DIALLEL ANALYSIS OF GRAIN NUMBER PER SPIKE IN TRITICALE

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Abstract

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In this paper the inheritance of grain number per spike in hexaploid (6x) winter triticale was investigated. Studies were performed on primary spikes of parents, F_1 and F_2 progenies of a 5 x 5 complete diallel crossing with reciprocals. The results highlighted the prevalence of dominance and over-dominance in the expression of this trait at majority of combinations of F_1 generation. Significant difference between direct and reciprocal crosses appeared in both generations and in generally with combinations of the most divergent parents. Analysis of variance for combining abilities demonstrated the existence of highly significant values for general combining ability (GCA), specific combining ability (SCA) and effects of reciprocal crosses (REC). GCA and SCA variations demonstrated similar values, which were for about three times higher than variation caused by reciprocal effects. The best SCA were expressed in generally in combinations of good x average or good x poor GCA of parents.

Key words: Triticale, diallel, grain number, spike, combining ability, heritability, inheritance

Introduction

Theoreticaly it is very important to prospect factors of heredity in new conditions of unfamiliar cytoplasm, in combinations of genomes of two divergent parental species as well as interaction of genes of different species which participated in creation of triticale [wheat (*Triticum* spp.) and rye (*Secale cereale* L.)]. Since, 6x triticale has genome of xenogamous rye added to tetraploide (4x) wheat genome, it has a divergent gene pool, which may result in more expressed role of nonadditive genes in the inheritance (Kaltsikes and Lee, 1973). Among some combinations have been found reciprocal effects, too (Chen, 1977). The number of grains per primary spike is very important quantitative traits (QT) for grain yield formation, which is given special attention in the selection process.

The aim of this study was to determine the genetic structure of inheritance of number of kernels per primary spike in the triticale. Knowledge regarding the mode of inheritance and gene action parameters in the number of kernels per spike may allow better choice of breeding methods and faster progress in improving some important characteristics. Also it can enable the creation of better strategies for the selection of parents for crossing and for manipulation with desirable genotypes.

Materials and Methods

For study were used the plants of parents and of theirs F_1 and F_2 progenies obtained by complete diallel crossing method with reciprocals (5 x 5). Five parental 6x winter triticale genotypes are considerable divergent and originate from the following countries and crosses: 1) Presto (PL), [(Tr.6A298 x C254.72) x (Tr.64 x rye Dankowskie Zlote)] x Lasko; 2) Lasko (PL), (Tr.57. x winter wheat C 1218/67) x 6TA 206; 3) Tr. Kg. 20 (SRB), the L284 x W 452 obtained by crossing *T. durum* N°43 x rye from Halle; 4) Tr.89 (MX), Inia x Armadillo "S", and 5) Tr.57 (MX), Maya 2 x Armadillo "S".

The experiment was conducted at the experimental field of the Center for Small Grains in Kragujevac, by the method of completely randomized block design with four replications during three years. Plants were grown in rows 1 m long, with spacing of 20 cm between rows and 10 cm within the rows. We apply the standard cultural practices with the use of 120 kg/ha of pure nitrogen and appropriate amounts of phosphorus and potassium fertilizers. From each of parents and of the F, progenies were analyzed 20 x 4 and of the each F, progenies 50 x 4 randomly selected plants grown in last year. Data for the number of kernels per primary spike were examined by comparing the averages of F₁ and F₂ progenies to averages of their parental genotypes. Experimental data were processed by variance analysis. Heritability was estimated according to Mather (1949), the GCA, SCA and REC effects were analyzed using a Method 1 - Model 1 of diallel cross (Griffing, 1956), components of variance and regression analysis were calculated according to Hayman (1958) and Mather and Jinks (1971) and mode of inheritance according to Kraljevic-Balalic et al. (1991). Data were processed by computer programs MSTAT-C and GEN.

