DIALLEL ANALYSIS OF SOME IMPORTANT GRAIN YIELD TRAITS IN BREAD WHEAT CROSSES

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ABSTRACT

One of the most important tasks in wheat breeding program is development of high yielding wheat cultivars by crossing the lines with good general combining ability (GCA) and selecting desirable genotypes within its segregating population for grain yield traits. The objective of this study was to estimate the combining ability and gene action involved in the expression of the traits grain weight per spike and grain weight per plant of wheat in F_1 generations, in 5 × 5 half diallel cross of bread wheat varieties (*Triticum aestivum* L.). The results of applying combining ability analysis indicated that among the parents, genotypes Sara, Pobeda and Renesansa were found to be the best general combiners for the both investigated traits. The best specific crosses for both traits were Sara/Partizanka, Pobeda/Sara, Renesansa/Partizanka, Partizanka/Pesma and Pobeda/Pesma. Most of the specific crosses involved high × high, high × low and low × low general combiners. The results of regression analysis, as well as the analyses of components of genetic variation indicated over-dominance in the inheritance of examined traits suggested that selection in later segregating generations may lead to fairly good improvement in these characters.

INTRODUCTION

Bread wheat (*Triticum aestivum* L.) is one of the most important crops providing one-fifth of the total calories for the world's population (Sehgal et al., 2015). It has been predicted that the world population would rise to over 9 billion by the year 2050 (United Nations, Population Division, 2015). This growth in population will increase the demand for wheat by 60% compared with current years. To meet this demand, global annual yield increases have to rise from the current level of 1% per year to 1.6% per year until 2050 (Wheat, 2014). For this reason, the wheat breeders have to share an urgent need to increase grain yield potential of wheat by developing new wheat varieties with desirable genetic make up (Erkul et al., 2010). This could be achieved by exploring maximum genetic potential from available wheat germplasm (Khan et al., 2007). Among the wheat traits, grain yield is one of the most important and complex polygenic trait, influenced by many components. Since that favorable combination of yield components may improved grain yield, analyzing various traits related to grain yield, as well as the selection of genetically suitable parents in crosses are the initial breeding steps

which could ensure success in breeding programs (Ilker et al., 2009). Keeping this in view, wheat breeders have been concentrated on development of high yielding wheat cultivars by crossing good general combining parental lines and selecting desirable transgressive segregants from resulting hybrids for grain yield traits (Istipliler et al., 2015; Kumar et al., 2015a). Information regarding general and specific combining ability of wheat genotypes, as well as the knowledge regarding the mode of inheritance and gene action parameters of the yield components, may allow better choice of breeding methods and could enhanced ability to select genetically suitable parents for developing desirable genotypes within its segregating population. The diallel analysis method has been frequently used for parent selection as an appropriate scheme to obtain genetic information of yield traits in a short period of time, which can be used for improving efficiency in wheat breeding programs (Kohan and Heidari, 2014). Among the various diallel techniques, combining ability analysis developed by Griffing (1956) is being considered to be more useful to the wheat breeders and provides valuable information about the ability of parents to transfer desirable traits to their progenies (Seboka et al., 2009). It also provides information about

the nature and magnitude of the gene action involved in the inheritance of characters. The combining abilities, gene actions and the mode of inheritance of the yield components in a complete diallel cross of bread wheat varieties have been investigated by several researchers (Ljubičić et al., 2014; Nazir et al., 2014; Yao et al., 2014, Kumar et al., 2015b; Shehzad et al., 2015). Given that improvement of grain yield is the main aim of wheat breeding programs, in an effort to fulfill this requirement, five leading Serbian bread wheat genotypes were selected as a parental line in this investigation. Therefore, the present study was carried out a) to estimate combining abilities of genotypes, b) to assess the nature and magnitude of gene action involved and c) to determine the mode of inheritance for the traits grain weight per spike and grain yield per plant of wheat, in a population of the 5×5 half diallel cross of wheat. The results of these crossing combinations could provide usable genetic variability for grain yield improvement and would be of great importance in the selection of desirable parents for an effective breeding program to develop the new wheat genotypes with high grain yield potential for food and nutritional security.

