

The analysis of the combining ability of stem height in barley hybrid

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Abstract: Diallel crossing of five divergent cultivars of the two-row barley (Vafa, Djerdap, NS-293, Jagodinac and Sladoran) gave 10 F_1 and F_2 hybrids for studying variability, the mode of inheritance, gene effects, heritability and the abilities of plant height.

The significance test of the mean values of the generation related to the parental mean was used to assess the mode of inheritance (Kraljevic-Balalic, 1991), and the analysis of variance of the combining abilities made following the method 2, mathematical model I, for the incomplete diallel (Griffing, 1956).

The inheritance of plant height is partially dominant, dominant or super-dominant, with prevalence of the partial dominance in the majority of the combinations.

The values of heritability were found to range from 35,25% to 72,85%. For plant height, the highest genetic difference between the cultivars was exhibited in the combination Jagodinac x Sladoran, with heritability amounting to 72,85%.

Highly significant differences for the general (GCA) and specific (SCA) combining ability in the F_1 and F_2 generation denoted that plant height had resulted from the genes with additive and non-additive, i.e. dominant impact. The variance of GCA was found to be higher in the F_1 and F_2 generation than that of SCA.

Key words: barley, plant height, heritability, gene effects, combining ability.

Introduction

Stem height is highly important component of resistance to lodging over barley breeding, with which, the genotypes of short, firm and flexible stem, withstanding an intensive highly dense growth, could be obtained

Stem shortening, which is necessary due to a highly problematic sensitivity of barley to lodging, is likely to lead to a higher yield. However, stem shortening must be done with utmost care because drastically shortened stems are likely to give rise to a considerable decrease in the total biomass and therefore in grain yield. Hence, the plant with somewhat shorter stems and considerably more resistant to lodging along with intensively distributed assimilates from leaves into grain which could offset adverse effects of the shorter stems on yield, is preferred.

The trait of a shorter stem predetermined by recessive genes and located in the first, second and third chromosome by Milohnic (1972) and in the seventh chromosome by Thomas et al., (1984). Sears et al., (1981) denoted that four recessive alleles brought about the trait of the shorter stem, while Mickelson and Rasmusson (1994) emphasized that the trait of a shorter stem of barley could be determined by one, two or three recessive genes, the most spread being *sdw* gene. The remaining two genes, contained in a minor number of the genotypes, have not been defined yet. Hellewell et al., (2000) also pointed out that the trait of a shorter stem and spike length of barley was influenced by *sdw* and *denso* alleles mapped in the same region of the second arm of 3H chromosome and that *sdw* alleles were likely to reduce the plant height by 10-20 cm. The genes, reducing stem height, possess the phenotypic effect in barley different from that in *Rht* gene of wheat; *dwarf* genotypes of barley actually possess a highly breakable stem, show higher sensitivity to diseases and have a poorer malt taste (Przulj et al., 2000).

Having in mind the significance of stem height in barley breeding, the mode of inheritance, gene effects and combining abilities have been studied to make sure that the utilisation potentials of these parental cultivars in further breeding programs of barley as well as those of choosing the highly yielding genotypes from the hybrid progenies in later generations are lawful.

Materials and Method

The material of the five parental cultivars (Vada, Djerdap, NS-293, Jagodinac and Sladoran) was used and their hybrids of the F₁ and F₂ generation obtained from diallel crossing, the parents being divergent for the stem height.

The crosses were made in the spring of 1997 following the method of diallel crossing (without reciprocal) with ten hybrid combinations obtained in the F₁ generation. The seeding of hybrid material was performed in October of the same year using thin seeding (in 1 m long rows, 10 cm of spacing among the kernels within the row and 20 cm of inter-row spacing) and the seed for F₂ generation obtained. In the autumn of 1999, the material for all the generations was seeded (in the same year) to enable an invariable impact of the environmental factors on all the generations. The trial was set up on the trial field of the Centre of Small Grains in Kragujevac according to random split block design with three replications. The seeding proceeded using thin seeding in 1 m long rows, spaced at 20cm, with plants at 10 cm of inter-row spacing. In such a manner, equal growing conditions for all the plants of the generations concerned were provided.

