, respectively), and low values of narrow-sense heritability (11.9% in 1997 and 12.2% in 1998).

Key words: silage maize, grain yield, heterosis, components of genetic variance, heritability, regression analysis

INTRODUCTION

A proper evaluation of heterosis, genetic variability and heritability of a trait is a very important from the aspect of practical selection. Heterosis as hybrid vigour of the F_1 generation in relation to parents is maximally used in the maize production. Heterosis evaluated and expressed in % in relation to values of superior-parent heterosis was named relative heterosis in contrast to absolute heterosis (FISHER, 1978), where an actual magnitude of a quantitative trait of F_1 generation is considered. According to FISHER (1978) absolute heterosis occurs if an average value of the trait of F_1 generation is higher than the average trait of the superior parent. However, heterosis is not a frequent phenomenon, and a case that the progeny is more superior in all traits than the superior parent is even rarer, hence the study is performed for each individual case.

HAYMAN (1954; 1954a) and JINKS (1954) genetically studied parental in-breds engaged in diallel crosses, while GRIFFING (1956) and KEMPTHORNE (1956) genetically analysed the initial population that had been a source of parental in-breds. According to methods of HAYMAN (1954a) genetic variance can be separated into the following components: D - variance based on the additive gene effects; F - sum of effects of interaction (additive x dominant); h^2 - heritability estimated on the basis of total genetic variance to phenotypic variance ratio. Besides, the following is presented: a figure presenting a relation of V_r variance and W_r covariance, limiting parabolas and an expected regression line according to which the character of gene effects is shown.

HANSON (1963) points out that heritability (h^2), as a part of variation due to the genetic constitution of parents, can be considered in a broad sense (genetic to phenotypic variance ratio) and in a narrow sense (additive genetic to phenotypic variance ratio). FALCONER (1960) indicates that when evaluating heritability one should bear in mind that obtained heritability for a certain trait is a value related to a particular population and specific environmental conditions.

According to analysis used by HAYMAN (1954, 1954a), MORENO-GONZALES and DUDLEY (1981), IVANOVIĆ (1982), DRAGANIĆ *et al.* (1982), BABIĆ (1993), PAJIĆ (1984), TRIFUNOVIĆ (1986) and TODOROVIĆ (1995) established that dominant genetic variance was more important than additive one, that dominant genes prevailed over recessive ones. The same authors also determined low values

of narrow-sense heritability and high values of broad-sense heritability and that grain yield was inherited by dominance or superdominance, while results obtained by OBILANA *et al.* (1979), who had studied genetic variance in intervarietal hybrids, confirmed that additive genetic variance was greater than dominant one for grain yield. Dominant variance was lower by approximately 50% than the value of additive variance.

GUNN (1975) emphasises that aims of selection for the silage maize development should not be orientated only towards the development of hybrids with high grain yields, but also to the development of hybrids which will have high yields of the total dry matter.

VATTIKONDA and HUNTER (1983) determined that the most grain yielding hybrid had silage yield lower by 10% than the record yielding silage maize. These results point out that there are justifiable reasons for a specific selection programme on silage maize. The genetic background of traits important for the increase of yield and quality of silage maize has not been significantly studied yet in relation to studies on inheritance of grain yield and its components (BARRIERE *et al.*, 1988; DHILLON *et al.*, 1990).

Based on the analysis of components of genetic variance it can be expected that dominant genes will have more important role in inheritance of grain yield in silage maize than additive genes.

MATERIAL AND METHODS

Six inbred lines of silage maize of the FAO maturity group 400 within the ZP collection (ZPL401, ZPL402, ZPL403, ZPL404, ZPL405, ZPL406) and 15 hybrids derived by diallel crosses of inbred lines were used in this study. A comparative field trial with inbreds and hybrids was set up according to the randomised complete-block design with four replications at Zemun Polje in 1997 and 1998. Each genotype was sown in one row per a replication with the density of 71,400 plants ha⁻¹. The elementary plot size was 2.8 m². Statistical processing of obtained results was done for each year due to a high significance of effects of a year on grain yield of silage maize. The following biometrical parameters were estimated: means, standard deviation, coefficient of variation and superior-parent heterosis. The analysis of components of genetic variance and regression analysis were done after the model used by HAYMAN (1954), JINKS (1954) and MATHER and JINKS (1971).