MATERIALS AND METHODS

The present investigation was carried out at the experimental trial field of the Institute of Field and Vegetable Crops in Novi Sad, Serbia, during the three growing seasons of 2009/2010, 2010/2011 and 2011/2012. The experimental material in the study was comprised of five Serbian winter wheat genotypes (*Triticum aestivum* L.) namely, Pobeda, Renesansa, Sara, Partizanka and Pesma (Table 1). The cultivars Pobeda, Renesansa, Sara and Pesma have been leading Serbian high yielding genotypes, while genotype Partizanka possesses excellent bread quality and lower yield, as well as considerable durability to abiotic stressful conditions. Above mentioned winter wheat genotypes were crossed following a 5 × 5 half diallel design and the first filial generation (F_1) of progenies was obtained. Half diallel design was used in the study because reciprocal differences are not significant in wheat crops. For the analysis, the average values of traits over the three years for the parents and hybrid generations were used to avoid the year interactions. 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 trial was sown in a randomized block design, with three replications. The main sample consisted of 10 plants per replication. At the stage of full maturity grain weight per spike (g) and grain weight per plant (g) of wheat were analyzed. General combining ability (GCA) and specific combining ability (SCA) were analyzed following the Method 2 (which includes parents and F_1 generation) Mathematical Model 1 of Griffing (1956). The components of genetic variance and regression analysis were calculated according to Hayman (1954) and Mather and Jinks (1971).

Table 1. The pedigree and origin of bread wheat genotypes used as parental genotypes for producing diallel crosses

Genotype	Pedigree	Origin
Pobeda	Sremica/Balkan	IFVCNS[a]
Renesansa	Jugoslavija/NS55-25	IFVCNS[a]
Sara	Partizanka/Jedina//Evropa	IFVCNS[a]
Partizanka	Bezostaja 1/NS 116	IFVCNS[a]
Pesma	NS51-37/Balkan	IFVCNS[a]

[a]IFVCNS: Institute of Field and Vegetable Crops, Novi Sad, Serbia

RESULTS AND DISCUSSION

Performance of wheat genotypes

The presented results revealed that significant differences among the parents and their F_1 progenies were observed. The highest mean value of the trait grain weight per spike (1.89 g) was expressed by the parent Renesansa against the lowest (1.51 g) by the parent Partizanka. Among cross combinations, the greatest mean value was observed in cross combination Sara/Partizanka (2.00 g), followed with crosses Pobeda/Sara (1.95 g) and Renesansa/Partizanka (1.85). The lowest mean value for F_1 crosses was recorded in the cross combination Renesansa/Pesma (1.65 g), followed with cross Sara/Pesma (1.69 g). With regard to the trait grain weight per plant, maximum mean value of the trait (9.34 g) was shown by the parent Renesansa against the lowest (7.57 g) by the parent Partizanka. Among cross combinations the greatest value (9.53 g) was observed in cross combination Pobeda/Sara (9.53 g), followed with cross combinations Sara/Partizanka (9.50 g) and Renesansa/Partizanka (9.43 g). The lowest value (8.26 g) was recorded in cross combinations Renesansa/Pesma and Sara/Pesma (8.28 g), Table 2.

Combining ability analysis

Based on the mean values of the five parents and their progenies in the F_1 generation, the analysis of variance of the combining ability was made. Results indicated that mean squares due to both general combining ability (GCA) and specific combining abilities (SCA) were non-significant for both characters under study. Mean squares for SCA were greater in magnitude than GCA means squares and the GCA/SCA ratio was less than unity, which indicated that non-additive gene effects were more important than the additive in the expression of these traits of wheat (Table 3). These results are in agreement with those obtained by Burungale et al. (2011) and Mandal et al. (2016). Estimates of general combining ability (GCA) effects of the parental lines used in the research are presented in Table 4. In case of both traits, negligible positive and negative GCA effects were observed between parental lines. Furthermore, it can be seen that the genotypes with the highest positive GCA effect had also

Table 2. Mean values of parents and F_1 in respect to studied traits in 5×5 wheat diallel cross

Genotypes	Grain weight per spike (g)	Grain weight per plant (g)
Parents		
Pobeda	1.82	9.08
Renesansa	1.89	9.34
Sara	1.78	8.90
Partizanka	1.51	7.57
Pesma	1.70	8.45
Crosses		
Pobeda/Renesansa	1.73	8.50
Pobeda/Sara	1.95	9.53
Pobeda/Partizanka	1.75	8.73
Pobeda/Pesma	1.75	8.67
Renesansa/Sara	1.72	8.46
Renesansa/Partizanka	1.85	9.43
Renesansa/Pesma	1.65	8.26
Sara/Partizanka	2.00	9.50
Sara/Pesma	1.69	8.28
Partizanka/Pesma	1.71	8.47
$LSD_{0.05}$[a]	0.35	1.42
$LSD_{0.01}$[b]	0.47	1.92

