

Combining abilities for spike traits in a diallel cross of barley

Kombinacione sposobnosti za osobine klasa ječma u dialelnom ukrštanju

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Abstract

Five two-row winter barley (*Hordeum vulgare* L.) cultivars divergent in spike traits were crossed in all possible combinations excluding reciprocals to produce 10 F₁ and F₂ hybrids for analysis of combining abilities. The analysis of variance of combining abilities showed significant differences for GCA and SCA in F₁ hybrids and F₂ generation, suggesting additive and non-additive gene action. The GCA/SCA ratio in F₁ and F₂ indicated the prevalence of the additive component of genetic variance for spike length, grain weight per spike and spike harvest index. By contrast, the SCA variance for grain weight per spike was higher than the GCA variance, indicating the dominance of non-additive gene action. Good GCAs were found in parents having high values for spike length (Djerdap, NS-293), grain number per spike (Vada, Jagodinac), grain weight per spike (Vada, NS-293) and spike harvest index (Djerdap, Jagodinac). None of the parents had good GCA for all traits, suggesting a potential increase in combining abilities for spike traits. The best SCA were obtained mostly from crosses between parents having high x low, high x high or average x low GCA values. Parents having high GCA values may be used to produce improved lines in hybridisation programmes. Combinations with high SCA values may yield good segregating lines in further selection programmes.

Keywords: barley, combining abilities, gene effect, spike traits

Rezime

Pet sorti ozimog dvoredog ječma (*Hordeum vulgare* L.), divergentnih za dužinu klasa, broj i masu zrna po klasu i žetveni indeks klasa dialelno je ukršteno (isključujući recipročna) i dobijeno je deset F₁ i F₂ hibrida za analizu kombinacionih sposobnosti. Analizom varijanse kombinacionih sposobnosti utvrđene su signifikantne razlike za OKS i PKS kod F₁ hibrida i F₂ generacije što ukazuje da su analizirana svojstva uslovljena genima sa aditivnim i neaditivnim delovanjem. Odnos OKS/PKS u F₁ i F₂ ukazuje na preovladavanje aditivne komponente genetičke varijanse u determinaciji dužine klasa, mase zrna po klasu i žetvenog indeksa klasa, dok je za broj zrna po klasu varijansa PKS veća od varijansi OKS i ukazuje na preovladavanje neaditivnog delovanja gena. Roditelji koji su imali visoke vrednosti za dužinu klasa (Djerdap, NS-

293), broj zrna po klasu (Vada, Jagodinac), masu zrna po klasu (Vada i NS-293) i žetveni indeks klasa (Djerdap, Jagodinac) su imali i dobre OKS. Nijedan od roditelja nije imao dobre OKS za sve osobine, što ukazuje na mogućnost povećanja kombinacionih sposobnosti za osobine klasa. Najbolje PKS su dobijene uglavnom iz ukrštanja roditelja visokih x niskih, visokih x visokih ili prosečnih x niskih vrednosti OKS. Roditelji visokih vrednosti OKS bi mogli biti upotrebljeni za dobijanje poboljšanih linija u programu hibridizacije. Kombinacije sa visokim vrednostima PKS bi u daljim programima selekcije mogli dati dobre segregirajuće linije.

Ključne reči: ječam, kombinacione sposobnosti, efekat gena, osobine klasa

Detailed abstract

Pet sorti ozimog dvoredog ječma Vada, Djerdap, NS-293, Jagodinac i Sladoran, divergentnih za dužinu klasa, broj i masu zrna po klasu, ukrštene su u svim kombinacijama (isključujući reciporočna) i dobijeno je 10 F₁ hibrida. Setva hibridnog semena obavljena je oktobra 2007. godine po principu retke setve za dobijanje biljaka za F₂ generaciju. Za analizu kombinacionih sposobnosti roditelji, F₁ hibridi i F₂ generacija, zasejani su u istoj godini (oktobra 2008) na zemljištu tipa vertisol, oglednog polja Centra za strna žita u Kragujevcu. Ogled je postavljen po slučajnom blok sistemu, u tri ponavljanja. U fazi pune zrelosti uzet je uzorak za analize i to za roditelje i F₁ hibride po 10 biljaka iz svakog ponavljanja (ukupno 30 biljaka) i po 50 biljaka za F₂ generaciju (ukupno 150 biljaka). Na pojedinačnim biljkama izmerena je dužina primarnog klasa (cm), i utvrđen broj zrna po klasu, masa ukupnog klasa i masa zrna po klasu (g). Žetveni indeks klasa izračunat je kao odnos mase zrna po klasu i ukupne mase klasa. Analiza varijanse kombinacionih sposobnosti je urađena po metodu 2, matematički model I, za nepotpuni dialel (GRIFFING, 1956) koristeći Gen stat softver 12.1 (2009).