Table 1. Mean squares of ANOVA for grain of yield

Sources of variance	df	Grain yield
Year (Y)	1	23.34**
Genotype (G)	20	98.82**
Y x G	20	2.66**
Error	126	1.18

Table 2. Mean values (\bar{x}), varieties (σ), coefficient of variation (CV%) and heterosis for grain yield (t ha⁻¹)

Genotype	\bar{x}		σ		CV (%)		Heterosis (%)	
	1997.	1998.	1997.	1998.	1997.	1998.	1997.	1998.
ZPLB401	5.775	6.745	0.395	0.257	6.83	3.81		
ZPLB402	5.977	6.798	0.686	0.282	11.48	4.15		
ZPLB403	4.887	6.128	0.282	0.837	5.76	13.66		
ZPLB404	5.375	5.640	0.630	0.368	11.72	6.52		
ZPLB405	3.253	3.150	0.736	0.653	22.61	20.73		
ZPLB406	5.347	4.528	0.490	1.013	9.17	22.37		
ZPLB401xZPLB402	13.233	13.403	1.079	1.256	8.15	9.37	121.4**	97.2**
ZPLB401xZPLB403	12.255	11.660	1.019	1.365	8.31	11.71	112.2**	72.9**
ZPLB401xZPLB404	9.645	7.657	1.772	0.404	18.37	5.27	67.0	13.5
ZPLB401xZPLB405	11.510	12.057	0.362	1.317	3.14	10.92	99.3**	78.7* *
ZPLB401xZPLB406	14.082	14.260	0.216	1.399	1.53	9.81	143.8**	111.4**
ZPLB402xZPLB403	4.083	6.052	0.914	0.213	22.39	3.52	-31.7	-11.0
ZPLB402xZPLB404	8.100	8.408	0.611	0.952	7.54	11.33	35.5	23.7
ZPLB402xZPLB405	11.863	13.577	0.747	1.411	6.30	10.39	98.5**	99.7**
ZPLB402xZPLB406	13.323	13.558	0.636	1.030	4.77	7.60	122.9**	99.4**
ZPLB403xZPLB404	7.028	8.330	0.566	0.632	8.06	7.59	30.7	35.9
ZPLB403xZPLB405	9.795	12.552	1.065	1.846	10.88	14.71	100.4**	104.8*
ZPLB403xZPLB406	11.287	12.542	0.780	1.481	6.91	11.81	111.1**	104.7**
ZPLB404xZPLB405	9.035	11.663	1.095	1.070	12.12	9.17	68.1*	106.8**
ZPLB404xZPLB406	12.770	14.910	1.446	0.454	11.33	3.04	137.6**	164.4**
ZPLB405xZPLB406	11.925	12.593	0.517	0.881	4.33	7.00	123.0**	178.1**

*,** significant at the probability levels of 0.05 and 0.01, respectively

RESULTS AND DISCUSSION

Obtained results of the two-factorial analysis of variance show very significant values of mean squares of a year, genotypes and the year x genotype (Y x G) interactions (Table 1).

The analysis of results indicates, as expected, a significantly higher yield of hybrids in relation to the yield of inbred lines in both years of investigation. The lowest, i.e. highest yield was recorded in the inbred ZPLB405 (3.253 t ha⁻¹ in 1997 and 3.150 t ha⁻¹ in 1998), i.e. ZPLB402 (5.977 t ha⁻¹ in 1997 and 6.798 t ha⁻¹ in 1998), respectively. The hybrid combination ZPLB402 x ZPLB403 had the lowest average yield in both years - 4.083 t ha⁻¹ in 1997 and 6.052 t ha⁻¹ in 1998. On the other hand, the highest average yields of 14.082 t ha⁻¹ and 14.910 t ha⁻¹ were recorded in the hybrids ZPLB401 x ZPLB406 (1997) and ZPLB404 x ZPLB406 (1998), respectively, (Table 2).