[a]LSD: Least significant difference test at P < 0.05 level; [b]LSD: Least significant difference test at P < 0.01 level;

Table 3. Mean squares values from combining ability analysis for the analyzed traits in 5×5 diallel cross of wheat

Source of variance	DF[e]	MS[f] Grain weight per spike	Grain weight per plant
GCA[a]	4	0.014[NS]	0.292[NS]
SCA[b]	10	0.015[NS]	0.311[NS]
E[c]	28	0.014	0.239
GCA/SCA		0.97	0.94

[a]GCA: General combining ability, [b]SCA: Specific combining ability, [c]E: Error; [e]DF: Degree of Freedom, [f]MS: Mean square, [d]NS: Non-significant; *: Significant at P < 0.05 level; **: Highly significant at P < 0.01 level.

Table 4. Estimates of of general combining abilities (GCA) effects and specific combining abilities (SCA) effects for the analyzed traits in a 5×5 diallel cross of bread wheat

Genotypes	GCA[a] values	
	Grain weight per spike (g)	Grain weight per plant (g)
Parents		
Pobeda	0.030[NS]	0.159[NS]
Renesansa	0.027[NS]	0.123[NS]
Sara	0.046[NS]	0.158[NS]
Partizanka	-0.040[NS]	-0.171[NS]
Pesma	-0.059[NS]	-0.269[NS]
$LSD_{0.05}$	0.13	0.54
$LSD_{0.01}$	0.17	0.72
SCA[b] values		
Crosses	Grain weight per spike (g)	Grain weight per plant (g)
Pobeda/Renesansa	-0.089	-0.526
Pobeda/Sara	0.125	0.467
Pobeda/Partizanka	-0.011	-0.004
Pobeda/Pesma	0.013	0.033
Renesansa/Sara	-0.108	-0.562
Renesansa/Partizanka	0.111	0.732
Renesansa/Pesma	-0.080	-0.343
Sara/Partizanka	0.223	0.769
Sara/Pesma	-0.089	-0.351
Partizanka/Pesma	0.063	0.167
$LSD_{0.05}$[c]	0.29	1.20
$LSD_{0.01}$[d]	0.39	1.62

[a]GCA: General combining ability; [b]SCA: Specific combining ability, [c]LSD: Least significant difference test at P < 0.05 level; [d]LSD: Least significant difference test at P < 0.01 level; [d]NS: Non-significant

the highest mean values of investigated traits, while negative GCA effects decreased the values in case of both traits. With regard to the trait grain weight per spike, it can be seen that genotypes Sara (0.046), Pobeda (0.030) and Renesansa (0.027) had a largest positive value of GCA effects. On the other hand, genotypes Pesma (-0.059) and Partizanka (-0.040) were found to be the poorest general combiners due to maximum negative GCA effects. Regarding to the trait grain weight per plant, the GCA estimates revealed that the tendency of the largest positive value of GCA effects were observed in genotypes Pobeda (0.159), Sara (0.158), and Renesansa (0.123), while genotypes Pesma (-0.269) and Partizanka (-0.171) were found to be the poorest general combiners with maximum negative GCA effects. Since in breeding program higher values of grain weight per spike and per plant is preferred, therefore positive GCA effects are preferred for these traits. In this view, for improving traits grain weight per spike, as well as the grain weight per plant, parents Sara, Pobeda and Renesansa are considered best for this task because they showed the highest positive values of GCA and they increased the grain weight per spike and grain weight per plant in its combinations in which they took a place (Table 2 and Table 4). The highest positive values of GCA suggest that these genotypes contain more genes with additive effects or additive×additive interaction effects which are readily transmissible from one generation to another. As these components are fixable and can be exploited effectively for the improvement of the trait, selection for these traits in early segregating generations would be effective. The crosses which displayed high SCA effects for both yield traits were obtained from parents with various types of GCA effects (high × high, high × low and low × low general combiner). The highest positive SCA effect was observed by the cross Sara/Partizanka (high × low general combiner), followed by crosses Pobeda/Sara (high × high), Renesansa/Partizanka (high × low), Partizanka/Pesma (low × low) and Pobeda/Pesma (high × low), Table 4. Greater SCA effects obtained from parents with various types of GCA effects has been also reported by Raj and Kandalkar (2013), Bagiu and Nedelea (2013) and Kohan and Heidari (2014). It was also observed that some crosses involving parents with good general combiners showed poor specific combiners, indicating that parents with high GCA effect might not always give crosses with high SCA effects. The highest negative SCA effects were shown by the cross Renesansa/Sara (high × high), followed by crosses Pobeda/Renesansa (high × high), Sara/Pesma (high × low) and Renesansa/Pesma (high × low general combiner). In this study it can be seen that three crosses with the highest positive SCA effect (Sara/Partizanka, Renesansa/Partizanka and Pobeda/Sara) had the highest values in terms of the studied traits among the all combinations (Table 2 and Table 4). Since that SCA effect represents the dominance and epistatic interactions, the highest positive SCA effect do not contribute remarkably in the improvement of self-fertilizing crops as wheat. According to Istipliler et al. (2015) even though specific combining ability (SCA) is

