



## Genetic Analysis of some Important Quantitative Traits in Bread Wheat (*Triticum aestivum* L.)

Nataša Ljubičić\* Sofija Petrović<sup>1</sup> Miodrag Dimitrijević<sup>1</sup> Nikola Hristov<sup>2</sup>

<sup>1</sup> University of Novi Sad, Faculty of Agriculture, Department of Genetics and Plant Breeding, 21000 Novi Sad, Serbia

<sup>2</sup> Institute of Field and Vegetable Crops in Novi Sad, 21000 Novi Sad, Serbia

\* Corresponding author e-mail: ljubicic.natasa@gmail.com

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### ABSTRACT

The estimation of gene effects in the inheritance of yield components is one of the most important tasks in wheat breeding programs. The objective of this study was to estimate gene effects for the number of grains and grain weight per spike in ten wheat crosses with five basic generations: parent cultivars (P1, P2), first and second filial generations (F1, F2) and first backcrosses (BC1). The gene effects responsible for inheritance of these two important traits were estimated on the basis of generation mean analysis, using an additive-dominant model with three and six-parameters. The adequacy of the additive-dominance model with three-parameters was tested using the Scaling test and Chi-square ( $\chi^2$ ) test. A three-parameter model was found as adequate to explain variation for the both traits in three crossing combinations. The magnitude of additive gene effects (d) was smaller than the corresponding dominance effects (h) in most crosses for both traits. The application of six-parameter models indicated the significant epistatic effects for explaining genetic variation for these traits. The inheritance of these traits was influenced by additive $\times$ additive (i) and dominance $\times$ dominance (l) type of non-allelic interactions in the study. Duplicate gene interactions were also observed in most crosses of both characters which are difficult to exploit in breeding programs. These results implied that the selection for the improvement of these traits should be applied in further generations in wheat breeding.

**Keywords:** Wheat, Additive-dominance model, Gene effects.

### Introduction

Wheat is one of the major cereal crops in the World, grown on over 220 million hectares, representing 26% of the total harvested area, on average (USDA, 2015). Considering growing demands rising approximately 2% per year, which is twice of the current gain rate in genetic yields potential, plant breeders have to put many efforts to improve the grain yield of wheat (Reynolds *et al.*, 2001). Wheat grain yield is a complex polygenic trait influenced by many components and can be improved through indirect selection on the basis of yield components. The increment in one component might have positive or negative effect on the other components (Chandra *et al.*, 2004). This is the reason why it is necessary to know the genetic architecture of yield components.

Therefore, information about the nature, magnitude of gene effects and their contribution to the inheritance of the yield and yield components is essential to plant breeders for improving wheat grain yield (Petrović *et al.*, 2001). In order to get information about gene action that is controlling the traits, plant breeders often use generation mean analysis. Generation mean analysis is a useful technique in plant breeding for estimating main gene effects (additive and dominance) and their digenic (additive $\times$ additive, additive $\times$ dominance, and dominance $\times$ dominance) interactions responsible for inheritance of quantitative traits (Singh and Singh, 1992; Kearsey and Pooni, 1996). As the number of grains and grain weight per spike are important quantitative traits of wheat which directly affects the yield, a large number of genetic studies have been made to investigate the genetic basis

of these traits of wheat. The importance of epistatic effects in controlling these traits was observed by many researches (Dvojković *et al.*, 2010; Zaazaa *et al.*, 2012; Ijaz and Kashif., 2013).

The present study was carried out to obtain information about the types of gene effects for the number of grains and grain weight per spike of different bread wheat genotypes.