The coefficient of variation for inbreds ranged from 5.76% (ZPLB403) to 22.61% (ZPLB405) in 1997 and from 3.81% (ZPLB401) to 22.37% (ZPLB406) in 1998. The corresponding values for hybrids ranged from 1.53% (ZPLB401 x ZPLB406) to 22.39% (ZPLB402 x ZPLB403), and from 3.04% (ZPLB404 x ZPLB406) to 14.71% (ZPLB403 x ZPLB405), (Table 2). The average values of the coefficient of variation were higher for inbreds than for hybrids in both years of investigation.

The majority of hybrids expressed highly significantly positive values of heterosis in both years, except the F₁ hybrids ZPLB401 x ZPLB404, ZPLB402 x ZPLB404 and ZPLB 403x ZPLB404 that had positive, but not significant values of heterosis in both investigation years. The hybrid combinations ZPLB404 x ZPLB405 (1997) and ZPLB403 x ZPLB405 (1998) had significant positive values of heterosis, while the hybrid ZPLB402 x ZPLB403 had negative heterosis in both years in relation to a superior parent. The maximum value of heterosis was recorded in 1998 in the F₁ generation ZPLB405 x ZPLB406 and amounted to 178.1%, while the combination ZPLB401 x ZPLB406 expressed the highest heterotic effect (143.8%) in 1997. The lowest positive heterosis in 1997 (30.7%) and 1998 (13.5%) was recorded in the F₁ generation ZPLB403 x ZPLB404 and ZPLB401 x ZPLB404, respectively (Table 2).

On the basis of the analysis of components of genetic variability for maize grain yield (Table 3) it can be concluded that the dominant component of variance (H_1 and H_2) was significantly higher than the additive component (D) in both years of investigations, and it points out to the greater participation of the dominant component in genetic variance. The value F (additive x dominant effect interaction) was positive, which means that dominant alleles prevailed over the recessive ones. This is also confirmed by the frequency of dominant alleles in relation to the recessive ones ($u=0.62$; $v=0.38$ in 1997 and $u=0.70$; $v=0.30$ in 1998). According to these results, dominant and recessive genes were not symmetrically arranged in parents as indicated by the ratio of $H_2/4H_1$ that was less than 0.25. The average degree of dominance $(H_1/D)^{1/2}$ was greater than unity indicating that grain yield in

maize is related to superdominance. The proportion of the total number of dominant and the total number of recessive genes Kd/Kr points out that parents have more dominant genes for this trait, since estimated values in both years were greater than unity (Table 3).

Table 3. Components of genetics variability of grain yield in 6x6 diallel crosses

Components of variance	Value	
	1997	1998
D	1,20	1,74
H ₁	50,13**	62,55**
H ₂	47,26**	52,78**
F	0,81	7,75
E	0,22	0,32
H ₂ /4H ₁	0,23	0,21
U	0,62	0,70
V	0,38	0,30
$\sqrt{H_1/D}$	6,45	6,00
Kd/Kr	1,11	2,18
\bar{v}_r	12,76	14,33
\bar{w}_r	0,45	-1,00
Vp	1,42	2,06
\bar{v}_r	0,84	0,97
H _{ns} ²	11,9%	12,2%
H _{bs} ²	98,4%	97,9%

The presence of epistasis was detected for grain yield in both years of investigation. By the elimination of each parent individually it was determined that the inbred ZPLB401 included epistasis in both years, while the inbred ZPLB402 included epistasis in 1997. The value of the parameter a was negative for both years ($a=-9.04$ and $a=-20.15$ in 1997 and 1998, respectively). The regression line intercepted Wr ordinate bellow the point of origin in both years indicating superdominance in inheritance of grain yield (Figures 1 and 2). It agreed with the average degree of dominance $(H_1/D)^{1/2}$ (Table 3), that was higher than unity. According to the distribution of parental genotypes in relation to the regression line it can be concluded that the inbreds ZPLB405 and ZPLB406 were donors of the majority of recessive genes, while the inbreds ZBLB403 and ZPLB404 were donors of dominant genes for grain yield in 1997 and 1998. The inbred ZPLB401 included epistasis and therefore it was eliminated from the analysis in both years. The inbred ZPLB402 was eliminated in 1997, while in 1998 it was characterised by a greater number of dominant genes (Figures 1 and 2).