Analizom varijanse kombinacionih sposobnosti utvrđene su signifikantne razlike za OKS i PKS kod F₁ hibrida i F₂ generacije što ukazuje da su dužina klasa, broj i masa zrna po klasu i žetveni indeks klasa uslovljeni genima sa aditivnim i neaditivnim delovanjem. Odnos OKS/PKS u F₁ i F₂ veći je od jedinice i ukazuje na preovladavanje aditivne komponente genetičke varijanse u determinaciji dužine klasa, mase zrna po klasu i žetvenog indeksa klasa.

Varijansa PKS je za broj zrna po klasu veća od varijansi OKS i ukazuje na preovladavanje neaditivnog delovanja gena. Roditelji koji su imali visoke vrednosti za dužinu klasa (Djerdap, NS-293), broj zrna po klasu (Vada, Jagodinac), masu zrna po klasu (Vada i NS-293) i žetveni indeks klasa (Djerdap, Jagodinac) su imali i dobre OKS. U ovim itraživanjima nijedan od roditelja nije se pokazao kao dobar opšti kombinator za sve osobine, što se može objasniti kompenzacijom komponenti prinosa i negativnim korelacijama koje su rezultat kompeticije između komponenti prinosa ili komplementacijom komponenti prinosa između dva roditelja. Najbolje PKS su dobijene uglavnom iz ukrštanja roditelja visokih x niskih, visokih x visokih ili prosečnih x niskih vrednosti OKS. Roditelji visokih vrednosti OKS bi mogli biti upotrebljeni za dobijanje poboljšanih linija u programu hibridizacije. Kombinacije sa visokim vrednostima PKS bi u daljim programima selekcije mogli dati dobre segregirajuće linije.

Introduction

Winter barley (*Hordeum vulgare* L.) is recognised as one of the very first grain crops to be domesticated both for livestock feed and human consumption. Barley is cultivated in temperate and tropical climates, and ranks fourth in acreage and third in terms of volume of production worldwide. It is grown on about 11% of the total global grain area. Barley is well adapted to diverse environmental conditions and, therefore, it is produced across a broad geographical range, including North America, Argentina, North Africa, the most of Asia and Australia. In the Republic of Serbia, barley is cultivated on about 100.000 ha, yielding 312.000 t annually (Przulj et al., 2010). Its versatility (used for human consumption and as livestock feed) and ability to tolerate unfavourable climate conditions make it a highly attractive crop even outside its traditional cultivation range. Due to relatively low rainfall in arid and semiarid regions and lower moisture requirements as compared to wheat, barley will spread to these areas in the coming period.

An increase in crop productivity involves a comprehensive approach and knowledge of the genetic background of crops. Productivity is the final result of the effect and interactions of several yield-determining traits, which are basically polygenic and, as such, they do not allow separate determination of their contribution. Identification of genetically superior parents is a prerequisite for obtaining promising progeny.

Analysis of combining abilities can provide useful information regarding the selection of adequate parents in the hybridisation programme, as well as the methods and strength of the effect of genes governing the expression of certain quantitative traits. Such findings on the traits determining crop productivity may be useful in the development of an efficient breeding program.

A number of biometric procedures are being used to detect and obtain an accurate estimate of different components of genetic variability. Diallel analysis (Hayman, 1954; Griffing, 1956; Mather and Jinks, 1971) is one of the methods which provides such estimates using results of testing of a particular number of genotypes in all possible crossing combinations. The objective of this study was to select barley genotypes as the best combiners for spike traits, and estimate the best combinations based on the evaluation of their general and specific combining abilities, suggesting the potential increase in yield component values and, hence, grain yield.

Materials and methods

Five two-row winter barley cultivars, including Vada, Djerdap, NS-293, Jagodinac and Sladoran, genetically divergent in spike length, grain number per spike and grain weight per spike were crossed in a complete set of combinations (excluding reciprocals) during 2005/2006 vegetation to produce 10 combinations in F_1 and F_2 generations. The trial is set up in central Serbia region, in the surrounding of Kragujevac, at the locality of the Small Grains Research Centre (N 44° 01'35" and E 20° 55' 38" elevation 210m) under open field conditions, during 2005-2008 vegetations.