Results and Discussion

The number of grains per spike is one of the most important components of yield and with the 1000 kernels weight dictates grain yield per spike. Parents of triticale who were used in the present diallel crosses were each amongst significantly different according to the number of grains per primary spike (Table 1). In doing so, it should be noted that the lines Tr. 89 and Tr. 57 had the largest number of grains, whereby in between them there was no significant difference. This diversity of parents has enabled to obtain significant differences among most of the progenies and thus facilitate the interpretation of the mode of inheritance of this complex trait. In most combinations of F_1 generation (in total 15) in the inheritance of grains number per spike was expressed over-dominance or dominance of better parent (BP). Incomplete dominance of BP was manifested in three combinations. Incomplete dominance of inferior parents (-id), and negative dominance (-d) are manifested only by a single combination of both. A significant and highly significant differences between direct and reciprocal crosses existed among seven combinations of mostly the most divergent parent pairs (Presto - Lasko, Presto - Tr. 89, Presto - Tr. 57, Lasko - Tr.Kg. 20, Lasko - Tr. 57, Tr. Kg. 20 - Tr.89 and Tr. 89 - Tr. 57).

On the existence of N-C heterosis in wheat due to the interactions pointed out Kihara (1979). Analyzing the effects of nucleus and cytoplasm of triticale, Yasumuro et al. (1981), have given importance for obtaining fixing heterosis in *interspecies* and *intergenus* hybridization. On the important role of nucleus-cytoplasm (N-C) interactions and double interactions of N-C in the expression of traits in triticale and wheat rye hybrids also indicated Sasaki et al. (1983), Nakata et al. (1983), (1986) and Yasumuro et al. (1983), (1985), (1987), (1988), (1989). Thus, in the breeding of triticale, N x C interactions must be actively used in addition to wheat rye interactions at the level of nuclei, as allowing new N-C combinations.

For most of combinations for investigated trait in the F_2 generation was observed significant decrease of value relative to the F_1 generation. The inheritance was different depending on the combination, moving in a range from negative dominance to positive over-dominance (Table 1). At three

Table 1

The number of grains per spike in parents, F_1 and F_2 generations of triticale (diallel 5 x 5)

Parents, generation		Presto	Lasko	Tr. Kg. 20	Tr. 89	Tr. 57
Presto		52.95	65.77 ^{od}	52.58 ^{id}	57.30 ^{id}	54.68 ^{-id}
Lasko		58.89 od	52.11	61.61 ^{od}	60.05 ^d	60.22 ^d
Tr. Kg. 20	F ₁	52.74 ^d	66.43 ^{od}	51.11	57.05 ^{id}	65.90 ^{od}
Tr. 89		60.59 ^d	59.17 d	59.87 ^d	58.93	63.99 ^{od}
Tr. 57		59.30 d	66.81 ^{od}	64.16 ^{od}	58.35 -d	58.70
Presto		52.95	56.72 ^{od}	53.07 ^d	58.31 d	54.32 -id
Lasko		55.19 od	52.11	54.75 ^{od}	54.88 -id	55.89 ⁱ
Tr. Kg. 20	F ₂	52.96 ^d	53.80 ^d	51.11	53.87 ^{-id}	56.25 ^{id}
Tr. 89		56.43 ⁱ	54.97 ⁱ	55.87 ⁱ	58.93	57.87 ^{-d}
Tr. 57		57.11 ^{id}	55.80 ⁱ	57.05 ^{id}	58.03 ^{-d}	58.70
	F ₁ LSD	0.05 = 2.43	F_2 LSD 0.05 =2.11			
		0.01 = 3.23	0.01 = 2.80			

d = positive dominance; -d = negative dominance; id = incomplete dominance of better parent; -id = incomplete dominance of inferior parent; od = over dominance; i = intermediate

combinations were maintained over-dominance in relation to BP, while in four combinations were expressed dominance of BP. Incomplete dominance of BP were found in three combinations, and in five combinations a intermediate mode of inheritance. Incomplete dominance of inferior parent (-id) was expressed in three combinations, whereas more inferior parent dominated (-d) in two combinations. Highly significant differences between direct and reciprocal crosses for the number of grains per spike were kept only in the combination of parents Presto - Tr. 57, while for the other combinations were not statistically significant.

By analysis of variance for the number of grains per spike in the F_1 generation of triticale was determined the existence of highly significant differences for GCA, SCA and reciprocal effects (REC). At that, the variance due to GCA was approximately the same value as the variance due to SCA, indicating equal importance of additive and dominant gene action in inheritance of grains number per spike. Variance due to the reciprocal effects had about three times smaller value of variance for GCA and SCA indicating on importance of impact of hereditary factors of cytoplasm in the expression of grains number in triticale (Table 2).