Low values of narrow-sense heritability were expressed for grain yield in both years of investigation ($h_{ns}^2=11.9\%$ in 1997 and $h_{ns}^2=12.2\%$ in 1998; Table 3). This was caused by a low proportion of additive variance in this trait expressing. Contrary to these results, broad-sense heritability had very high values ($h_{bs}^2=98.4\%$

in 1997 and $h^2_{bs}=97.9\%$ in 1998), pointing out to a great proportion of dominant genes in total genetic variance (Table 3).

Grain yield is an important and a complex trait consisting of a greater number of components of quantitative nature with a polygenic base. According to the presented data on grain yield (Table 2) all hybrid combinations, except ZPLB402 x ZPLB403, expressed positive heterotic effects. The stated hybrid combination had the lowest mean in both investigation years. Heterosis was estimated in relation to average superior-parent heterosis and was named absolute and relative heterosis after FISHER (1978). High heterosis usually occurs when effects of non-additive genes are higher, especially in the case of superdominance, as in this study. The hybrid combination ZPLB402 x ZPLB403 did not have a positive heterosis for ear length as its mean was lower than parental means in both years (Table 2). High values of heterosis for grain yield of maize were determined by TODORVIĆ (1995). Obtained values of coefficients of variance for grain yield were lower than those obtained by KOJIĆ (1982) and BABIĆ (1993).

Components of genetic variance for grain yield in both years were calculated from systems of equations (JINKS, 1954; HAYMAN, 1954; MATHER and JINKS, 1971) (Table 3). Obtained results are in accordance with results gained by MORENO-GONZALES and DUDLEY (1981), KOJIĆ (1982), PAJIĆ (1984), BABIĆ (1993) and TODORVIĆ (1995).

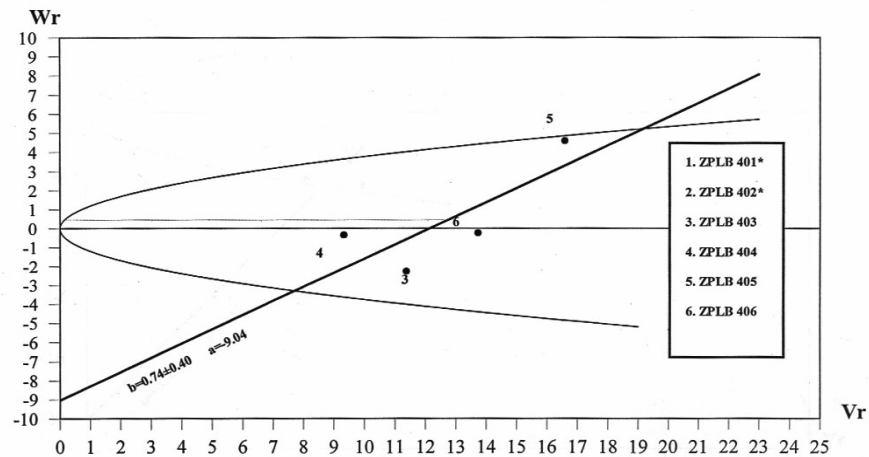


Fig. 1. V_r/W_r regression analysis for grain yield of six maize inbred lines in 1997 (* parent which includes epistasis)

The complete picture on gene actions according to MATHER and JINKS (1971) is established by the regression analysis. In the absence of the interallelic interaction the scatter of array points on the V_r/W_r graph should lie inside the limiting parabola and be distributed along the regression line. The degree of dominance is estimated from the point of intersection of the regression line with the W_r ordinate. When the regression line intersects the W_r ordinate above the point of origin ($D>H$; $a=+$) it indicates partial dominance. When the regression line passes

through the point of origin ($D=H$; $a=0$) it indicates complete dominance. When the regression line passes below the point of origin, as in the present study on ear length ($H>D$; $a=-$), it indicates superdominance (Figures 1 and 2) what is in accordance with results achieved by KOJIĆ (1982), PAJIĆ (1984) and TODORVIĆ (1995).