Parents, F_1 hybrids and F_2 generation were planted at the experimental field in a randomised block design with three replications during 2007/2008 vegetation. The experimental materials were planted in 5 m² plots in 5 rows 1 m in length, at a row spacing of 20 cm and within-row spacing of 10 cm. The experiment was conducted on vertisol, using common cultural practices as regards basic soil tillage and seedbed preparation. During seedbed preparation, 40 kg N ha⁻¹, 70 kg P ha⁻¹ and 70 kg K ha⁻¹ were incorporated into the soil. The crop was fertilised in spring before the onset of the growing season with 60 kg N ha⁻¹. At full maturity, sampling was made for analyses involving 10 plants from each replication for parents and F_1 hybrids (a total

of 30 plants) and 50 plants for F₂ generation (150 plants in total). Data were recorded on individual plants for length of primary spike, grain number per spike and grain weight per spike. Spike harvest index was calculated as the ratio of grain weight per spike to total spike weight. The analysis of variance of combining abilities was carried out according to method 2, mathematical model I, for incomplete diallel (Griffing, 1956) using GenStat 12.1 (2009).

Results and discussion

The analysis of variance shows that the significant differences observed for all traits between parents, F₁ hybrids and F₂ progeny suggest genetic divergence of the material selected (Table 1). Significant differences between genotypes as a prerequisite for diallel analysis in a different set of materials were also reported by Bhatnagar and Sharma (1995), Sharma et al. (2003a), Kakani et al. (2007) and Singh et al. (2007). The analysis of variance of combining abilities (Table 2) reveals the significance of general combining ability (GCA) and specific combining ability (SCA) variances for all traits in F₁ and F₂ generations i.e. the importance of additive and non-additive gene effects in determining the inheritance of the traits.

Table 1. Analysis of variance of spike traits in barley

Tabela 1: Rezultati analize varijanse osobina klasa kod ječma

Sources of variation	df	Spike length		Grain number per spike		Grain weight per spike		Spike harvest index	
		F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
		MS ^a	MS	MS	MS	MS	MS	MS	MS
Replications	2	0.04	0.16	1.30	0.23	0.01	0.01	3.56	0.39
Treatments ^b	14	5.62**	4.11**	10.75**	10.26**	1.16**	0.90**	15.48**	29.36**
Error	28	0.58	0.12	1.11	0.33	0.01	0.001	3.30	2.08

* and ** Significant at 5% and 1% levels of significance, respectively

a – mean squares

b – parents, F₁ hybrids and F₂ progeny

The significance of means of squares for GCA and SCA for length of primary spike in F₁ hybrids and their ratio (GCA/SCA=13.48) suggests that length of primary spike is generally governed by additive gene action and, to a very low extent, by non-additive gene action. In F₂ generation, the GCA/SCA ratio (36.31) shows the predominance of additive gene action for length of primary spike. Positive values of GCA for length of primary spike in F₁ were obtained for Djerdap, NS-293 and Jagodinac (Table 3). The GCA values for parents in F₂ generation were very similar to those in F₁ hybrids, with a change in parental order, however, being observed. The best general combiners in F₂ generation included NS-293, followed by Djerdap and Jagodinac. In F₁ generation, higher SCA values relative to the other combinations were found in Vada x NS-293, Djerdap x NS-293, Djerdap x Sladoran and Djerdap x Jagodinac combinations. A significantly higher SCA value in F₂ generation was found in Djerdap x NS-293 and Djerdap x Sladoran combinations. Significant SCA values were identified mostly from crosses between parents having high x high and high x low GCA values (Table 4).

Table 2. Analysis of variance of general combining ability (GCA) and specific combining ability (SCA) for spike traits in barley

Tabela 2. Analiza varijanse opštih kombinacionih sposobnosti (OKS) i posebnih kombinacionih sposobnosti (PKS) za osobine klasa ječma

Sources of variation	Spike length		Grain number per spike		Grain weight per spike		Spike harvest index		
	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	
	df	MS ^a	MS	MS	MS	MS	MS	MS	
GCA	4	7.77**	5.45*	2.45*	3.11*	0.05**	0.04**	20.50**	22.53*
SCA	10	0.58**	0.15**	3.68**	3.33**	0.03**	0.02**	3.71**	6.52*
Error	28	0.04	0.04	0.69	0.64	0.005	0.001	1.60	0.66
GCA/SCA		13.48	36.31	0.67	0.93	2.15	1.54	5.52	3.45

* and ** Significant at 5% and 1% levels of significance, respectively

a – mean squares

Table 3. Estimates of general combining ability (GCA) effects for spike traits in barley