Agrotechnical measures, weed control, irrigation and digging proceeded as usual.

In the phase of full maturity, a unique random sample was taken to analyse the following generations:

- for all the parents and F₁ combinations (3 x 10) entirely 30 plants
- for all the F₂ combinations (3x50) entirely 150 plants

For studying the variability and inheritance mode of the stem height for the parents, F₁ and F₂ generation, the statistical parameters of the mean value ($\bar{x}$), standard deviation (sd), standard error of the mean value (S x) and variability coefficient (V%) were calculated.

LSD test was used for testing the significance of the differences between the mean values of the trait in question.

Significance test of the mean values of the generations compared with the parental mean was utilised to assess the inheritance mode (Kraljevic-Balalic, 1991).

The values of heritability (h^2) were determined according to the formula of Mather (after Allard, 1960) considering that the parents, F₁ and F₂ generation had been grown during the same year.

$$h^2 = \frac{\sigma^2_{F_2} - \frac{\sigma^2_{P_1} + \sigma^2_{P_2} + \sigma^2_{F_1}}{3}}{\sigma^2_{F_2}}$$

The analysis of variance of the combining abilities was made following the method 2, mathematical model 1 for the incomplete diallel (Griffing, 1956).

Results

The mean values and variability of the stem height

Of the parents chosen for diallel crosses, the cultivar Sladoran had the shortest (55,3 cm) and Vada the tallest stem (74,1 cm) (Tab.1).

In the F₁ generation, the stem height was found to be lower than the taller parent except for the crossing combinations of Vada x Djerdap and Djerdap x Jagodinac.

The mean values of the F₂ generation were mainly lower than those in the F₁ generation, the lowest progeny being in the combination Djerdap x Sladoran (58 cm).

The cultivar Sladoran had the lowest height and variability (6,4%), whereas NS-293 had the highest variability (9,3%).

A higher variability of the stem height in the F₁ generation was mainly found in those combinations of Sladoran and Vada included as parents, i.e. the parents with the lowest and the highest stem height. The coefficient of variability ranged from 6,9% in the combination of Jagodinac x Sladoran to 11,7% in that of Vada x Sladoran.