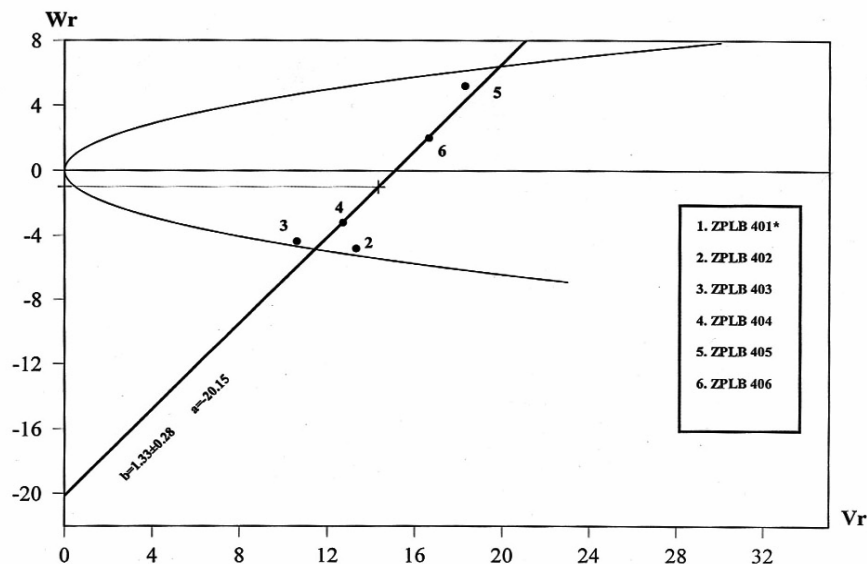


Fig. 2. V_r/W_r regression analysis for grain yield of six maize inbred lines in 1998 (* parent which includes epistasis)

The scatter of array points along the expected regression line indicates the distribution of dominant and recessive genes among the parents. The points nearest the point of origin represent the parents with the highest number of dominant genes, while points furthest from the point of origin represent the parents with the highest number of recessive genes.

The similarity between the parents and the offspring depends on magnitude of genetic variance and its components. The ratio between genetic variance and total phenotypic variance represents broad-sense heritability, while narrow-sense heritability is the ratio between additive genetic variance and total phenotypic variance. Low values of narrow-sense heritability for grain yields were obtained in both investigation years (Table 3). Such low values are caused by a small proportion of additive gene effects, great effects of environmental factors on the expression of grain yield and high frequency of dominant alleles. When the frequency of dominant alleles is above 0.5 narrow-sense heritability decreases as confirmed by obtained results. Low values of narrow-sense heritability were gained by PAJIĆ (1984), BABIĆ (1993) and TODORVIĆ (1995). Obtained very high values of broad-sense heritability indicate a high proportion of dominant gene effects in total genetic variance. Lower values of broad-sense heritability were obtained by

TRIFUNOVIĆ (1986). FALCONER (1960) indicates that when evaluating heritability one should bear in mind that obtained heritability for a certain trait is a value related to the particular population and specific environmental conditions.

The regression analysis has a practical application in quantitative genetics as a method of studying the intensity and the degree of dependence among observed phenomena. This method facilitates the determination of the genetic system of inheritance of quantitative traits. According to obtained results inheritance of grain yield (Fig. 1 and 2) indicates superdominance what is in accordance with results gained by PAJIĆ (1984) and TODOROVIĆ (1995).