Tabela 3: Procena efekata opštih kombinacionih sposobnosti (OKS) za osobine klasa ječma

Parents	Spike length		Grain number per spike		Grain weight per spike		Spike harvest index	
	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
Vada	-1.37**	-1.30**	0.61*	0.54**	0.06**	0.04	-0.99**	-1.19**
Djerdap	0.98**	0.65**	-0.30	-0.04	-0.02	-0.03	1.66**	1.85**
NS-293	0.91**	0.74**	-0.08	-0.03	0.12**	0.11**	-0.39	-0.02
Jagodinac	0.33**	0.50**	0.55*	0.53*	-0.05	-0.03	1.38**	1.72**
Sladoran	-0.85**	-0.52**	-0.74*	-0.88**	-0.10	-0.07*	-2.13**	-1.62**

* and ** Significant at 5% and 1% levels of significance, respectively

The analysis of variance of combining abilities for grain number per spike suggests significant differences in GCA and SCA, indicating additive and non-additive gene action for grain number per spike in this study. SCA variances were higher in both generations than GCA variances, suggesting non-additive genetic effects for the trait. Cultivars Vada and Jagodinac were very good combiners for grain number per spike in F₁ and F₂. Significant SCA values in both generations were determined in Vada x Djerdap, NS-293 x Jagodinac, NS-293 x Sladoran and Jagodinac x Sladoran combinations. The best SCAs were obtained mostly from crosses between parents having high x low GCA. Kakanl et al. (2007) also report that the GCA/SCA ratio for spike length and grain number per spike in F₂ generation, as opposed to F₁, was above unity, suggesting greater importance of additive genetic effects in the inheritance of the traits. The results by Singh et al. (1996), Bhatnagar and Sharma (1997), Bouzerzour and Djakoune (1998), Esparza Martinez and Foster (1998) Sharma et al. (2003b) and Verma et al. (2007) indicate that non-additive genetic variance is the major component of the genetic variance of different economically important traits of barley. Conversely, Kalashnik and Smyalovskaya (1986) and Yang and Lu (1991) indicated a higher contribution of the additive component, whereas Choo et al. (1998), Bhatnagar and Sharma (1995), Singh et al. (1996), Budak (2000) and Madić et al. (2012) highlighted the importance of both additive and non-additive genetic variance components in determining grain yield and yield components in barley.

Table 4. Estimates of specific combining ability (SCA) effects for spike traits in barley

Tabela 4: Procena vrednosti posebnih kombinacionih sposobnosti (PKS) za osobine klasa ječma

Crosses	Spike length		Grain number per spike		Grain weight per spike		Spike harvest index	
	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
VA x DJ ^a	-0.09	0.31	1.63**	1.27*	-0.08*	0.08	-1.30	-1.03
VA x NS	0.76**	-0.27	-1.02	-0.91	0.02	-0.14**	2.15	1.99*
VA x JA	0.38*	-0.54*	-0.66	-1.20*	0.19**	-0.02	0.39	-1.44
VA x SL	-0.30	0.30	0.95	1.26*	0.16**	0.17**	-0.40	-0.36
DJ x NS	1.20**	0.45*	-0.58	-0.51	0.23**	-0.07	-1.86	-1.87
DJ x JA	0.54*	0.09	-0.79	-0.64	0.09*	-0.01	1.05	2.89**
DJ x SL	0.87**	0.69**	-0.71	-0.59	0.07*	0.06	0.02	0.90
NS x JA	-0.20	0.04	1.92**	1.59**	-0.02	0.31**	2.40*	2.45*
NS x SL	-0.40*	0.16	1.81*	1.42*	-0.04	-0.05	2.81*	3.40**
JA x SL	-0.31	-0.61**	1.58*	1.67**	0.10*	0.12**	1.02	2.41*

* and ** Significant at 5% and 1% levels of significance, respectively;

Crosses (parents): VA- Vada; DJ- Djerdap; NS- NS-293; JA- Jagodinac; SL- Sladoran

The results of the analysis of variance of combining abilities for grain weight per spike are in agreement in F₁ and F₂ generations. The significant differences for GCA and SCA suggest the significant role of both additive and non-additive gene action in the inheritance of grain weight per spike. Cultivars NS-293 and Vada were identified as the best general combiners for grain weight per spike in F₁ hybrid, whereas NS-293 was the best general combiner in F₂ generation. Significant SCA values in F₁ were obtained in Djerdap x NS-293, Vada x Jagodinac, Djerdap x Jagodinac, Vada x Sladoran and Jagodinac x Sladoran combinations. A significantly higher SCA value in F₂ generation was found in the Vada x Sladoran, Djerdap x Sladoran and Jagodinac x Sladoran combinations. Significant SCA values were obtained mostly from crosses between parents having high x low and average x low GCA values.

