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THE MODE OF INHERITANCE AND GENE EFFECTS FOR THE GRAIN NUMBER PER SPIKE IN DIFFERENT WHEAT GENOTYPES

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Summary: In order to estimate the gene effects and the mode of inheritance of the grain number per spike, five wheat genotypes (Pobeda, Renesansa, Sara, Partizanka and Pesma) were selected. The above mentioned genotypes were diallel crossed and F_1 , F_2 , and F_{3C} were obtained. The gene effects were estimated using additive-dominant model which was adequate for three crossing combinations: Renesansa x Sara, Renesansa x Partizanka and Partizanka x Pesma. In the most crosses the value of the dominant gene effect was more significant than additive. The inheritance of the grain number per spike was influenced by additive x additive and dominance x dominance type of non-allelic interactions. The mode of inheritance of the number of grains per spike in F_1 , F_2 and BC_1 generations differed depending from the crossing combinations.

Key words: wheat, inheritance, additive-dominance model

INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the most important cultivated crops in Serbia and has been grown in the area which has been varied, in recent five years, from 480 000 ha to 600 000 ha (USDA, 2014). Considering the importance of wheat in contemporary production, the main goal of breeding programs is to obtain the varieties with a high genetic potential for grain yield (Petrović et al., 2012). Wheat production in the country can be increased either by bringing more area under cultivation or by developing new, high yielding varieties (Ljubičić, 2014).

Grain yield is a complex trait, influenced by a number of other quantitative traits and environmental effects. Because of these complex interactions it is difficult to improve yield through breeding, especially in the early

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generations, if the yield is the only factor recorded, suggesting that component traits should also be used as selection criteria for yield improvement. This is the reason why it is essential to know the genetic architecture of yield components (Dimitrijević et al., 1995; Fatehi et al., 2008; Petrović et al., 2013; Dimitrijević et al., 2013).

In an efficient breeding program, an understanding of the inheritance of yield and yield related traits in advance would be important to maximize the use of genetic potential. Plant breeders often use generation mean analysis to get information about gene action which is controlling the traits. Generation mean analysis is a simple and useful technique for estimating gene effects for a polygenic trait. Its greatest merit lying in an ability to estimate epistatic gene effects such as additive×additive (i), dominance×dominance (j) and additive×dominance (l) effects (Singh and Singh, 1992; Novoselović et al., 2004; Ljubičić et al., 2014).

As one of the main components of yield, the number of grains per spike is a result of the number of spikelets per spike and the number of flowers per spike, as well as, the result of the success of fertilization and crop setting in these grains flowers. As each of these traits are variable, the number of grains per spike as a result of all these traits and many other factors, is especially highly variable (Petrović et al., 2001; Hristov et al., 2008;).

The aim of the study is to evaluate the mode of inheritance and the gene effects for grain number per spike in different wheat genotypes.

MATERIAL AND METHODS

Five varieties of hexaploid wheat (*Triticum aestivum* L.), namely, Pobeda, Renesansa, Sara, Partizanka and Pesma, which were diallely crossed and it was obtained F₁ and F₂ generations of progenies. Also, it was derived Fbc₁ (F₁ generation crossed with one of the parents). The trial was set up on the trial field of the Institute of field and vegetable crops in Novi Sad, according to random block design with three replications, in three growing seasons (2009/2010, 2010/2011 and 2011/2012). The cultivars were sown in 2 m long rows with 20 cm of inter-row spacing and 10 cm spacing between plants in the row. Grain yield component, number of grains per spike of wheat plants were analyzed, at the stage of full maturity. The main sample consisted of 10 plants per replication. The gene effects were estimated on the basis of Generation mean analysis, an additive-dominance model of three parameters (Mather, 1949) and marked was according to Hayman (1960) as follows:

m = Mean effect.

d = Additive gene effects.

h = Dominance gene effects.

i = Additive×additive epistatic gene effects.

j = Additive×dominance epistatic gene effects.

l = Dominance×dominance epistatic gene effects.