CONCLUSION

The results of the analysis variance for grain yield show highly significant differences among observed genotypes, as well as, significant influence of the year and the year x genotype interaction on variability of this trait. The highest grain yield was recorded in the hybrids ZPLB401 x ZPLB406 (1997) and ZPLB404 x ZPLB406 (1998). As expected, hybrids had higher average yields than inbreds due to the depression of this trait in inbreds that occurs during inbreeding. The majority of hybrid combinations had high values of heterosis (from -31.7 to 178.1 %), while the hybrid ZPLB402 x ZPLB403 had a negative value of heterosis for grain yield (from -11.0 % in 1998 to -31.7% in 1997). The analysis of genetic variance show that dominant components (H_1 and H_2) were higher than additive (D) and that their role in inheritance of grain yield in the F_1 generation was more important. The positive component F for this trait indicates that dominant genes prevailed over recessive ones. The estimated value of the average degree of dominance $(H_1/D)^{1/2}$ is greater than unity and indicates superdominance in inheritance of these traits. The frequency of dominant genes (u) was greater than the frequency of recessive genes (v) for all traits in both years. The ratio of dominant genes to recessive genes in parental genotypes indicates prevalence of dominant genes over recessive ones in grain yield ($Kd/Kr > 1$) during both years. Results of the Vr/Wr regression analysis point to superdominance in inheritance of grain yield. The presence of non-allelic interaction was determined for this trait. It points out to the need to study effects of epistasis as it can have a greater significance in some hybrids. High, i.e. low values of broad-sense, i.e. narrow-sense heritability for grain yield, respectively, were obtained (98.4% i.e. 11.9% in 1997 and 97.9% i.e. 12.2% in 1998).

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**KOMPONENTE GENETIČKE VARIJABILNOSTI I HERITABILNOST
PRINOSA ZRNA SILAŽNOG KUKURUZA**Mile SEČANSKI¹, Tomislav ŽIVANOVIĆ², Goran TODOROVIĆ¹ i Gordana ŠURLAN-MOMIROVIĆ²¹ Institut za kukuruz "Zemun Polje", Slobodana Bajića 1, 11185 Zemun Polje,² Poljoprivredni fakultet Univerziteta u Beogradu, Nemanjina 6, 11080 Zemun, Srbija i Crna Gora

Izvod

Pravilna procena heterozisa, genetičke varijabilnosti i heritabilnosti neke osobine je veoma bitna sa stanovišta praktične selekcije, što je i bio cilj ovih istraživanja. Rezultati analize varijanse pokazuju visoko značajne razlike između ispitivanih genotipova za prinos zrna, kao i značajan uticaj godine i interakcija godina x genotip na varijabilnost ove osobine. Najveći prinos zrna su imali hibridi ZPLB401 x ZPLB406 (1997) i ZPLB404 x ZPLB406 (1998). Hibridi su u odnosu na linije ispoljili veće prosečne vrednosti za prinos zrna što je i očekivano obzirom da pri inbridingu dolazi do depresije ove osobine kod linija. Za većinu hibridnih kombinacija utvrđene su visoke vrednosti heterozisa, dok je hibrid ZPLB402 x ZPLB403 pokazao negativnu vrednost heterozisa za prinos zrna (-11.0 do -31.7%). Analiza komponenti genetičke varijanse pokazuje da su dominantne komponente (H_1 i H_2) bile veće od aditivne (D) i imale važniju ulogu u nasleđivanju prinosa zrna u F_1 generaciji. Komponenta F je pozitivna za ovu osobinu što ukazuje da dominantni geni preovlađuju nad recesivnim. Izračunata vrednost prosečnog stepena dominacije $(H_1/D)^{1/2}$ je veća od jedinice za ovu osobinu i pokazuje da se u nasleđivanju ovih osobina radi o superdominaciji. Odnos dominantnih gena prema recesivnim kod roditeljskih genotipova pokazuje da su kod prinosa zrna preovladavali dominantni geni nad recesivnim ($Kd/Kr > 1$) u obe godine. Rezultati Vr/Wr regresione analize ukazuju na superdominaciju u nasleđivanju prinosa zrna. Prisustvo nealelne interakcije ustanovljeno je za ovu osobinu. To ukazuje na potrebu proučavanja efekta epistaze pošto može imati veći značaj kod pojedinih hibrida. Za prinos zrna su dobijene visoke vrednosti heritabilnosti u širem smislu (98.4% (1997) i 97.9% (1998)) i niske vrednosti heritabilnosti u užem smislu (11.9% (1997) i 12.2% (1998))

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