### Materials and Methods

Five, diallely crossed, winter wheat varieties (*Triticum aestivum* L.), namely, Pobeda, Renesansa, Sara, Partizanka and Pema, were used in the study. Five plant material categories were obtained: parental varieties ( $P_1, P_2$ ), progenies ( $F_1, F_2$ ) and back-crosses ( $BC_1$ ) of ten cross combinations (Pobeda/Renesansa, Pobeda/Sara, Pobeda/Partizanka, Pobeda/Pema, Renesansa/Sara, Renesansa/Partizanka, Renesansa/Pema, Sara/Partizanka, Sara/Pema and Partizanka/Pema). The trial was sown in a randomized block design, with three replications, during the three successive seasons of 2009/2010, 2010/2011 and 2011/2012. Field experiment was conducted at the experimental field of the Institute of Field and Vegetable Crops in Novi Sad, Serbia. 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. The main sample consisted of 10 plants per replication. At the stage of full maturity grain yield components, namely the number of grains per spike and grain weight per spike (g) were analyzed. The gene effects of the grain yield components, number of grains and grain weight per spike of wheat, were estimated for each cross combination by Generation mean analysis ( $P_1, P_2, F_1, F_2$  and  $BC_1$ ), using an additive-dominance model of three-parameters (Mather, 1949). The adequacy of the additive-dominance model was tested using the Scaling-test (A, B and C) and Chi-square ( $\chi^2$ ) 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-parameter genetic model i.e. (m, d, h, i, j and l) according to Mather and Jinks (1982). According to the methodology of Hayman (1960) the following notation for gene effects were used, where (m) represents mean effect, (d) additive gene effects, (h) dominance gene effects, (i) additive  $\times$  additive epistatic effects, (j) additive $\times$ dominance epistatic effects and (l) dominance  $\times$  dominance epistatic gene effects. The type of epistasis was determined only when dominance (h) and dominance  $\times$  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).

### Results and Discussion

The additive-dominance model with three-parameter revealed that dominance effects (h) showed higher values than the additive effects (d) for number of grains per spike, indicating that dominance gene effects play the major role in controlling the genetic variation of this trait for all crosses. These results are in accordance with results reported by Petrović (1995) and Fethi and Mohamed (2010). The results of applying Scaling test and Chi-square ( $\chi^2$ ) test showed that the additive-dominance model, with three-parameter, was sufficient to explain genetic variation for the number of grains per spike for three crosses: Renesansa/Sara, Renesansa/Partizanka and Partizanka/Pema. The results of Scaling test indicated that each of A, B or C was significant or highly significant for the number of grains per spike in the remaining seven crosses: Pobeda/Renesansa, Pobeda/Sara, Pobeda/Partizanka, Pobeda/Pema, Renesansa/Pema, Sara/Partizanka and Sara/Pema. Thus, it indicated the presence of non-allelic gene interaction for these crosses and revealed that simple model with three-parameter is inadequate for explaining the inheritance of number of grains per spike (Table 1).

In controlling inheritance for the grain weight per spike, the additive-dominance model with three-parameter revealed that both additive and dominance gene effects were important, with prevalence of dominance gene action, which is in accordance to the results reported by Dvojković *et al.*, (2010). For the grain weight per spike, Scaling test and Chi-square ( $\chi^2$ ) test showed that the three-parameter model, was sufficient to explain genetic variation for three crosses: Pobeda/Sara, Renesansa/Sara and Sara/Partizanka, while in the remaining cross combinations three-parameter model failed and was found to be inadequate to explain genetic variation the inheritance of this trait (Table 1).

Therefore, the six-parameter model was applied and was fitted for explaining genetic variation for both traits. The estimates of the six parameters, i.e. means (m), additive (d), dominance (h), additive  $\times$  additive (i), additive  $\times$  dominance (j) and dominance  $\times$  dominance (l) are presented in Table 2.

Using the six-parameter model it was observed that the mean effects were highly significant for both traits in the most crosses, indicating that these traits are quantitatively inherited. For the number of grains per spike it confirmed the presence of significant epistatic effects in all cross combinations, except the three cross combinations: Pobeda/Renesansa, Renesansa/Partizanka and Partizanka/Pema. In the cross combination Pobeda/Renesansa, Scaling test in previous model, indicated the presence of epistasis, while those are not determined, which suggested the presence of three-genic or polygenic epistasis. Similar results were reported by Mather and Jinks