The adequacy of the additive-dominance model could be tested in two ways, using the Scaling-test (A, B and C) and Chi-square (χ^2) test. The simple genetic model (m, d and h) was applied when epistasis was absent, whereas in the presence of non-allelic interaction the analysis was proceeded to estimate the interaction types involved using the six parameters genetic model i.e. (m, d, h, i, j and l) according to Mather and Jinks (1982). According to the methodology of Kearsey and Pooni (1996) the type of epistasis was determined only when dominance (h) and dominance×dominance (l) effects were significant. When these effects had the same sign, the type of epistasis was complementary, while different signs indicated duplicate epistasis (Kearsey and Pooni, 1996). The best-fit model was used for obtaining the degree of freedom. This model excludes gene effects which do not have a significant influence on the expression of the studied trait. The values of significant gene effects could be obtained using a matrix system. The mode of inheritance was estimated using the test of significance of mean generation values in relation to the parental means (Dimitrijević et al., 1994).

RESULTS

The results of additive-dominance model with three-parameter revealed that the dominance effects (h) showed higher values than the additive effects (d), (Table 1). The adequacy of the additive-dominance model was tested using Scaling test and Chi-square (χ^2) test. The results of these tests showed that the additive-dominance model with three-parameter was sufficient to explain genetic variation for grain number per spike for three crosses: Renesansa x Sara, Renesansa x Partizanka and Partizanka x Pesma. The results of the Scaling tests indicated that each of A, B or C were significant or highly significant for the grain number per spike in the remaining seven cross combinations: Pobeda x Renesansa, Pobeda x Sara, Pobeda x Partizanka, Pobeda x Pesma, Renesansa x Pesma, Sara x Partizanka and Sara x Pesma which indicated the presence of non-allelic gene interaction for these crosses (Table 1).

Table 1. Estimated values of additive and dominance gene effects for the grain number per spike of wheat

Cross combination					
Gene effect	Pobeda x Renesansa	Pobeda x Sara	Pobeda x Partizanka	Pobeda x Pesma	Renesansa x Sara
m	42.12	39.35	35.41	38.67	38.95
d	0.50	-0.09	-1.86	-0.81	0.08
h	1.46	1.71	6.24	3.90	1.37
Scaling test					
A	6.27	-0.08	-8.25*	-0.94	-6.71
B	5.79	0.03	-2.84	1.37	-6.13
C	13.13*	-17.61**	-25.59**	-15.48*	-4.56
$\chi^2(3)$	8.49 *	13.6**	36.27**	10.91*	7.41
P (probability)	< 0.05	< 0.01	< 0.01	< 0.01	> 0.05
Cross combination					
Gene effect	Renesansa x Partizanka	Renesansa x Pesma	Sara x Partizanka	Sara x Pesma	Partizanka x Pesma
m	37.62	41.57	35.58	41.48	36.17
d	-2.29	-1.44	-1.76	-0.79	1.34
h	2.59	3.47	4.94	5.12	3.11
Scaling test					
A	-1.40	14.50	-13.41**	14.08**	1.28
B	4.50	17.28	-8.10*	16.28**	-1.83
C	-2.21	2.04	-17.90**	0.14	-2.12
$\chi^2(3)$	3.00	42.08**	25.21**	50.58**	0.56
P (probability)	> 0.05	< 0.01	< 0.01	< 0.01	> 0.05

*Significant at 0.05, ** significant at 0.01

Therefore, the six-parameter model was applied in order to assess the digenic types of interaction which controlling the genetic variations for this character. The estimates of the six parameters, i.e means (m), additive (d), dominance (h), additive×additive (i), additive×dominance (j) and dominance×dominance (l) are presented in Table 2.