The presence of both additive and non-additive gene action (significant GCA and SCA values) was observed in the inheritance of spike harvest index in F₁ and F₂. The GCA/SCA ratio was above unity in both generations, suggesting the preponderance of additive gene action. Significant GCA values in both generations were identified in Djerdap and Jagodinac genotypes. Significant SCA values in F₁ were found in NS-293 x Sladoran and NS-293 x Jagodinac, and those in F₂ in Vada x NS-293, Djerdap x Jagodinac, NS-293 x Jagodinac, NS-293 x Sladoran and Jagodinac x Sladoran combinations. Significant SCA values were obtained mostly from crosses between parents having high x low, average x low and low x low GCA values. Kakani et al. (2007) identified all major positive SCA values from crosses between parents having high x average, average x average and average x low GCA values, indicating the predominance of non-additive gene effects in the combinations. Singh et al. (2007) report that crosses between parents having good and bad GCA values often result in good SCA values. Bhatnagar and Sharma (1995) obtained the highest SCA values from crosses between average x high or high x high GCA values.

Parents having high values for spike length (Djerdap, NS-293), grain number per spike (Vada, Jagodinac), grain weight per spike (Vada, NS-293) and spike harvest index (Djerdap, Jagodinac) also showed good GCA values (parental values are not

presented). None of the parents in this study was found to be good general combiner for all or most of the traits tested, which can be attributed to yield component compensation and negative correlations resulting from the competitive relationship between yield components or yield component complementation between two parents (Kakani et al., 2007; Verma et al., 2007). Kakani et al. (2007) report that none of the parents having good GCA for yield showed good GCA for yield components, suggesting the ability to increase combining abilities for yield components. Good combining abilities for yield components in barley in a different set of materials were identified by Bhatnagar and Sharma (1997), Yilmaz and Konak (2000), Sharma et al. (2003a; 2003b).

Verma et al. (2007) report that significant GCA values suggest the importance of additive gene action and the additive x additive method of interaction, indicating the potential use of such parents for obtaining improved lines in the hybridisation programme. Kakani et al. (2007) identified one of the parents to have good GCA in most crosses, suggesting that these crosses may produce desirable transgressive segregants. The same authors determined that crosses having continuously positive SCA values in both generations also show significant positive heterosis, due to which SCA values can serve as criteria in the selection of best crosses. Verma et al. (2007) report that combinations having high SCA values may produce good segregating lines in further selection cycles.

Parents having high values of the traits tested mostly have good GCA values. As GCA values are associated with additive effects and additive x additive type of interaction, these parents have a good potential to increase the value of the traits and can be used in hybridisation programmes to develop dynamic populations that would have most desirable genes for yield increase. In order to create such dynamic populations, hybridisation programmes should involve the use of parents which emerged as good combiners for most of the traits tested. Being related to dominant effects and epistatic interactions, SCAs are not particularly important in self-pollinating plants. However, in barley as a self-pollinating plant, the additive x additive type of interaction can be fixed in later generations. Therefore, the superiority of hybrids is seen as a possible indication of their ability to produce transgressive segregants for a trait in later generations of selection, suggesting the potential use of SCA value as a satisfactory criterion in the selection process. The inclusion of parents showing good GCAs into simple crossing and/or diallel selective crossing programmes i.e. F_1 hybrids having high SCA values can provide a justified approach to breeding barley for increased grain yield.

Conclusion

The analysis of variance of combining abilities showed significant differences for GCA and SCA in F_1 hybrids and F_2 generation, suggesting additive and non-additive gene action. The GCA/SCA ratio in F_1 and F_2 indicated the prevalence of the additive component of genetic variance for spike length, grain weight per spike and spike harvest index. By contrast, the SCA variance for grain weight per spike was higher than the GCA variance, indicating the dominance of non-additive gene action. Good GCAs were found in parents having high values for spike length (Djerdap, NS-293), grain number per spike (Vada, Jagodinac), grain weight per spike (Vada, NS-293) and spike harvest index (Djerdap, Jagodinac). The best SCAs were obtained mostly from crosses between parents having high x low, high x high or average x low GCA values. Parents having high GCA values may be used to produce improved lines in

hybridisation programmes. Combinations with high SCA values may yield good segregating lines in further selection programmes.

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