Tab.1. Statistical parameters and inheritance of the stem height in barley

Combination	Generation	No. of plants	$\bar{X} \pm s_{\bar{x}}$	S	$V(\%)$	h^2
K-1 Vada x Djerdap	P ₁	30	74.1 ± 1.01	5.54	7.95	61.13
	F ₁	30	79.9 ± 1.06 <i>sd</i>	5.84	7.60	
	F ₂	90	76.5 ± 0.92 <i>sd</i>	8.73	10.93	
	P ₂	30	72.4 ± 0.89	4.90	6.61	
K-2 Vada x NS-293	P ₁	30	74.1 ± 1.01	5.54	7.95	35.25
	F ₁	30	75.7 ± 0.89 <i>d</i>	4.86	6.42	
	F ₂	90	73.2 ± 1.02 <i>pd</i>	9.69	13.24	
	P ₃	30	66.1 ± 1.12	6.16	9.32	
K-3 Vada x Jagodinac	P ₁	30	74.1 ± 1.01	5.54	7.95	35.95
	F ₁	30	74.9 ± 1.39 <i>d</i>	7.59	10.13	
	F ₂	90	66.5 ± 0.79 <i>pd</i>	7.54	11.34	
	P ₄	30	62.9 ± 0.79	4.33	6.90	
K-4 Vada X Sladoran	P ₁	30	74.1 ± 1.01	5.54	7.95	48.91
	F ₁	30	60.6 ± 1.30 <i>i</i>	7.12	11.74	
	F ₂	90	62.0 ± 0.82 <i>pd</i>	7.84	12.64	
	P ₅	30	55.3 ± 0.65	3.58	6.47	
K-5 Djerdap x NS-293	P ₂	30	72.4 ± 0.89	4.90	6.61	38.21
	F ₁	30	72.6 ± 1.34 <i>d</i>	7.36	10.43	
	F ₂	90	70.1 ± 0.72 <i>pd</i>	6.82	9.73	
	P ₃	30	66.1 ± 1.12	6.16	9.32	
K-6 Djerdap x Jagodinac	P ₂	30	72.4 ± 0.89	4.90	6.61	57.24
	F ₁	30	75.3 ± 1.01 <i>sd</i>	5.54	7.36	
	F ₂	90	61.6 ± 0.80 <i>pd</i>	7.58	12.30	
	P ₄	30	62.9 ± 0.79	4.33	6.90	
K-7 Djerdap x Sladoran	P ₂	30	72.4 ± 0.89	4.90	6.61	65.85
	F ₁	30	63.2 ± 0.98 <i>pd</i>	5.38	8.51	
	F ₂	90	58.0 ± 0.84 <i>pd</i>	8.02	13.83	
	P ₅	30	55.3 ± 0.65	3.58	6.47	
K-8 NS-293 x Jagodinac	P ₃	30	66.1 ± 1.12	6.16	9.32	50.07
	F ₁	30	65.2 ± 1.24 <i>pd</i>	6.82	10.46	
	F ₂	90	71.1 ± 0.87 <i>sd</i>	8.30	11.67	
	P ₄	30	62.9 ± 0.79	4.33	6.90	
K-9 NS-293 x Sladoran	P ₃	30	66.1 ± 1.12	6.16	9.32	55.49
	F ₁	30	60.2 ± 0.83 <i>i</i>	4.53	7.52	
	F ₂	90	60.5 ± 0.77 <i>i</i>	7.91	12.07	
	P ₅	30	55.3 ± 0.65	3.58	6.47	
K-10 Jagodinac x Sladoran	P ₄	30	62.9 ± 0.79	4.33	6.90	72.85
	F ₁	30	56.1 ± 0.99 <i>pd</i>	5.43	6.96	
	F ₂	90	63.1 ± 0.91 <i>d</i>	8.59	13.61	
	P ₅	30	55.3 ± 0.65	3.58	6.47	
F ₁ LSD	0.05	3.39	F ₂ LS	0.05	2.28	
	0.01	4.57		D	0.01	3.08

i-intermediary; *pd*- partial dominance; *d*-dominance; *sd*-superdominance

The highest variability in the F₂ generation was recorded in the crossing combinations, the parents of which considerably varied in the stem height. Thus, the variability coefficient amounted to 13,8% in the combination Djerdap x Sladoran and to 13,6 % in that of Jagodinac x Sladoran.

The lowest variability coefficient (10,9%) was recorded in the combination in which the parents did not significantly vary in the stem height, being Vada x Djerdap (Tab.1.).

The mode of inheritance and heritability of the stem height

Stem height in the F₁ and F₂ generation displayed differing modes of inheritance from intermediarity to super-dominance. The intermediary mode of inheritance was mainly found in those crossing combinations in which the parents significantly varied in the stem height., such as the combination of NS-293 x Sladoran, whereas in those ones in which the parents scarcely varied in the stem height, super-dominance was manifested in the inheritance of this trait in the F₁ and F₂ generation (Vada x Djerdap) (Tab.1).

Excluding the crossing combination of Vada x Jagodinac with dominant inheritance mode, the prevalence of partial dominance inheritance was mainly observed in the remaining crossing combinations in the F₁ generation.

The partial dominance was also found to prevail in the inheritance of stem height in the F₁ generation (Tab.1).

The values of heritability ranged from 35,25% to 72,85%. The highest genetic variation between the cultivars for stem height was revealed in the combination Jagodinac x Sladoran, with heritability amounting to 72,85% (Tab.1).

The analysis of variance of the combining ability

Based on the mean values of the parents and their progenies in the F₁ and F₂ generation, the analysis of variance of the combining ability was made. The results of the analysis indicated highly significant differences for the general (GCA) and specific (SCA) combining ability in the F₁ and F₂ generation, meaning stem height having resulted from the genes with additive and non-additive, i.e. dominant effects. The variance of GCA proved to be higher in the F₁ and F₂ generation than that of SCA (Tab.2.).