(1982) and Sharma *et al.*, (2012). Also, it was revealed that the magnitude of additive gene (d) effects were slightly smaller relative to the corresponding dominance effects (h) in most cases, indicating that dominance gene effects play the major role in controlling the genetic variation of the number of grains for all crosses. These results suggesting that in these crosses pedigree selection method is a useful breeding program for improving these populations. The importance of dominance effects in controlling of the number of grains was observed by Fethi and Mohamed (2010). On the contrary, according to Dvojković *et al.*, (2010), additive effects predominate in controlling the number of grains. The prevailing type of non-allelic gene interactions which was observed in many crosses was additive  $\times$  additive (i) and dominance $\times$ dominance (l). Additive  $\times$  additive type of non-allelic gene interactions were noticed in cross combinations: Pobeda/Sara, Pobeda/Partizanka, Renesansa/Pesma and Sara/Pesma. Dominance  $\times$  dominance type of non-allelic gene interactions were noticed in cross combinations: Pobeda/Pesma, Renesansa/Sara, Renesansa/Pesma, Sara/Partizanka and Sara/Pesma. In crosses Pobeda/Pesma, Renesansa/Sara, Renesansa/Pesma and Sara/Pesma duplicate type of non-allelic interaction was apparent since dominance effects (h) and dominance $\times$ dominance epistatic effect (l) were significant and in opposite sign. In this case success of the selection would be affected negatively by these interactions. The presence of duplicate epistasis is unfavorable from the breeder's point of view because it causes decreasing effect on the analyzed trait. Duplicate epistasis in the number of grains inheritance has been reported also by Erkul *et al.*, (2010) and Ijaz and Kashif (2013). Contrary to these results, the presence of non-allelic gene interaction caused by complementary genes was indicated Novoselović *et al.*, (2004). In the cross combinations: Pobeda/Pesma, Renesansa/Pesma and Sara/Pesma the less favorable case of duplicate type of epistasis was observed as the sign of the value of epistatic effects dominance  $\times$  dominance (l) were negative, which causes reducing the effects of dominant gene and decreasing phenotypic expression of the trait. These results are less favorable for breeders, than if the values of dominance  $\times$  dominance epistatic effects (l) were positive, as the crosses Renesansa/Sara. In this cross combination epistatic effect in a small amount masked the phenotypic expression of the trait. The presence of significant epistatic effects additive  $\times$  additive (i), which has been observed in cross combination: Pobeda/Sara, Pobeda/Pesma, Renesansa/Pesma and Sara/Pesma, is more favorable for breeders as these effects increase the ability for successful selection of more superior genotypes. However, when non-additive effects are larger than additive, the improvement of the trait

needs intensive selection through later generation. In cross combinations: Pobeda/Sara, Pobeda/Pesma and Sara/Pesma fixable additive gene effect was not significant, yet significant epistatic effects additive  $\times$  additive (i) was observed which could be a result of some preferred interaction between the genes which are controlling this trait. The favorable situation was observed in the cross combinations Pobeda/Sara and Pobeda/Partizanka, considering in this crosses only epistasis additive  $\times$  additive (i) significantly controlled the inheritance of the number of grains and this effect additionally draws gene effects in the direction to the additivity. When additive effects are larger than the non-additive, it is suggested that selection in early segregating generations would be effective. The results of six-parameter model also indicated that epistasis was not found in the inheritance of the number of grains for the crosses Pobeda/Renesansa, Renesansa/Partizanka and Partizanka/Pesma, which suggested that for this crosses an additive-dominance model was adequate. Absence of epistatic effects in these crosses greatly makes easier the selection for this trait, considering that the presence of epistasis complicated procedures for improving quality of traits. The results obtained here, revealed the importance of epistatic effects in the inheritance of the number of grains per spike and should not be ignored in establishment a new breeding program to improve wheat genotypes for this trait.

Regarding to the grain weight per spike, the six-parameter model was fitted for explaining genetic variation for the grain weight per spike and it confirmed the presence of significant epistatic effects in cross combinations: Pobeda/Renesansa, Pobeda/Pesma, Renesansa/Pesma and Sara/Pesma. The inheritance of the grain weight per spike was differing depending on cross combination and it was controlled by additive and non-additive gene effects. This indicated that both gene effects were equally important in controlling the genetic variation of the grain weight. This result is in accordance to the results reported by Dvojković *et al.*, (2010). On the contrary, according to Zaza *et al.*, (2012) additive genetic variation predominates in the inheritance of this trait. The type of non-allelic gene interactions, which had been observed in many crosses, were additive $\times$ additive (i) and dominance $\times$ dominance and were noticed in cross combinations: Pobeda/Renesansa, Pobeda/Pesma, Renesansa/Pesma and Sara/Pesma (Table 2.)