The best general combiners were genotypes Tr. 57 and Lasko, who had the highest values of GCA (Table 3). Cul-

tivars Presto and Tr.Kg. 20 were poor general combiners. Good values for the SCA in direct crosses demonstrated the combinations of Presto x Lasko, Presto x Tr. 89, Lasko x Tr.Kg. 20 and Tr.Kg. 20 x Tr. 57 (a combination of good x poor general combiners). In reciprocal crosses, good SCA had only combinations of Presto x Lasko and Tr. 57 x Tr. 89 (good x poor and good x average general combiners). Significant differences between the SCA values of direct and reciprocal crosses demonstrated the combinations of parents: Presto - Tr.Kg. 20, Presto - Tr. 89, Lasko - Tr.Kg. 20, Lasko - Tr. 89, Lasko - Tr. 57, Tr.Kg. 20 - Tr. 57 and Tr. 89 - Tr. 57.

Previous results indicate that at the number of grains per spike, choice of parents and plants of triticale with a high mean value is not completely reliable way to get better progenies and for selection of promising plants in the next generations, but should nevertheless take also into account the parents who stand by their overall "per se performance". The coincidence between the "per se" performance and GCA effects were found also by Gill et al. (1978), which can be used as a selection criterion. They found a weak correlation between the "per se" performance and SCA, after their crossing among of good general combiners in triticale have not resulted in higher SCA effects. The contrasting results in terms of agreement "per se" performance of GCA and

Artova of combining admittes for number of grains per spike in trutcate							
Sources of variation	D.f.	S.S.	M.S.	F _e	F _{10.05}	F _{t 0.01}	
General combining abilities (GCA)	4	129.15	32.29	43.41**	2.50	3.59	
Specific combining ability (SCA)	10	339.10	33.91	45.60**	1.97	2.58	
Reciprocal effects (REC)	10	100.66	10.07	13.53**	1.97	2.58	
Error (E)	72	M'e =	0.74				

 Table 2

 ANOVA of combining abilities for number of grains per spike in triticale

D.f.= degrees of freedom; S.S.= Sums of squares; M.S.= Means of squares; Fe = F value experimental; $F_t = F$ theoretical; ** = High statistical significance

Table 3

Values of GCA (per diagonal), SCA (above diagonal) and reciprocal values (below diagonal) for number of grains	
per spike in triticale	

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Parents			Presto	Lasko	Tr. Kg. 20	Tr. 89	Tr. 57
Presto			-2.519	4.661++	-4.091	2.130++	-1.566-
Lasko			3.615++	1.240++	4.861++	-1.240	1.204
Tr. Kg. 20)		1.109	-2.575	-1.034	0.242	4.931++
Tr. 89			-1.456-	0.576	-1.421-	0.353	-0.239
Tr. 57			-2.311	-3.298	0.814	2.837++	1.959++
LSD	0.05	0.01	SE				
(GCA)	0.768	1.023	0.386				
(SCA)	1.329	1.770	0.668				
(REC)	1.715	2.284	0.862				

SCA effects, pointed out Dhinsa et al. (1985) and Brar et al. (1983). They suggest the use of good general combiners for desirable traits in order to speed progress in breeding.

Genetic variability and heritability of F₁ and F₂ generations in triticale are shown in Table 4. In the F₁ generation, the variance due to dominant effects of genes (H, and H₂) had a more important role in the inheritance of grains number per spike compared with the additive component of variance (D), although the proportion of the additive component was not negligible. This is consistent with the results of individual crosses in the F_1 generation, where most of the combinations showed over-dominance, dominance or incomplete dominance in relation to BP. In the F, generation, the additive component (D) and components of dominance effects of genes (H₁ and H₂) were similar in value, which indicated an equal effect of additive and dominance in the inheritance of these trait. The value of the parameter F (additive x dominance interaction effect) in both generations was positive, indicating that for the number of grains per spike predominated genes of better parent (dominant over recessive), which is consistent with the ratio of activity Kd/ Kr, which in both generations was in favor of dominance alleles (greater than 1). The dominant alleles (u) were more frequent than recessive (v). On the asymmetric distribution of dominant and recessive alleles for all the parents used in diallel, points that the value H₂/4H₁ in both generations was less than the theoretical value of 0.25. The average degree of dominance $(\sqrt{H1/D})$ was greater than unity (especially in F₁), which indicates that if one takes into account all the crosses; at the inheritance of number of grains per spike it was the case of over-dominance. In the F, generation, the

