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COMBINING ABILITIES OF SILAGE MAIZE GRAIN YIELD

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Abstract: The aim of the present study was to evaluate the following parameters of maize grain yield: variability of inbred lines and their diallel hybrids, superior-parent heterosis and general and special combining abilities. According to obtained results of the two-year study, it can be concluded that variability of this trait is significantly affected by a genotype, year and their interaction. As expected, hybrids had higher average grain yields than inbreds due to the depression of this trait that occurs in inbreds during inbreeding. The highest average value of heterosis for gain yield was detected in the hybrid ZPLB405 x ZPLB406 (123.0% and 178.1% in 1997 and 1998, respectively).

The estimation of combining abilities was done on the basis of diallel hybrids after the method established by Griffing, 1956, (method II, mathematical model I). The analysis of variance of combining ability for grain yield indicated highly significant values of GCA and SCA for the observed trait in both study years. Grain yield inheritance was more affected by non-additive genes (dominance and epistasis) as indicated by the GCA to SCA ratio that was smaller than unity. The inbreds ZPLB401 and ZPLB406 had high GCA effects, while the hybrid combinations ZPLB401 x ZPLB402, ZPLB401 x ZPLB403, ZPLB401 x ZPLB405, ZPLB402 x ZPLB406, ZPLB403 x ZPLB406, ZPLB404 x ZPLB406, ZPLB405 x ZPLB406 had high SCA effects in both study years. These hybrid combinations include one parent with high GCA effects and other with low GCA effects. Furthermore, there are combinations ZPLB402 x ZPLB405, ZPLB403 x ZPLB405 and ZPLB404 x ZPLB405 with significant SCA effects that include parents with low GCA effects. This is probably the result of the additive type (additive x additive) of interaction between parents.

Key word: silage maize, heterosis, combining abilities, GCA, SCA, grain yield.

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Introduction

A proper evaluation of combining abilities of genotypes can be made on the basis of intercrossing. Heterosis as hybrid vigour of the F_1 generation in relation to parents is maximally used in maize production. 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. Therefore, it is necessary to recognize combining abilities of parents prior to their crossing with the aim to develop a hybrid. Consequently, the estimation of combining abilities, done according to crosses, is a very important stage in developing highly productive maize hybrids. Combining ability implies the capacity of a parent to produce superior progenies when crossed with another parents. Combining abilities are classified into two groups: general combining ability (GCA) and special combining ability (SCA). GCA and SCA were initially presented by Sprague and Tatum, 1942, according to whom GCA was used to indicate an average performance of the inbred in the hybrid combinations, while SCA was used to point out cases in which performed combinations had been better or worse than expected according to average performances of inbreds included into such combinations. Griffing, 1956, 1956a, Sprague and Tatum, 1942, Falconer, 1960, Borojević, 1981, determined that GCA was the result of additive genetic variance, while SCA was the result of non-additive genetic variance, i.e. of dominance and epistasis.

Diallel cross techniques are the most reliable method for analysing combining abilities. There are several methods to evaluate combining abilities: method proposed by Hayman, 1954, 1954a, and modified by Jones, 1965, and the analysis used by Griffing, 1956. The diallel cross techniques for the analysis of GCA proposed by Griffing, 1956, encompasses four experimental methods and two mathematical analyses: Method 1 (encompasses parents, F_1 hybrids and reciprocal crosses), Method 2 (encompasses parents and F_1 hybrids without reciprocal crosses), Method 3 (includes F_1 hybrids and reciprocal crosses), Method 4 (includes F_1 hybrids without reciprocal crosses), Model 1 (fixed model implies that parents are not a random sample of a certain population) and Model 2 (i.e. a random model implies that parents are a sample of a population analysed on the basis of a diallel cross). Methods used by Griffing, 1956, point out to significance of GCA and SCA of inbreds indicating additive and dominant gene effects.

Singh and Gupta, 1969, Kraljević-Balalić, 1974, reported that high positive values for SCA were often obtained by crosses of a parent with high GCA and a parent with low GCA as well as by crosses of parents with low GCA. Similar results were obtained by Pajić, 1984, Babić, 1993, Todorović, 1995, who emphasised that parents with low GCA can produce positive and high values of SCA. Borojević, 1981, established that parents with good GCA could produce potential inbreds in later generations and that high values of combining abilities were in many cases related to a heterosis phenomenon.

