



Gene action for grain yield and its correlation with yield components in a diallel cross of winter wheat (*Triticum aestivum* L.)

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Summary: Magnitude and type of gene actions in a specific population are the main criteria for the parents' selection that will develop the best recombinants after hybridization. Information about the genetic control of complex traits is useful for the further development of efficient breeding programs. In order to identify action of genes for grain yield plant⁻¹ and its correlation with main yield components, incomplete diallel crossing was applied. The field trial was conducted at the experimental field of the Agricultural Advisory Service in southeastern Europe, during season 2012-2013. Mean values of F₁ generation showed that crosses Apache × Prima had the highest value of grain yield plant⁻¹ and Jackson × Balkan had the lowest. Common type of inheritance for grain yield plant⁻¹ was over dominance. The ANOVA revealed that this trait was controlled by additive and non-additive effects. The best general combiner for grain yield plant⁻¹ was Apache, and two crosses (Dragana × Jackson; Balaton × Nevesinjka) showed significant SCA effects. Components of genetic variance showed that dominant was more important than additive component, and the total number of dominant genes were in excess over the number of recessive genes in all parents. Furthermore, moderately low value of narrow sense heritability ($h^2=31.96\%$) was observed for grain yield plant⁻¹. Parent Sana contained maximum dominant genes, whereas parent Jackson had maximum recessive genes. Grain yield plant⁻¹ was significantly correlated with tillers numbers plant⁻¹ at genotypic level ($r_g=0.494$). The results from this study might be helpful for creating new wheat cultivars with high-yielding potential.

Key words: combining ability, diallel cross, grain yield, wheat

Introduction

In order to create new cultivars, the key point of the wheat breeding program is to develop populations with high genetic variations. The main criteria for the selection of parents that after hybridization are likely to develop the best recombinants for desirable traits, is the magnitude and type of gene action in a particular population. The prerequisite for combining desirable genes in a single genotype is the evaluation of available genetic material to evaluate the genetic variability for economically important traits (Nazir et al., 2014). Knowledge of the inheritance pattern of the target traits is substantial for the success of selection within a breeding program.

Three main components (number of spikes per unit area, number of grains per spike and 1000 grain weight) determine the yield of wheat (Tian et al., 2006). The grain yield is the result of the plants life cycle, generative and vegetative, reflecting the interaction of the environment with all growth and development processes that occur throughout the life cycle (Mirosavljević et al., 2018).

Significant estimates of general and specific combining ability variances for yield and yield related traits have been reported by many researchers. Crosses displaying high SCA effects for grain weight and

yield were derived from parents having various types of GCA effects (high \times high, high \times low, low \times low and medium \times low) (Fasahat et al., 2016).

The high ratio of GCA to SCA mean squares indicate the role of additive gene effects in the appearance of grain yield plant⁻¹ (Gomaa et al., 2014). Moreover, it was stated that grain yield plant⁻¹ possibly could be result of epistatic genetic effects too, as from additive and dominant genes. Heritability of some trait determines the extent in which it is transferred from one generation to the next, and is an important tool when used with other parameters for predicting genetic gain within a selection process (Xu et al., 2017).

Evaluating the performance of eight bread wheat cultivars under three diverse environments through an 8 \times 8 diallel cross, Ahmad et al. (2011) established low heritability in the narrow sense (10.13%) compared to the broad sense heritability (80.69%), which indicates a greater influence of the dominant gene action in the overall genetic variability for grain yield plant⁻¹. Similar to these findings, low, medium, and high narrow sense heritability estimates were reported for grain yield per plant⁻¹ (Watson et al., 2019). Previous studies stated that grain yield plant⁻¹ is closely associated with its components (Philipp et al., 2018).

The aim of this study was to determine the modes of inheritance, combining ability and to identify gene action for grain yield plant⁻¹ and its relationship with yield components. Knowing the genetic control of this complex trait may be used for developing an efficient breeding and selection programs for creating new cultivars with improved genetic basis for high yield potential.

Materials and Methods

The trial was conducted as a randomized block design with three replications at the Experimental Field of the Agricultural Advisory Service (Sremska Mitrovica) in southeastern Europe (typical Pannonian Plain). For this study eight winter wheat (*Triticum aestivum* L.) genotypes were selected (Apache, Balaton, Balkan, Dragana, Jackson, Nevesinjka, Sana, and Prima). Genotypes were chosen based on their divergent background and variability among studied traits (Table 1). These eight cultivars were crossed according to the diallel model without reciprocals during the season 2011-2012, resulting in 28 hybrid combinations. During the next crop season, 2012-2013, the seeds of eight parents and 28 F₁ hybrids were sown. Standard agricultural practices were applied. In trials, weeds were periodically manually removed, while pests and diseases were controlled by appropriate chemical applications in spring.