Further, the cultivars Sladoran and Jagodinac were found to be highly good combiners for a short stem owing to their highly significant negative values of GCA. By contrast, the cultivars Vada and Djerdap were found to be poor combiners for short stem as evidenced by the significantly positive values of GCA (Tab.3).

The crossing of Vada x Sladoran exhibited the lowest value in the F₁ generation, which was highly significantly lower than the remaining values, meaning this combination being fairly good for stem height. This crossing combination consisted of one parent with a good GCA for tall stem (+ value GCA) and of the other having a good GCA for the short one (- value GCA).

In the F_2 generation, the crosses Vada x Jagodinac, Vada x Sladoran, Djerdap x Jagodinac and Djerdap x Sladoran were found to have highly significant SCA values for short stem, whereas that of Vada x Djerdap had a significant SCA value for tall stem (Tab.4).

Tab.2. ANOVA of the combining ability of the stem height in barley

Variation source	Generation	DF	MS	F_c	F_t	
					0.01	0.05
GCA	F_1	4	185.46	135.69**	4.08	2.72
SCA		10	10.32	7.55**	3.04	2.19
E		28	1.37			
OKS/PKS				17.97		
GCA	F_2	4	137.65	221.6**		
SCA		10	15.17	24.42**		
E		28	0.62			
GCA/SCA				9.07		

Tab.3. GCA values for stem height

Parents	GCA values F_1	Rank	SE	GCA values F_2	Rang	SE
Vada	5.231**	5		5.028**	5	
\erdap	3.832**	4		2.234**	4	
NS-293	0.076	3	0.235	1.086	3	0.807
Jagodinac	-1.224*	2		-1.688*	2	
Sladoran	-7.905**	1		6.660**	1	

F_1 LSD 0.05 1.280 F_2 LSD 0.05 0.901
0.01 1.727 0.01 1.216

Tab.4. SCA values for stem height

Crossing combinations	SCA values F_1	SE	SCA values F_2	SE
Vada x \erdap	-0.233		5.484**	
Vada x NS-293	2.684		0.442	
Vada x Jagodinac	3.315**		-3.911**	
Vada x Sladoran	-4.337		-3.366**	
\erdap x NS-293	1.289	0.266	0.903	0.544
\erdap x Jagodinac	5.023**		-4.847**	
\erdap x Sladoran	-0.366		-4.118**	
NS-293 x Jagodinac	-1.296		4.625**	
NS-293 x Sladoran	0.751		-0.806	
Jagodinac x Sladoran	-3.049**		4.337**	

F_1 LSD 0.05 2.862 F_2 LSD 0.05 1.92
0.01 3.861 0.01 3.86

Discussion

Of the quantitative traits, stem height of barley showed a continual variability, with normally distributed frequency as a result of the impact of a larger number of the genes. According to the analysis, the mean values of both parents denoted the presence of significant varietal differences. Thus, the mean values were decreased in the majority of the combinations of the F_1 and F_2 generation compared to the taller parent, which was in agreement with results obtained by Bede (1981), Drezner et al., (1984), for wheat, as well as with those obtained by Lalic et al., (1984) and Mersikov (1990) for barley.

Stem shortening, inevitable for highly problematic sensitivity of barley to lodging, is likely to give rise to a higher yield, but it has to be approached with great caution because the drastically shortened stems might bring about a considerable decrease in the total biomass and subsequently about a worse grain yield. This is corroborated by the research results denoting positive correlations between stem height and yield (Kovacevic 1987, Ore 1989 and 1991 and Przulj et al., 2000).

The variations of parental varieties for stem height were found to be slight with variability coefficient ranging from 6.9% to 11.7%. So obtained results were in agreement with those obtained by Dimitrijevic et al., (1996) and Zecevic (1996), whereas Pavlovic (1997) pointed at a high variability of the trait in question in wheat, with the variability coefficient in hybrid generations of up to 26%.