proposed for cross pollinated species, SCA effects may be also used for selection homozygous lines that show transgressive segregation, as well as for the exploitation of hybrid wheat where non-additive genetic variability could be utilized. Since that success of selection in a population depends on additive variance, it is possible to use crosses obtained from parents with high GCA effects because the GCA is based on additive variance. In this regard, greater SCA effects in crosses which involved both parents with high GCA, such as a cross Pobeda/Sara (high × high) is being considered to be more important in this study, since it contain the additive×additive type of interaction. This kind of interaction is fixable in later generations and can be used in future plant breeding. The greater SCA effects obtained in this cross indicated the possibility of genetic improvement for the grain weight per spike as per plant, through pedigree method of selection. The importance of greater SCA effects in crosses which were involving both parents with high GCA in self-pollinated crops was pointed out by Joshi et al. (2004). Greater SCA effects obtained in crosses which were involving one parent with high and other with low GCA (Sara/Partizanka, Renesansa/Partizanka and Pobeda/Pesma) indicated the involvement of additive×dominance gene interaction in expression of this trait. Higher positive SCA effects exhibited by the crosses Partizanka/Pesma which involving both parents with low general combiner proves that promising combinations could be also obtained from crossing of genotypes with low GCA and indicated the presence of non-allelic interaction at heterozygous loci. Given that this interaction is unfixable, it is suggested utilizing these crosses through single plant selection in the later generations. According to Jinks and Jones (1958) in parental lines which involving both parents with low general combiner, compared with parents of high GCA, heterozygous were highly responsive to the environment due to non-additive effects such as dominance and epistasis. However, higher contribution of dominance or non-additive effects in cross pollinated plants could be valuable in hybrid breeding programs, while for wheat are more important parents that show a high GCA and they are used in cases where the selection is performed in subsequent generations.

Graphical representation for the traits

The graphical (Vr/Wr) representation showed that the regression line cuts the covariance (Wr) axis below the origin, implying that inheritance of the trait grains weight per spike was controlled by over-dominance gene action. The assumption of absence of non-allelic interaction seemed to satisfy as the regression line did not significantly deviate from unit slope (b = 0.550 ± 0.440) and all results were acceptable for use in genetic analysis. The distribution of arrays points on regression line indicated that the genotypes Pobeda, Renesansa and Pesma, owing to proximity to the origin, possessed maximum dominant genes. On the other hand, genotype Partizanka being far away from the origin, possess maximum recessive genes, while genotype Sara had an equal proportion of both genes. The arrays that correspond