In crosses Pobeda/Renesansa, Pobeda/Pesma and Renesansa/Pesma duplicate type of non-allelic interaction was confirmed since dominance effects (h) and dominance  $\times$  dominance epistatic effect (l) were significant and in opposite sign. In this case success of the selection would be affected negatively by these interactions and causes decreasing effect on the analyzed trait.

Also in these crosses the less favorable case of duplicate type of epistasis, was observed as the sign of the value of epistatic effects dominance $\times$ dominance (l) were negative, which causes decreasing phenotypic expression the trait and effect of dominant gene effects. Duplicate epistasis in the inheritance grain weight has been reported also by Zaazaa *et al.*, (2012) and Dvojković *et al.*, (2010). Contrary to these results, where non-allelic gene interactions have been found in the inheritance of grain weight per spike as revealed by Garole and Monpara (2005) and Munir *et al.*, (2007). Complementary type of epistasis was only found in the cross combination Sara/Pesma, as the significant dominant gene and significant epistatic effect dominance $\times$ dominance had the same sign. This situation is more favorable than the presence of duplicate type of epistasis due to a greater chance of breeding success. The presence of non-allelic gene interaction caused by complementary genes for the grain weight was also reported by Novoselović *et al.*, (2004). The presence of significant epistatic effects additive $\times$ additive (i) which has been observed in this cross combination is more favorable for breeders as these effects increases the ability to successfully selection superior genotypes. This type of epistasis significantly controlled the inheritance of the grains weight and additionally draws gene effects in the direction to the additivity. In cross combination Renesansa/Pesma the negative sign of additive  $\times$  dominance (j) interaction was observed and in most cases suggested dispersion of genes in the parents. These results are in agreement with those obtained by Khattab *et al.*, (2010). The results of six-parameter model also indicated that epistasis wasn't found in the inheritance of the grain weight at the crosses: Pobeda/Sara, Pobeda/Partizanka, Renesansa/Sara, Renesansa/Partizanka, Sara/Partizanka and Partizanka/Pesma. This suggests that for this crosses an additive-dominance model was adequate, which greatly makes easier the selection for this trait, considering that

the presence of epistasis complicated procedures for improving quality of traits.

### Conclusions

In light of the present findings it can be concluded that the examined traits in this study have shown complex genetic behavior. The inheritance of the number of grains per spike was controlled by additive and non-additive genetic effects, with prevalence of dominance gene action in the most crosses. The results also revealed the importance of epistatic effects (additive  $\times$  additive and dominance  $\times$  dominance) in the inheritance of the number of grains per spike in cross combinations: Pobeda/Sara, Pobeda/Partizanka, Pobeda/Pesma, Renesansa/Sara, Renesansa/Pesma, Sara/Partizanka and Sara/Pesma. Therefore, selection in the advanced generations might be effective for number of grains due to dominance and epistatic effects.

The inheritance of the grain weight per spike was differing depending on cross combination and revealed that both additive and non-additive gene effects were important in controlling the genetic variation of the grain weight per spike of wheat. The results also revealed the importance of epistatic effects (additive $\times$ additive and dominance  $\times$  dominance) in the inheritance of the grain weight per spike in cross combinations: Pobeda/Renesansa, Pobeda/Pesma, Renesansa/Pesma and Sara/Pesma. Therefore, breeding strategies which can exploit additive as well as non-additive gene effects could be used for improving these traits of wheat yield.

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Table 1. The estimates of gene effects for the number of grains and grain weight per spike using the three-parameter model in ten winter wheat crosses