The inheritance of plant height in the F_1 and F_2 generation is characterised by the partial dominance, dominance and by the intermediary type of inheritance. In general, the plant height is said to be inherited partially dominantly, which comly with results of Bode et al., (1900), Prodanovic (1992), Pavlovic (1993).

The analysis of variance of the combining ability pointed to the highly significant differences for GCA and SCA. Thus, the values of the GCA were more significant indicating that the additive genetic effects prevailed in this diallel in the inheritance of the plant height. Significant differences among the GCA and SCA with plant height of barley were evidenced throughout the researches performed by Lalic et al., (1984), Vasquez et al., (1989), Knezevic et al., (1993) and Madic (1995).

Certain cultivars seem to be good general combiners for a short stem, while the crossings with good SCA for a short stem typically include one parent with good GCA for a high stem and one parent with proper GCA for the short one. These results comply with those obtained by Lalic et al., (1984) having concluded that good crossing combinations most often involved one parent with a high and the other with a low GCA value.

Conclusion

Highly significant differences for stem height were found to exist between the genotypes of barley and their progeny, with the highest stem height established in the cultivar Vada and the lowest one in that of Sladoran.

In the F_1 generation, plant height was shorter than being in the taller parent with an exception to the crossing combinations Vada x Djerdap and Djerdap x Jagodinac.

The mean values of the F_2 generation were mainly lower than those in the F_1 generation, while the shortest progeny was evidenced in the crossing combination of Djerdap x Sladoran.

The variability of the F_1 generation and parents was found to be low, with somewhat higher variability found in the F_2 generation.

The inheritance of the stem height was partially dominant, dominant or overdominant with prevalence of the partial dominance in the majority of the combinations.

The heritability ranged from 35.25% to 72.85%, with its highest value found in the combination Jagodinac x Sladoran.

The highly significant differences for the GCA and SCA in the F_1 and F_2 generation denoted that the plant height over the current researches had resulted from the genes with additive and non-additive, i.e. dominant impact. The relationship between GCA and SCA was in both F_1 and in F_2 generation higher than one.

Lastly, Sladoran and Jagodinac proved to be remarkably good combiners for a short stem due to their negatively highly significant values of GCA, with the best crossings obtained between one good and one bad general combiner.

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ANALIZA KOMBINACIONIH SPOSOBNOSTI VISINE STABLIKE KOD HIBRIDA JEČMA

- originalni naučni rad -

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Rezime

Dialelnim ukrštanjem pet divergentnih sorti dvorednog ječma (Vada, Verdap, NS-293, Jagodinac i Sladoran) dobijeno je 10 F_1 i F_2 hibrida, radi proučavanja varijabilnosti, načina nasleđivanja, efekata gena, heritabilnosti i kombinacionih sposobnosti za visinu stabljike.

Za ocenjivanje načina nasleđivanja primenjen je test signifikantnosti srednjih vrednosti generacija u odnosu na roditeljski prosek (*Kraljević-Balalić, 1991*), a analiza varijanse kombinacionih sposobnosti je urađena po metodu 2, matematički model I, za nepotpuni dialel (*Griffing, 1956*).

Nasleđivanje visine stabljike je parcijalno dominantno, dominantno ili superdominantno uz preovladavanje parcijalne dominacije kod većine kombinacija.

Vrednosti za heritabilnost kretale su se u rasponu od 35,25% do 72,85%. Najveća genetska razlika između sorti, za visinu stabljike se ispoljila u kombinaciji Jagodinac x Sladoran gde je heritabilnost iznosila 72.85%.

Visoko signifikantne razlike za opšte (OKS) i posebne (PKS) kombinacione sposobnosti u F_1 i F_2 generaciji, ukazuju da je visina stabljike u ovim istraživanjima bila uslovljena genima sa aditivnim i neaditivnim, odnosno dominantnim delovanjem. Varijansa OKS bila je veća i u F_1 i F_2 generaciji od varijanse PKS.