to parents were similarly distributed along the regression line and indicate that the parents were genetically divergent for the analyzed trait (Figure 1a). The importance of over-dominance in the inheritance of the grain weight per spike of wheat were pointed out by Petrović et al. (2012) and Adel and Ali (2013). Contrary to these results, the importances of partial dominance in the inheritance of this trait were reported by Kohan and Heidari (2014). However, the selection in early generations for the trait grain weight per spike would be difficult due to over-dominance type of gene action which indicates that the selection for this trait in advanced segregating generations would be more effective.
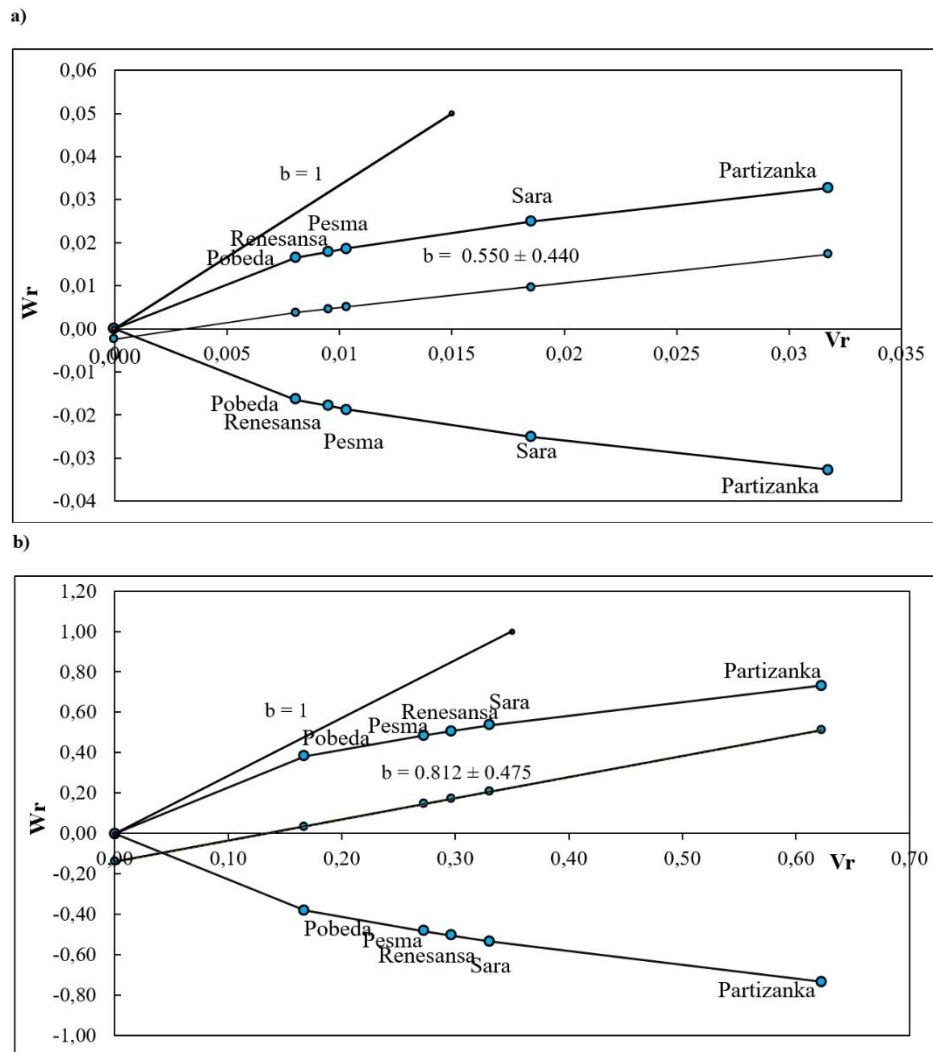
a)

b)

Figure 1 (a) and (b): a) Vr/Wr regression analysis for grain weight per spike of wheat
b) Vr/Wr regression analysis for grain weight per plant of wheat
b: Coefficient of Regression, Wr: Covariance, Vr: Variance

As it is seen in Figure 1b, the Vr/Wr graphical presentation revealed that regression line intercepted the covariance (Wr) axis below the point of origin, suggesting that the trait grains weight per plant has been governed by the dominant gene action with over-dominance. Since that regression line did not deviate significantly from the unit slope (b = 0.812 ± 0.475), the absence of epistasis was confirmed. The distribution of array points along the regression line indicated that the genotype Pobeda contains most of dominant genes as being nearest to the point of origin, while variety Partizanka contain maximum recessive genes being furthest from the origin for this trait.

Varieties Pesma, Renesansa and Sara had an equal proportion of both genes. The arrays that correspond to parents were similarly distributed along the regression line and indicate that the parents were genetically divergent for the analyzed trait. These findings correspond with the results published by other authors who also indicated over-dominance type of gene action in the inheritance of the trait grain weight per plant (Nazir et al., 2014; Yao et al., 2014; Shehzad et al., 2015). Contrary to these results, partial dominance in the inheritance of this trait was observed by Farooq et al. (2011) and Rashid et al. (2013).