The analysis of combining abilities of heterogeneous and heterozygous genetic material (populations and varieties) show that GCA was more important than SCA for inheritance of grain yield and its components. This was also confirmed by the results gained by Lamkey and Hallauer, 1984, Vančetović, 1992, Delić, 1993.

Pajić, 1984, Babić, 1993, Todorović, 1995, studied combining abilities of grain yield in maize inbred lines and their diallel series of F_1 hybrids. Very significant values of GCA and SCA were determined. Non-additive gene effects prevailed in grain yield inheritance as a greater effect of dominant genes was established (GCA/SCA<1).

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 comparison to studies on inheritance of grain yield and its components, Barriere et al., 1988, Dhillon et al., 1990.

The existence of a difference between GCA and SCA for grain yield inheritance in maize inbred lines was a starting point in this study.

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 m^2. Statistical processing of obtained results was done for each year due to a high significance of effects of a year, genotype and their interaction 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 combing abilities was performed after Griffing, 1956, Method 2, mathematical model I, without reciprocal crosses according to the following model:

Source of variation	d.f.	sum of squares	mean squares	Expected mean squares
GCA	p-1	Sg	Mg	$\sigma^2 + (p+2)(\frac{1}{(p-1)}\Sigma gi^2$
SCA	P(p-1)/2	Ss	Ms	$\sigma^2 + \frac{2}{p(p-1)}\frac{\Sigma\Sigma}{i \le j}S_{ij^2}$
Error	M	Se	Me	σ^2

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 interaction (Tab. 1).

T a b. 1. - Mean squares of ANOVA for grain 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

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 (Tab. 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) (Tab. 2). The average values of the coefficient of variation were higher for inbreds than for hybrids in both study years.

The majority of hybrids expressed highly significantly positive values of heterosis in both years, except the F_1 hybrids ZPLB401 x ZPLB404, ZPLB402 x ZPLB404 and ZPLB 403x ZPLB404 that had positive, but not significant values of heterosis in both study 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 F_1 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 F_1 generation ZPLB403 x ZPLB404 and ZPLB401 x ZPLB404, respectively (Tab. 2).

T a b. 2. - Mean values ($\overline{X}$), varieties (σ), coefficient of variation (CV%) and heterosis for grain yield (t ha[-1])

Genotype	$\overline{X}$		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	3.233	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

On the basis of obtained data (Tab. 3), it can be observed that there are highly significant differences for GCA and SCA in F_1 generation in both study years. It is obvious that grain yield is affected by additive and non-additive gene effects with the prevalence of non-additive gene effects (dominance and epistasis), which is indicated by the GCA to SCA ratio lower than unity (GCA/SCA=0.60 in 1997 and GCA/SCA=0.23 in 1998).

T a b. 3. - ANOVA for combining ability for grain yield

Sources of variance	Degrees of freedom	Mean square	
		1997	1998
GCA	5	8.005**	3.799**
SCA	15	13.401**	16.475**
E	60	0.246	0.350
GCA/SCA		0.60	0.23

Highly statistically positive effects of GCA in 1997, i.e. 1998, were recorded in the inbreds ZPLB406 and ZPLB401, i.e. the inbred ZPLB406, respectively. Negative effects of GCA in both years were determined in the inbreds ZPLB402, ZPLB403 and ZPLB404, while the inbred ZPLB405 had a negative value of GCA in 1997 (Tab. 4).