Table 4

Components of genetic variance and heritability for number of grains per spike in F_1 and F_2 generations of triticale

Components of	F ₁	F,
variance	1	
D	13.430	13.597
H ₁	78.740	14.764
H ₂	66.373	12.442
F	13.174	13.992
E	0.725	0.558
u	0.698	0.710
v	0.302	0.290
$H_{2}/4H_{1}$	0.211	0.211
$\sqrt{\frac{1}{H_1}/D}$	2.421	1.042
Kd/Kr	1.508	2.951
Heritab. in narrow sense, %	0.267	0.208
" broader sense, %	0.969	0.880

average degree of dominance was very close to the unit which means that the dominance played an important role in the inheritance.

Low values in both generations were established for narrow-sense heritability (20.8% and 26.7%), while its value in a broader sense in both generations are very high (96.9% and 88.0%). This indicates partial lack of diversity and number of parents in general for more precise diallel analysis, taking into account that the dominance and over-dominance had a major role in the inheritance of this complex quantitative trait. Therefore, we can not say with certainty that offsprings of investigated F_1 and F_2 hybrid progenies plants will be similar to them, especially if parents are not substantially different in the number of grains per spike.

Based on the results of regression analysis in the F, generation (Figure 1), one can argue that the regression line had significant departure from the unit but not from zero (b± Sb = 0.316 ± 0.146 , t ₍₃₎ = 3.18 and 5.85 for P = 0.05 and 0.01, from where the P < 0.05 > 0.01 accordingly P > 0.05). The points in the diagram are quite scattered, indicating the presence of inter-allelic interactions in the inheritance. In that sense regression analysis is also affirming the importance of genetic system of dominance and over-dominance in heritability. Limiting parabola is very distant from the regression line, which indicates on importance of the genetic system of domination, which is consistent with the value of the average degree of dominance $\sqrt{H1/D}$, that was higher than unit in both generations (Table 4). The value of parameter "a" is negative (-2.818), indicating the importance of overdominance in the inheritance of grains number per spike. Layout of points of scattering diagram and its distance along the expected regression line indicates on a high diversity of parents, as well as that the genotypes Tr. 89 (4) and Tr. 57 (5) had a greater number of dominant genes compared to recessive. Other parents (Presto, Lasko and Tr.Kg. 20) were more distant from the coordinate origin, indicating that they posses more recessive in relation to dominant genes for number of grains per spike. The point of the diagram of line Tr. 89 (4) was very close to the intersection with the parabola line and near to the coordinate origin, indicating that it has almost all the dominant alleles for this trait.

The expected regression line on WrW ' chart was not significantly deviant from b = 1/2 (b' ± Sb '= 0.596 ± 0.348), but the distribution of points was significantly altered compared to VrWr regression. However, again the lines Tr.89 (4) and Tr. 57 (5) were the closest to the coordinate origin, which again proves that they had mostly dominant genes, while other genotypes had mostly recessive. Changing of distribution of points and their position relative to b = 1 and b = 1/2 in comparison VrWr and WrW' charts indicates the

presence of inter-allelic interactions. Point of distribution diagram for Tr.57 (5) was in the third quadrant, which again shows the importance of over-dominance for the inheritance of grains number per spike (Figures 1 and 3).

By regression analysis of the F₂ generation were obtained similar results, although the distribution of points on diagram of distribution was little changed. Here, the expected regression line was not significantly deviant than unity (b=1.156 \pm 0.470), but was closer to limiting parable and cut the Wr axis above the coordinate origin (a = 1.541), suggesting that incomplete dominance and additivity had a more important role in the F2 generation compared to the F1 (Figures 1 and 2). Here, at the genotypes Tr. 57 (5) and Lasko (2) were the most frequent dominant alleles. Changes in the distribution of individual points along the line of expected regression at WrW' in relation to VrWr chart, as well as in relation to b = 1/2 and b = 1, indicates that in the F₂ generation

also inter-allelic interaction played an important role in the inheritance of this trait (Figures 2 and 4). It is known that the additive and dominant gene action can not be accurately determined if it is present in a significant volume of epistasis (Hayman, 1958).