Plant to plant spacing was 15 cm and row to row spacing was 30 cm. One healthy seed was planted per site. The parent plants and F₁ hybrids were sown in a plot comprised of 3 rows with 3 m in length, having 20 healthy plants in one row. Observations for different traits were recorded on 45 (15 per plot) random plants for both, parent plants and F₁ offspring. Plants were tagged prior to heading, and observations are made on fertile tillers plant⁻¹, number of grains spike⁻¹, 1000 grain weight and grain yield plant⁻¹.

In order to determine the mode of inheritance for grain yield plant⁻¹, test of significance mean values (t-test) between F₁ generation and the parents was applied. The analysis of combining ability were made following the method 2, model 1 proposed by Griffing (1956). Analysis of genetic components of variance was done according to methods used by Mather & Jinks (1971). Narrow sense heritability was calculated using genetic components of variance according to the formula by Mather and Jinks (1982). Test for regression coefficient (b) and correlation coefficients was calculated using Infostat.

Results and Discussion

Mean Values and Modes of Inheritance

This study was undertaken to determine inheritance patterns, combining ability and action of genes for grain yield in wheat, along with its correlations with yield components. In order to accumulate a desirable gene pool in improved wheat germplasm, it is necessary to comprehend the extent of genetic variation and the inheritance pattern of the measurable traits in relation to the targeted environment for which genotypes are to be developed (Fellahi et al., 2015). Wide spread commercial varieties contain

valuable of internal variability which depicts that a selection within the varieties may be important for increasing the grain yield and other quantitative or qualitative traits (Greveniotis et al., 2020).

The main purpose of wheat breeding is to increase grain yield which is a quantitative trait and is affected by many genetic and non-genetic factors. The success of selection in the cross populations depends on the knowledge of inheritance pattern of the important traits. Wheat yield improvement requires certain breeding program.

Significant differences in mean values for grain yield plant⁻¹ between F₁ hybrids were observed (Table 2). Combination Apache × Prima had the highest mean value for grain yield plant⁻¹ (18.13 g), and Jackson × Balkan had the lowest value (10.54 g). An intermediate type of inheritance in F₁ generation was observed in three combinations (Dragana × Apache, Apache × Jackson, Sana × Balkan). Five combinations (Sana × Balaton, Dragana × Nevesinjka, Dragana × Jackson, Apache × Balkan and Jackson × Balkan) were significantly different from their parents. In other crosses, we reported partial or full dominance.

Table 1. Origin, year of introduction and mean values for yield related traits of the parents

Genotype	Introduced	Grain yield plant ⁻¹ (g)	Tillers plant ⁻¹	No. grain spike ⁻¹	1000 grain weight (g)
Dragana (RS)	2002	15.02	6.20	59.75	41.20
Apache (FR)	1998	18.17	6.48	68.28	40.93
Sana (HR)	1983	16.09	5.67	74.68	38.30
Balaton (AT)	2005	16.27	7.04	61.53	37.85
Prima (RS)	1995	14.74	5.57	56.75	46.87
Nevesinjka (RS)	1992	14.02	5.37	61.67	41.96
Jackson (US)	1993	14.14	6.10	59.07	39.73
Balkan (RS)	1979	13.87	5.23	64.07	42.44

Table 2. Mean values and modes of inheritance for grain yield plant⁻¹

Parents	Dragana	Apache	Sana	Balaton	Prima	Nevesinjka	Jackson	Balkan
Dragana	<u>15.02</u>	16.45 ⁱ	15.54	16.22	13.55	17.61 ^{h+}	17.95 ^{h+}	13.23
Apache		<u>18.17</u>	15.19	15.32	18.13 ^{d+}	17.05 ^{pd+}	16.10 ⁱ	11.38 ^{h-}
Sana			<u>16.09</u>	11.24 ^{h-}	13.23	14.03	14.79	15.19 ⁱ
Balaton				<u>16.27</u>	13.65	17.62	14.17 ^{d-}	13.47 ^{d-}
Prima					<u>14.74</u>	16.48	13.18	14.32
Nevesinjka						<u>14.02</u>	12.97	13.89
Jackson							<u>14.14</u>	10.54 ^{h-}
Balkan								<u>13.87</u>
LSD	0.05							2.13
	0.01							3.04

h-heterosis occurred (over dominance); pd-partial dominant; d-dominant; i-intermediate inheritance
+, - = positive and negative type of inheritance mode