Crossing combinations										
Gene effect	Pobeda/Renesansa		Pobeda/Sara		Pobeda/Partizanka		Pobeda/Pesma		Renesansa/Sara	
	NG	GW	NG	GW	NG	GW	NG	GW	NG	GW
m	42.12	1.88	39.35	1.79	35.41	1.63	38.67	1.65	38.95	1.80
d	0.50	0.03	-0.09	-0.13	-1.86	-0.13	-0.81	-0.15	0.08	-0.07
h	1.46	-0.13	1.71	0.15	6.24	0.02	3.90	0.09	1.37	-0.15
Scaling test										
A	6.27	0.40*	-0.08	0.10	-8.25*	0.34*	-0.94	0.11	-6.71	-0.36
B	5.79	0.34*	0.03	0.14	-2.84	0.03	1.37	0.44*	-6.13	-0.26
C	13.13*	-0.15	-17.61**	-0.32	-25.59**	0.75**	-15.48*	-0.40	-4.56	-0.09
$\chi^2$ (3)	8.49*	13.63**	13.6**	2.26	36.27**	13.74**	10.91*	3.14**	7.41	4.48
P probability	<0.05	<0.01	<0.01	>0.01	<0.01	<0.01	<0.01	<0.01	>0.05	>0.01
Crossing combination										
Gene effect	Renesansa/Partizanka		Renesansa/Pesma		Sara/Partizanka		Sara/Pesma		Partizanka/Pesma	
	NG	GW	NG	GW	NG	GW	NG	GW	NG	GW
m	37.62	1.69	41.57	1.75	35.58	1.57	41.48	1.85	36.17	1.46
d	-2.29	-0.17	-1.44	-0.16	-1.76	-0.06	-0.79	-0.23	1.34	-0.02
h	2.59	-0.06	3.47	0.08	4.94	0.31	5.12	0.08	3.11	0.18
Scaling test										
A	-1.40	-0.37	14.50	0.38*	-13.41	-0.40	14.08**	14.08**	1.28	-0.08
B	4.50	0.01	17.28	0.78**	-8.10*	-0.13	16.28**	16.28**	-1.83	-0.06
C	-2.21	-1.01*	2.04	0.14	-17.90**	-0.60	0.14	0.14	-2.12	-0.57
$\chi^2$ (3)	3.00	10.65*	42.08**	8.55**	25.21**	5.15	50.58**	50.58**	0.56	9.31*
P probability	>0.05	>0.01	<0.01	<0.01	<0.01	>0.01	<0.01	<0.01	>0.05	>0.01

NG=Number of grains, GW=Grain weight,  
\*Significant at 0.05, \*\* Significant at 0.01.

Table 2. The estimates of gene effects for the number of grains and grain weight per spike using the six parameter model in ten winter wheat crosses

Crossing combinations										
Gene effect	Pobeda/Renesansa		Pobeda/Sara		Pobeda/Partizanka		Pobeda/Pesma		Renesansa/Sara	
	NG	GW	NG	GW	NG	GW	NG	GW	NG	GW
m	41.55**	0.97**	22.63**	1.20**	23.04**	1.28**	23.21**	0.70*	48.71**	2.34**
d	-0.24	-0.03	0.05	0.02	2.71	0.16*	1.15	0.16*	0.29	0.05
h	10.46	2.40**	37.42*	1.61	24.29	0.48	36.65**	2.54**	-28.41*	-1.77
i	-1.06	0.89	17.57*	0.61	14.50*	0.39	15.89**	0.95**	-8.27	-0.50
j	0.48	0.06	-0.11	-0.04	-5.41	-0.31	-2.30	-0.33	-0.58	-0.11
l	-11.01	-1.64**	-17.52	-0.85	-3.41	-0.02	-16.34*	-1.50**	21.11*	1.12

  

Crossing combination										
Gene effect	Renesansa/Partizanka		Renesansa/Pesma		Sara/Partizanka		Sara/Pesma		Partizanka/Pesma	
	NG	GW	NG	GW	NG	GW	NG	GW	NG	GW
m	32.47**	1.02**	9.60	0.67**	41.11**	1.58**	8.82	0.01	34.81**	1.07**
d	2.95**	0.19**	1.39*	0.20**	2.65*	0.14	1.10	0.15	-1.56	0.01
h	15.94	1.14	92.50**	3.16**	-22.08	-0.04	94.88**	5.73**	5.65	0.94
i	5.31	0.68	29.74**	1.02**	-3.61	0.07	30.23**	0.01	1.58	0.43
j	-5.89	-0.38	-2.78	-0.40*	-5.31	-0.27	-2.20	0.15*	3.11	-0.02
l	-8.41	-0.32	-61.52**	-2.18**	25.12*	0.46	-60.59**	5.73**	-1.04	-0.30

NG=Number of grains, GW=Grain weight,

\*Significant at 0.05, \*\* Significant at 0.01.

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