Table 2. Estimated values of additive and dominance gene effects for the grain number per spike of wheat using the six parameter model

Cross combination					
Gene effect	Pobeda x Renesansa	Pobeda x Sara	Pobeda x Partizanka	Pobeda x Pesma	Renesansa x Sara
m	41.55**	22.63**	23.04**	23.21**	48.71**
d	-0.24	0.05	2.71*	1.15	0.29
h	10.46	37.42*	24.29	36.65**	-28.41*
i	-1.06	17.57*	14.50*	15.89**	-8.27
j	0.48	-0.11	-5.41	-2.30	-0.58
l	-11.01	-17.52	-3.41	-16.34*	21.11*
Cross combination					
Gene effect	Renesansa x Partizanka	Renesansa x Pesma	Sara x Partizanka	Sara x Pesma	Partizanka x Pesma
m	32.47**	9.60	41.11**	8.82	34.81**
d	2.95**	1.39*	2.65*	1.10	-1.56
h	15.94	92.50**	-22.08	94.88**	5.65
i	5.31	29.74**	-3.61	30.23**	1.58
j	-5.89	-2.78	-5.31	-2.20	3.11
l	-8.41	-61.52**	25.12*	-60.59**	-1.04

*Significant at 0.05, ** significant at 0.01

Using the six-parameter model it was confirmed the presence of significant epistatic effects in all crossing combinations, except the three cross combinations: Pobeda x Renesansa, Renesansa x Partizanka and Partizanka x Pesma. The type of non-allelic interactions which was observed were: additive×additive (i) and dominance×dominance (l). For the all investigated crosses was observed the preponderance dominance effects (h) and showed higher values than the corresponding additive effects (d), (Table 2).

The application of the best fit model was indicated very similar gene effects which were presented by a model with six parameters. Interactions caused by the presence of complementary genes, in which significant values (h) and (l) had the same sign, for the trait number of grains per spike of wheat, in this experiment has not been determined (Table 3).

Table 3. Estimated values of gene effects for the grain number per spike of wheat using the best fit model

Cross combination	Gene effect	Estimated values	SE	t-test	Cross combination	Gene effect	Estimated values	SE	t-test
Pobeda x Renesansa	m	42.75	0.85	50.45**	Renesansa x Partizanka	m	38.92	0.87	44.82**
	$\chi^2(5)$	3.30				d	2.81	1.46	1.93
	P	> 0.01				$\chi^2(5)$	2.10		
Pobeda x Sara	m	32.88	3.60	9.15**	Renesansa x Pesma	P	> 0.01		
	h	10.13	4.76	2.13*		m	9.88	9.11	1.08
	i	7.60	3.88	1.96		h	91.77	22.19	4.14**
	$\chi^2(3)$	0.54				i	29.60	8.98	3.29**
	P	< 0.01				l	-61.04	13.94	-4.38**
Pobeda x Partizanka	m	39.37	0.97	40.66**	$\chi^2(2)$	1.04			
	d	2.06	1.27	1.62	P	< 0.01			
	i	-2.77	1.75	-1.58	Sara x Partizanka	m	35.52	1.14	31.21**
	$\chi^2(3)$	20.30				d	1.75	1.35	1.30
P	< 0.01			l		7.37	2.60	2.83*	
Pobeda x Pesma	m	23.31	9.14	2.55**	$\chi^2(3)$	4.18			
	h	36.35	21.71	1.67	P	< 0.01			
	i	15.89	8.99	1.77	Sara x Pesma	h	115.25	7.13	16.17**
	l	-16.12	13.62	-1.18		i	38.84	8.20	4.74**
	$\chi^2(2)$	0.48				l	-72.14	6.50	-11.10**
P	< 0.01			$\chi^2(3)$		1.10			
Renesansa x Sara	m	40.36	1.93	20.93**	P	> 0.01			
	h	-8.48	7.79	-1.09	Partizanka x Pesma	m	37.66	0.78	48.09**
	l	9.53	7.13	1.34		χ^2	4.00		
	$\chi^2(3)$	5.60				P(5)	> 0.01		
	P	> 0.01							