The findings of this research showed that most the common mode of inheritance for grain yield plant⁻¹ was over dominance. Two crosses (Dragana × Nevesinjka and Dragana × Jackson) showed

positive over dominance. Similar to these findings, Yao et al. (2014) also established super dominant and intermediate inheritance pattern for grain yield plant⁻¹.

Table 3. Analysis of variance for combining ability for grain yield plant⁻¹

Source of	DF	SS	MS	Fe	Ft	0.05	0.01
GCA	7	44.10	6.30	7.73**	2.14		2.91
SCA	28	84.30	3.01	3.69**	1.64		2.01
E	70	57.07	0.82				

** Significant at 1% level

Table 4. GCA effects for grain yield plant⁻¹

Parents	GCA	Rank
Dragana	0.692	2
Apache	1.195**	1
Sana	-0.226	6
Balaton	0.056	4
Prima	-0.163	5
Nevesinjka	0.403	3
Jackson	-0.567	7
Balkan	-1.392	8
LSD	0.05	0.81
	0.01	1.07

** Significant at 1% level

Table 5. SCA effects for grain yield plant⁻¹

Parents	Apache	Sana	Balaton	Prima	Nevesinjka	Jackson	Balkan
Dragana	-0.285	0.223	0.621	-1.830	1.667	2.970*	-0.928
Apache		-0.634	-0.782	2.247	0.604	0.617	-3.278
Sana			-3.444	-1.235	-0.995	0.735	1.957
Balaton				-1.097	2.307*	-0.167	-0.045
Prima					1.390	-0.941	1.021
Nevesinjka						-1.717	0.025
Jackson							-2.349
LSD 0.05							2.28
0.01							3.03

* Significant at 5% level

Table 6. Components of genetic variance

Components	Values
D	1.22
H₁	11.22
H₂	9.28
F	0.21
E	0.82
u	0.71
v	0.29
√(H₁/D)	3.03

K_D/K_R	1.06
h^2 (%)	31.96

Combining ability

The analysis of variance for combining ability showed the highly significant genotypic variation for grain yield plant⁻¹ (Table 3). Results showed the importance of additive and non-additive effects with the preponderance of additive gene action for grain yield plant⁻¹. Similar to these findings, significant differences due to GCA effects for grain yield plant⁻¹ were also reported by Chaudhry et al. (1994).

Estimates of GCA effects of the parent cultivars ranged from -1.392 to 1.195 (Table 4). Cultivar Apache was the best general combiner for grain yield plant⁻¹, followed by cultivar Dragana. Cultivar Balkan showed the poorest general combining ability.

Significant and positive SCA effects for grain yield plant⁻¹ were revealed in two crosses (Dragana × Jackson and Balaton × Nevesinjka) (Table 5). Estimates of SCA effects ranged from -3.278 to 2.970.

Estimates of combining ability showed that GCA value of Apache was significant and higher than values of other cultivars involved in the research. Our results indicate that cultivar Apache was the best general combiner for grain yield plant⁻¹ and may be useful as genetic source in wheat breeding programs for higher grain yield. The high grain yield plant⁻¹ of certain crosses (Dragana × Jackson and Balaton × Nevesinjka) showed strong positive SCA effects. Since at least one good combining parent was included in these crosses, their progenies had increased grain yield plant⁻¹ than overall means and yielded valuable transgressive segregations. The superior performance of crosses between parents from diverse origins (Serbia, France, Austria and US) also demonstrated the role of a wider genetic base in the crossing program.

Components of genetic variance for grain yield plant⁻¹

Estimates of the genetic and environmental components of grain yield plant⁻¹ variation showed that dominance component (H) was more important than additive component (D), considering the greater values of H₁ and H₂ than D component (Table 6).