T a b. 4. – General combining ability for grain yield of the parents

Parents	GCA		Range		SE	
	1997	1998	1997	1998	1997	1998
ZPLB401	1.095**	0.474	2	2	0.248	0.296
ZPLB402	-0.120	-0.018	3	4		
ZPLB403	-0.161	-0.668	6	5		
ZPLB404	-0.773	-0.812	5	6		
ZPLB405	-0.361	0.001	4	3		
ZPLB406	1.321**	1.022**	1	1		

$LSD_{0.05}$ = 0.496 and $LSD_{0.01}$ = 0.660 for 1997 and $LSD_{0.05}$ = 0.592 and $LSD_{0.01}$ = 0.787 for 1998

Statistically very significant positive values of SCA in 1997 were detected in the majority of hybrid combinations except in F_1 generations ZPLB402 x ZPLB403, ZPLB402 x ZPLB404 and ZPLB403 x ZPLB404 that were characterised by a negative value of SCA (Tab. 5). The combination ZPLB401 x ZPLB404 had a positive SCA value, but this value was not statistically significant. Unlike 1997, in 1998, a significant positive SCA value was detected only in the combination ZPLB405 x ZPLB406, while a negative SCA value was recorded in the combination ZPLB401 x ZPLB404 (Tab. 5).

T a b. 5. - Specific combining ability of grain yield of the hybrid combinations

Parents	Year	ZPLB 402	ZPLB 403	ZPLB 404	ZPLB 405	ZPLB 406	SE
ZPLB401	1997	3.184**	3.248**	0.250	1.702**	2.593**	0.608
	1998	3.127**	2.034**	-1.824	1.763**	2.944**	0.724
ZPLB402	1997		-3.710	-0.080	3.269**	3.048**	
	1998		3.081	-0.582	3.775**	2.734**	
ZPLB403	1997			-0.109	2.243**	2.054**	
	1998			-0.010	3.400**	2.369**	
ZPLB404	1997				1.095**	3.149**	
	1998				2.654	4.875**	
ZPLB405	1997					1.891**	
	1998					1.750*	

$LSD_{0.05}$ = 1.216 and $LSD_{0.01}$ = 1.617 for 1997 and $LSD_{0.05}$ = 1.448 and $LSD_{0.01}$ = 1.926 for 1998

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 (Tab. 2), all hybrid combinations, except ZPLB402 x ZPLB403, expressed positive heterotic effects. The stated hybrid combination had the lowest mean in both study years. Heterosis was estimated in relation to mid-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. High values of heterosis for grain yield of maize were determined by Todorović, 1995. Obtained values of coefficients of variance for grain yield were lower than those obtained by Šatarić, 1978, Kojić, 1982 and Babić, 1993.

The analysis of general and special combining abilities was performed on the basis of results obtained on diallel crosses. Intercrossing of all inbred lines does not result in heterosis, hence, this study was devoted to observance of combining abilities of selected inbreds. According to the consideration that GCA is a parameter of additive genetic variance, and SCA is a parameter of non-additive genetic variance (dominance and epistasis) (Griffing, 1956, Falconer, 1960, Borojević, 1981) grain yield in our two-year experiment was affected by non-additive gene effects as it was confirmed by the GCA/SCA ratio lower than unity (Tab. 3). Gained results are in accordance with results obtained by Kojić, 1982, Pajić, 1984, Babić, 1993, Todorović, 1995. Other authors indicate that grain yield is caused by additive gene effects, and also point out to a greater significance of GCA for heterozygous material (populations and varieties), Vančetović, 1992, Delić, 1993, Lamkey and Hallauer, 1984.

According to the evaluation of GCA, the inbred ZPLB406 was the best combiner for grain yield in both study years (Tab. 4). The importance of inbreds with high values of GCA is great in the maize breeding programme for the development of new, higher yielding hybrids and the development of new synthetic populations. The hybrid combination ZPLB404 x ZPLB406 had the highest value of SCA in 1998 (Tab. 5). Crosses with a high SCA value usually include a parent with high GCA and a parent with a low GCA value (Singh and Gupta, 1969, Kraljević-Balalić, 1974). This means that GCA of certain inbred is related only to an actual combination and that it does not have to be an inferior combiner for a certain trait in the combination with another inbred. The hybrid combination ZPLB402 x ZPLB405 had the highest SCA value in 1997. Since parents of this hybrid were defined as inferior general combiners, the high SCA value was probably a result of the additive genes x additive genes interaction (Tab. 5). The hybrid ZPLB402 x ZPLB403 had not only the lowest SCA value in both study years, but also expressed a negative heterotic effect, and also included inbred lines with a low effect for GCA.