*Significant at 0.05, ** significant at 0.01

DISCUSSION

The results obtained using by the additive-dominance model with three-parameter revealed that dominance gene effects (h) had a higher values than the additive effects (d), indicating that dominance gene effects play the major role in controlling the genetic variation of the grain number per spike of wheat for all crosses. The higher estimates of dominance effects than for additive, for this trait, indicated that the parents were in dispersion phase and that there was an accumulation of dominant parental genes in their progenies. The similar finding, which indicated the major role of dominance gene effects in controlling the genetic variation of grain number per spike for all crosses, was also obtained by Dhanda and Sethi (1996); Petrović (1995); Fethi and Mohamed (2010). The results of Scaling test and Chi-square (χ^2) test showed that the additive-dominance model with three parameters was sufficient to explain genetic variation for the grain number per spike for three crosses: Renesansa x Sara, Renesansa x Partizanka and Partizanka x Pesma. These tests also showed that three-parameter model was inadequate for explaining the inheritance of the grain number per spike in in the remaining seven crosses (Pobeda x Renesansa, Pobeda x Sara, Pobeda x Partizanka, Pobeda x Pesma, Renesansa x Pesma, Sara x Partizanka and Sara x Pesma)

which indicated the presence of non-allelic gene interaction for these crosses. Presence of non-allelic interactions (epistasis) suggests that a digenic epistatic model of inheritance could be adequate in such cases.

The results obtained using by the additive-dominance model with six-parameter also showed the preponderance of dominance effects (h) for the all investigated crosses. The six-parameter model confirmed the presence of significant epistatic effects in all crossing combinations, except the three cross combinations: Pobeda x Renesansa, Renesansa x Partizanka and Partizanka x Pasma. The type of non-allelic interactions which was observed in remain crosses were: additive×additive (i) and dominance×dominance (l). In the cross combination Pobeda x Renesansa tests indicated the presence of epistasis, while those are not determined, which may be the consequence of the presence of threegenic or polygenic epistasis. Similar results were obtained by Mather and Jinks (1982) and Sharma et al. (2012). The mean effect (m) was significant for all studied crosses, except for the two crosses (Renesansa x Pasma and Sara x Pasma). According to Khattab et al. (2010) highly significance of the estimated values of mean effects (m) indicated that studied trait was quantitatively inherited. Crossing combination Renesansa x Partizanka had a highly significant only the mean value (m) and value of additive gene effects (d), while significant epistatic effects were not identified, which makes easier the selection on this trait. When additive effects are larger than the non-additive, it is suggested that selection in early segregating generations would be effective. Similar results have pointed out by Dvojković et al. (2010). Also, the favorable situation was observed in the cross combination Pobeda x Partizanka, as in this cross combination was expressed a significant value of the additive gene effects (d) and significant additive×additive epistatic effects were (i), which additionally draws gene effects in the direction to the additivity. In the cross combination Pobeda x Sara, genes with dominant effects (h), as well as epistasis additive×additive (i) significantly controlled the inheritance of the number of grains per spike. Duplicate type of epistasis was detected in crosses: Pobeda x Pasma, Renesansa x Sara, Renesansa x Pasma and Sara x Pasma, since dominance effects (h) and dominance×dominance (l) epistatic effects were significant and in opposite signs. The success of the selection could be affected negatively by these interactions. Similarly, Fethi and Mohamed (2010) also reported that dominance effects (h) and dominance×dominance epistasis (l) were more important than additive effects and other epistatic components in the inheritance of the grain number per spike. The presence of the duplicate type of epistasis in the inheritance of grain per spike were also indicated by Kobiljski (1999); Singh et al. (2004); Erkul et al. (2010); Ijaz and Kashif (2013). Contrary to these results, the presence of non-allelic gene interaction caused by complementary genes indicated Novoselović et al. (2004). In the cross combination Renesansa x Pasma additive (d) and dominance effects (h) were significant, whereas dominance effects were relative higher than additive effects. In the crosses Renesansa x Pasma, Pobeda x Pasma and Sara x Pasma was observed the less favorable case of duplicate type of epistasis. The sign of the value of epistatic effects dominance×dominance (l) were negative, which causes reducing the effects of dominant gene, in the crosses listed above. These results are less favorable for breeders, than if the values of dominance×dominance epistatic effects (l) were positive, while the values of the dominant gene effects (h) appeared to be negative. Also, the favorable side of these crossing combinations lies in the fact that in these crosses was significant epistatic effects additive×additive (i), which increases the ability to successfully selection more superior genotypes. More favorable results were obtained in the cross combination Pobeda x Pasma. The value of the significant duplicate type of epistasis, as well as highly significant values of additive×additive type of epistasis ($i = 15.89^{**}$, $l = 16.34$), suggest that epistatic effects additive×additive (i) pushed gene effects toward additivity.