The results from our study showed that the F value, which estimates the relative frequency of dominant alleles to recessive in the parents, was positive. This indicates the excess of dominant alleles present in the parents, which was further supported by the frequency of dominant (u) and recessive alleles (v). The degree of dominance measured by $\sqrt{(H_1/D)}$ was found to be larger than unity (3.03), indicating over dominance for the inheritance of grain yield plant⁻¹. The K_D/K_R ratio (1.06) demonstrate that the total number of dominant genes were higher over the total number of recessive genes in all the parents included in this research. Estimates of narrow sense heritability (h^2) were moderately low for grain yield plant⁻¹.

The estimates of genetics of variation for grain yield plant⁻¹ showed greater magnitude of H₁ and H₂ than D component, and revealed that genes with non-additive effects were more important. The positive value of F revealed the excess of positive alleles present in the parents, which was additionally sustained by the value of K_D/K_R (>1). The degree of dominance ($\sqrt{(H_1/D)}$) was more than unity which supported the higher influence of non-additive genes in the inheritance for grain yield plant⁻¹. These results are in agreement with those of Akram *et al.* (2009) and Ojaghi (2010). Preponderance of dominance effects for this trait indicate that the early generations selection may not be useful and it had to be in later generations of segregation. Narrow sense heritability value was moderately low, indicating that non-additive effects had greater impact for expression of this trait. Such low narrow sense heritability for grain yield plant⁻¹ have been previously reported (Watson *et al.*, 2019).

Regression analysis Vr/Wr for grain yield plant⁻¹

The Vr/Wr graph present that the regression line intercepted the Wr-axis below the point of origin (a=-1.36), which indicates that the trait was controlled by the over dominant type of gene action (Figure 1). Parents Sana and Balkan contained maximum dominant genes, which was indicated by the

distribution of array points along the regression line. Being farthest from the origin, parent Jackson carried maximum recessive genes.

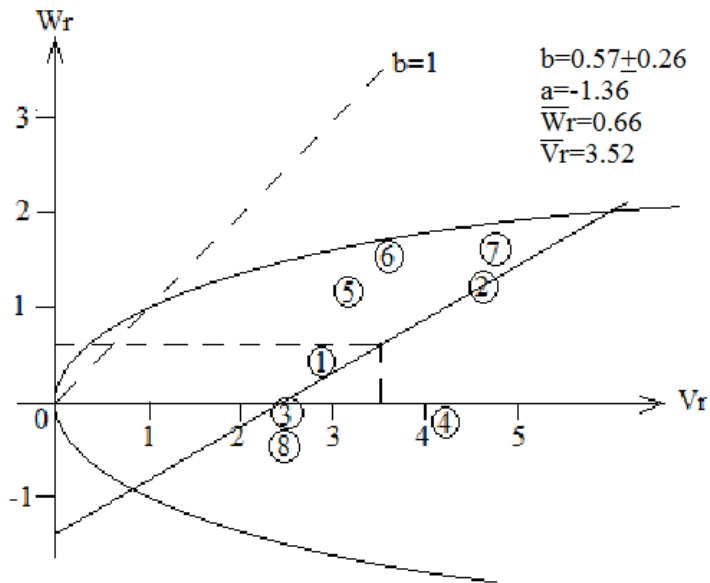


Figure 1. V_r/W_r graph for grain yield plant^{-1}

1-Dragana; 2-Apache; 3-Sana; 4-Balaton; 5-Prima; 6-Nevesinjka; 7-Jackson; 8-Balkan

Table 7. Genotypic (r_g) and phenotypic (r_p) correlation coefficients between grain yield plant^{-1} and yield components

Character	r	Tillers plant^{-1}	No. grains spike^{-1}	1000 grain weight
Grain yield plant^{-1}	r_g	0.494**	0.131	0.105
	r_p	0.302	-0.185	0.047
Tillers plant^{-1}	r_g		-0.101	-0.083
	r_p		-0.027	-0.022
No. grains spike^{-1}	r_g			-0.389*
	r_p			-0.135

*, ** Significant at 5, 1% level

The average level of dominance is expressed by the range between the point where the regression line intersects the covariance's (W_r) axis and the point of origin (a), showed over dominant type of gene action for grain yield plant^{-1} . It means that the genotypes are efficient for developing increased grain yields in hybrid condition. Similar results have been earlier reported by Chaudhry (2002) and Kashif & Khaliq (2004). Being closest to the origin, Sana and Balkan contained maximum dominant genes, while parent Jackson carried maximum recessive genes being furthest from the origin.