According to Hatileva et al. (1987) and Farooq et al. (2012), in the inheritance of grains number per spike of triticale and wheat was observed dominance or incomplete dominance. Our results generally agree with some results from the literature (Grebennikova et al., 2011). The reason for the partial disagreement with the mode of inheritance of certain traits in triticale is best explained by Kaltsikes and Lee (1971). They said that 6x triticale, since it has added the genome of allo-pollinated rye to genome of 4x wheat, may have a more diverse "gene pool", which can result in more pronounced role of non-additive genes in the inheritance of some of its properties.

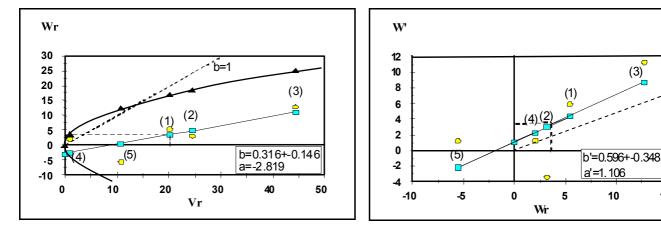


Fig. 1. Regression analysis VrWr of number of grains per spike in triticale (P and F1)

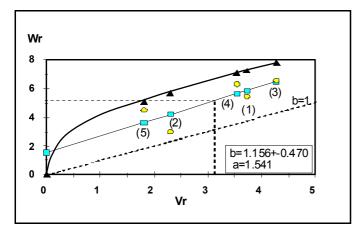


Fig. 2. Regression analysis VrWr of number of grains per spike in triticale (P and F2)

Fig. 3. Regression analysis - WrW' for number of grains per spike in triticale (P and F1)

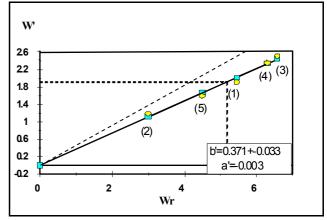


Fig. 4. Regression analysis - WrW' for number of grains per spike at triticale (P and F2)

(3)

10

15

Conclusions

Results showed the prevalence of dominance and overdominance in expression of number of grains per spike in most winter triticale combinations of F₁ generation. It was found the existence of significant differences between direct and reciprocal crosses in both generations and mostly in combinations of the most divergent parents. Analysis of variance for combining abilities revealed the existence of highly significant values for GCA, SCA and effects of reciprocal crosses. Variations in GCA and SCA showed similar values, which were about three times larger than the variations due to reciprocal effects. Top SCA are manifested mainly in a combination of good x average or good x bad general combiner. Obtained results indicate that at the number of grains per spike, a selection of plants with a high mean value in early generations is not completely reliable way to get better and promising future progenies and plants, but should nevertheless take into account also the plants which stand by their overall "performance" for more properties ("per se").

Analysis of components of genetic variation showed in the F_1 generation that the variance due to dominant gene action (H_1 and H_2) had a more important role in the inheritance of grains number per spike compared with the additive component (D). In the F_2 generation, both of said components had similar values indicating equal effect of additivity and dominance. The value of the average degree of dominance $\sqrt{H1/D}$ was greater than unity in both of generations, indicating that taking into account all combinations, in the heritability of this trait was case of overdominance. Narrow-sense heritability was low in both generations (20.8 and 26.7%), while its values in the broad sense were very high (96.9 and 88.0%).

Regression analysis indicates the presence of inter-allelic interactions in inheritance, affirming the importance of genetic system of dominance and over-dominance in heritability. The presence inter-allelic interactions make difficult more precise determination of the additive and dominant gene action, but its presence is encourage in relation of increasing possibility of promotion of breeding process and fixation of heterosis for this trait. Hexaploid triticale, since it has the genome of allo-pollinated rye added to genome of 4x wheat, it may have a more diverse "gene pool", which can result in more pronounced role of non-additive genes in the inheritance of some of its properties, such making demand for use of more parents and broader diversity in diallel analysis of complex quantitative traits than in this study, in order to obtain more precise data.

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