Analysis of components of genetic variation showed that the variance due to dominant effects of genes (H_1 and H_2) were more important in the inheritance of the trait grain weight per spike compared with the additive component of variance (D), indicating that the expression of this trait is conditioned by dominance (non-additive) gene action. Unequal values of non-additive components suggested that positive and negative alleles were unequal among parent cultivars. The frequency of the dominant allele (u) was found to be greater than the frequency of recessive allele (v), which was in agreement with the calculated F value (interaction additive × dominant effect), which was positive. The proportion of genes with positive and negative effects in the parents ($H_2/4H_1$) was found to be less than its theoretical value (0.25) for this trait which indicated asymmetrical distribution of positive and negative alleles in the parents. Since that estimates for degree of dominance ($\sqrt{H_1/D}$) were found to be more than

unity in F_1 generation, it becomes clear that over-dominance type of gene action in the inheritance of the trait has been present (Table 5). This result was in accordance with the results obtained by regression analysis. The ratio of the total number of dominant against recessive alleles (Kd/Kr) was greater than 1, indicating the presence of more dominant alleles in inheritance of this trait. Similar results, which indicated a larger value of the dominant component in the genetic variance and over-dominant inheritance of the grain weight per spike, have been also pointed out by Petrović et al. (2012) and El-Hosary et al. (2015). Contrary to these results, the greatest part of the additive component and partial dominance responsible for the inheritance of grain weight per spike was observed by Minhas (2012) and Kohan and Heidari (2014). In view of over-dominance type of gene action and preponderance of dominance effects for grain weight per spike, selection in early generations would not be fruitful and indicates that it had to be delayed till late segregating generations.

Table 5. Estimation of genetic components of variation for the analyzed traits of wheat

Components	Grains weight per spike (g)	Grains weight per plant (g)
D[a]	0.01	0.24
H_1[b]	0.03	0.80
H_2[c]	0.02	0.51
F[d]	0.02	0.46
E[e]	0.01	0.24
$H_2/4H_1$[f]	0.15	0.16
u = p[g]	0.82	0.80
v = q[h]	0.18	0.20
$\sqrt{(H_1/D)}$[i]	2.20	1.81
K_D/K_R[j]	3.55	3.18

[a]D: Measures additive effect, [b]H_1 and [c]H_2: Measures dominance effect, [d] F: Determines frequencies of dominant to recessive alleles in parents, [e]E: Shows environment effect, [f]$H_2/4H_1$: Determines proportion of genes with positive and negative effects in the parents, [g] u: The values of dominant alleles, [h] v: The value of recessive alleles, [i] $\sqrt{(H_1/D)}$:Measures average degree of dominance, [j] (K_D/K_R): Ratio of the total number of dominant against recessive alleles.

In the inheritance of the trait grain weight per plant of wheat, the non-additive components (H_1 and H_2) were found to be greater than additive (D), indicating that non-additive gene effects play a predominant role in the inheritance of this trait. Unequal values of non-additive components suggested that positive and negative alleles were unequal among parent cultivars. The frequency of the dominant allele (u) was greater than the frequency of recessive allele (v), which was in agreement with the calculated positive F value. The proportion of genes with positive and negative effects in the parents ($H_2/4H_1$) was found to be less than its theoretical value (0.25) which confirmed asymmetrical distribution of positive and negative alleles in the parents. The estimates for degree of dominance ($\sqrt{H_1/D}$) were found to be slightly more than unity in F_1 generation, indicated the existence of over-dominance in the inheritance of the trait. These results are in accordance with the results previously obtained by regression analysis. The ratio of the total number of dominant against recessive alleles (Kd/Kr) was greater than 1, indicating the presence of more dominant alleles in inheritance of this trait (Table 5). The greatest value of the

dominant component in the genetic variance and over-dominant inheritance of the grains weight per plant, has been also pointed out by Yao et al. (2014), El-Hosary et al. (2015) and Kumar et al. (2015b). Considering the fact that selection in early generations for the trait grain weight per plant could be difficult due to the over-dominance type of gene action, it is expected to obtain desired grain weight per plant of wheat by selection through later generations and could be much slower in a selection program.

In light of the present findings it can be concluded that parents Pobeda, Renesansa and Sara were found to be the best general combiners for the examined traits of wheat. If the general combining abilities and the mean values of these genotypes were considered, these three parents could be used in hybridization program for the improvement of varieties towards higher grain weight per spike, as well as for the grain weight per plant of wheat. On the other hand, if the specific combining abilities and the mean values of the cross combinations are considered, than F_1 cross combinations such as Sara/Partizanka,

Renesansa/Partizanka and Pobeda/Sara could be effective to improve these traits. The predominance of non-additive type of gene actions, as well as over-dominant inheritance of these traits in bread wheat, clearly showed that selection in early generation may not be useful. Therefore, for the improvement of these traits of wheat, selection of superior plants should be delayed through later generations. Information in this regard would help breeders to make better selection of desirable parents to develop an efficient breeding program to obtain new wheat cultivars with high grain yield potential for food and nutritional security.

ACKNOWLEDGMENTS

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