Correlation analysis

The highly significant and positive genotypic correlation was observed between grain yield plant^{-1} and tillers plant^{-1} ($r_g=0.494$), while phenotypic correlation between these traits was also positive ($r_p=0.302$) but non-significant (Table 7). Moreover, grain yield plant^{-1} showed a positive but non-significant genotypic correlation with number of grains spike^{-1} and 1000 grain weight. Among the yield components, number of grains spike^{-1} and 1000 grain weight were in significant negative correlation on genotypic level ($r_g=-0.389$), and in negative but non-significant correlation on phenotypic level.

Correlations between the traits depends on genetic and environmental factors (Mladenov et al. 2012). In general, genotypic correlation coefficients had higher magnitudes than the phenotypic ones,

which was in accordance with the findings of El-Mohsen et al. (2012) that in general genotypic correlation coefficients were higher than the corresponding phenotypic values. This could be explained by the depressing effect of environment on trait relationship. Grain yield plant⁻¹ had a significant positive genotypic correlation with number of tillers plant⁻¹, positive but non-significant genotypic correlation with the number of grains spike⁻¹, and it showed positive and non-significant correlation with 1000 grain weight. These findings are in accordance with findings of Srećkov et al. (2011) who also reported positive but non-significant genotypic correlation between grain yield and grain weight. This suggests that increase in tillers plant⁻¹ would increase grain yield plant⁻¹. Results of this research are in agreement with the findings of Tilley *et al.* (2019) who stated that reproductive tillers make up a considerable proportion of the total grain yield plant⁻¹. Genotypic correlation between number of grains spike⁻¹ and 1000 grain weight was negative and significant. Similar results have also been reported by Khan et al. (2010), while contrary to these findings Mecha et al. (2017) reported positive correlation between number of grains spike⁻¹ and 1000 grain weight.

Conclusions

The results from our study indicate that there was a significant genotypic variation for the studied character. The most common mode of inheritance for grain yield plant⁻¹ was over dominance. Cultivar Apache showed significant and higher GCA value than values of other cultivars involved in this research, and therefore it could be used as donor parent for the improvement of grain yield. Crosses Dragana × Nevesinjka and Balaton × Nevesinjka holds promise for yielding better segregates with improved grain yield plant⁻¹.

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Delovanje gena za prinos zrna i njegova povezanost sa komponentama prinosa u dijalelnom ukrštanju ozime pšenice

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Sažetak: Opseg i tip delovanja gena u novim populacijama su glavni kriterijumi za odabir roditelja koji će stvoriti najbolje potomstvo nakon hibridizacije. Informacije o genetičkoj kontroli kompleksnih osobina su korisne za dalje stvaranje efikasnih oplemenjivačkih programa. U cilju identifikacije prirode delovanja gena na prinos zrna po biljci i njegovu korelaciju sa komponentama prinosa upotrebljeno je nepotpuno dijalelno ukrštanje. Ogled je izveden u jugoistočnoj Evropi na oglednom polju Poljoprivredne savetodavne službe tokom sezone 2012-2013. Prema srednjim vrednostima F_1 generacije, ukrštanje Apache × Prima je imalo najveći prinos zrna po biljci, a Jackson × Balkan najmanji. Najčešći način nasleđivanja za prinos zrna po biljci bila je puna dominacija. ANOVA je pokazala da je ova osobina kontrolisana i aditivnim i neaditivnim efektima. Apache se pokazao kao generalno najbolji kombinator za prinos zrna po biljci, a kod dva ukrštanja (Dragana × Jackson; Balaton × Nevesinjka) je ustanovljena značajnost posebnih kombinacionih sposobnosti. Komponente genetičke varijanse su pokazale da je dominacija važnija od aditivne komponente, a ukupan broj dominantnih gena je veći od broja recesivnih kod svih roditelja. Ustanovljena je umereno niska vrednost ($h^2=31,96\%$) heritabilnosti u užem smislu za prinos zrna po biljci. Maksimalan broj dominantnih gena je utvrđen kod roditelja Sana, dok je Jackson imao maksimalan broj recesivnih gena. Na genotipskom nivou, prinos zrna po biljci bio je u značajnoj korelaciji sa brojem produktivnih vlati ($r_g=0,494$). Rezultati ovih istraživanja bi mogli biti od koristi za stvaranje novih varijeteta pšenice sa visokim potencijalom za prinos.

Ključne reči: dijalelno ukrštanje, kombinaciona sposobnost, prinos zrna, pšenica