Conclusion

The results of the analysis of variance for grain yield show highly significant differences among observed genotypes as well as a significant influence of the environment (year) and the year x genotype interaction. The highest grain yield was recorded in 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 that occurs in inbreds during inbreeding. The majority of hybrid combinations had high values of heterosis (ranging from -31.7 to 178.1%), while the hybrid ZPLB402 x ZPLB403 had a negative value of heterosis for grain yield (ranging from -11.0 % in 1998 to -31.7% in 1997). The analysis of variance of combining abilities show highly significantly positive values of GCA and SCA for grain yield in both study years. The non-additive gene effect has a significant role in grain yield inheritance as confirmed by the GCA to SCA ratio lower than unity. As the inbred ZPLB406 had highly significantly positive GCA values for grain yield in both study years, it is the best general combiner. The hybrid combinations ZPLB402 x ZPLB405 (1997) and ZPLB404 x ZPLB406 (1998) had highly significant SCA values for grain yield in both study years. All hybrid combinations with good SCA include both parents with good or one parent with good GCA and another with more inferior GCA or both parents with poor GCA. In both study years, hybrid combinations ZPLB402 x ZPLB405, ZPLB403 x ZPLB405 and ZPLB404 x ZPLB405 had significant SCA effects and also included parents with inferior GCA values. This is probably due to additive gene effects (additive genes x additive genes interaction between parents).

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KOMBINACIONE SPOSOBNOSTI PRINOSA ZRNA SILAŽNOG KUKURUZA

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Rezime

U radu za prinos zrna kukuruza izvršena je procena varijabilnosti inbred linija i njihovih dialelnih hibrida, heterozis u odnosu na boljeg roditelja i opšte i posebne kombinacione sposobnosti. Na osnovu dobijenih rezultata dvogodišnjeg istraživanja može se zaključiti da na varijabilnost ove osobine značajno utiču

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genotip, godina i njihova interakcija. 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. Najveći prinos zrna su imali hibridi ZPLB401 x ZPLB406 (1997) i ZPLB404 x ZPLB406 (1998). Za većinu hibridnih kombinacija utvrdjene su visoke vrednosti heterozisa (-31.7 do 178.1 %), dok je hibrid ZPLB402 x ZPLB403 pokazao negativnu vrednost heterozisa za prinos zrna (-11.0 do -31.7%). Najviša prosečna vrednost heterozisa za prinos zrna je utvrdjena za hibrid ZPLB405 x ZPLB406 (123.0% (1997) i 178.1% (1998).

Procena kombinacionih sposobnosti je izvršena na bazi dialelnih hibrida po metodi Griffing-a, 1956, (metod II, matematički model I). Analiza varijanse kombinacionih sposobnosti za prinos zrna je pokazala da postoje visoko značajne vrednosti OKS i PKS za ovu ispitivanu osobinu u obe godine. Za nasledjivanje prinosa zrna utvrdjen je veći značaj neaditivnih gena (dominacije i epistaze) što pokazuje odnos OKS/PKS koji je bio manji od jedinice. Najbolji opšti kombinatori su bile linije ZPLB401 i ZPLB406, a hibridne kombinacije ZPLB401 x ZPLB402, ZPLB401 x ZPLB403, ZPLB401 x ZPLB405, ZPLB402 x ZPLB406, ZPLB403 x ZPLB406, ZPLB404 x ZPLB406, ZPLB405 x ZPLB406 su sa značajnim efektima PKS u obe godine ispitivanja. Sve hibridne kombinacije sa dobrim *PKS* uključuju oba roditelja sa dobrim ili jednog roditelja sa dobrim *OKS* i drugog sa lošijim *OKS* ili oba sa lošim *OKS* sposobnostima. Takodje, imamo i hibridne kombinacije ZPLB402 x ZPLB405, ZPLB403 x ZPLB405 i ZPLB404 x ZPLB405 koje su u obe godine ispitivanja imale značajne efekte *PKS*, a uključuju roditelje sa lošim *OKS* vrednostima. Ovo je verovatno posledica delovanja aditivnog tipa (aditivni x aditivni) interakcije medju roditeljima.

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