Application of the best fit model indicated a very similar gene effects which were presented by a model with six parameters. Interactions caused by the presence of complementary genes, in which significant values (h) and (l) had the same sign, for the trait number of grains per spike in this experiment has not been determined.

In the cross combination Pobeda x Renesansa, due to the absence of statistically significant difference it was not determined the mode of inheritance in the F_1 , F_2 and BC_1 generations. In the cross Pobeda x Sara it wasn't possible to determine the mode of inheritance in the F_1 , F_2 and BC_1 generations, as a consequence of the absence of statistically significant difference. In the cross combination Pobeda x Partizanka, domination of better parent in the F_1 generation, was observed, while in the F_2 generation due to the absence of statistically significant difference, the mode of inheritance could not be determined. That also goes for the BC_1 . In the cross combination Pobeda x Pasma, due to the absence of statistically significant difference, the mode of inheritance in the F_1 , F_2 and BC_1 generations was not determined. In the cross combination Renesansa x Sara, the mode of inheritance in F_1 , F_2 and BC_1 generations, could not be determined, due to the absence of statistically significant difference. The same goes for the cross combination Renesansa x Partizanka, in F_1 , F_2 and BC_1 generations, followed by the cross combination Renesansa x Pasma, in F_1 and F_2 generations. In the backcross progeny, BC_1 , a positive heterotic effect, was noted. The positive heterotic effect was denoted in the cross combination Sara x Partizanka, as well, while in F_2 generation the mode of inheritance could not be determined, due to the absence of statistically significant difference between the mean values of that trait for parents and progeny. In the back cross progeny, BC_1 , the dominance of the parent with

the lower mean value of the trait, was determined. In the backcross generation, BC₁, a positive heterotic effect was observed.

Generally, it can be concluded that the inheritance of the number of grains per spike is caused by different effects differing depending on cross combination.

CONCLUSION

Additive-dominant model was adequate for the three cross combinations: Renesansa x Sara, Renesansa x Partizanka and Partizanka x Pesma. The inheritance of the grain number per spike was controlled by additive and non-additive genetic effects, with a greater value of the dominance gene effect in the most cases. The dominance effects showed higher values than the additive effects, indicating that dominance gene effects play the major role in controlling the genetic variation of the grain number per spike for all the crosses. Therefore, given that the non-additive effects are larger than additive, the improvement of the number of grain per spike needs intensive selection through later generation.

Results obtained in this study also revealed the importance of epistatic effects (additive×additive and dominance×dominance) in the inheritance of grain number per spike which all suggests that it cannot be ignored when establish a new breeding program to improve wheat population for this trait. The mode of inheritance of the number of grains per spike in F₁, F₂ and BC₁ generations were differed depending from the crossing combinations.

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NAČIN NASLEĐIVANJA I EFEKAT GENA ZA BROJ ZRNA PO KLASU RAZLIČITIH GENOTIPOVA PŠENICE

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Izvod: U cilju procene genskih efekata i načina nasleđivanja broja zrna po klasu u radu je odabrano pet genotipova pšenice (Pobeda, Renesansa, Sara, Partizanka i Pema). Navedeni genotipovi su ukršteni dialelno i dobijena je F₁ i F₂ generacija i generacija povratnog ukrštanja, Fbc₁. Procena efekata gena je rađena uz primenu aditivno-dominantnog modela, koji bio adekvatan za kombinacije ukrštanja Renesansa x Sara, Renesansa x Partizanka i Partizanka x Pema. U većini ukrštanja dominantni efekat gena je bio značajniji od aditivnog. U nasleđivanju broja zrna po klasu biljke zapažena je interakcija gena aditivni x aditivni i dominantni x dominantni. Način nasleđivanja broja zrna po klasu se u F₁, F₂ generaciji, kao i kod generacija povratnih ukrštanja, BC₁, razlikovalo u zavisnosti od kombinacije ukrštanja.

Ključne reči: pšenica, nasleđivanje, aditivno-dominantni model.

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