



Estimation of some genetic parameters through generation mean analysis in two winter wheat crosses

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Abstract

Background and Purpose: The objectives of this study were to estimate gene effects and heritability for three important quantitative traits (grain yield components) in two wheat crosses (Divana/Srpanjka and Soissons/Žitarka).

Materials and Methods: Eight generations (namely; P_1 , P_2 , F_1 , F_2 , $Bc_{1.1}$, ($P_1 \times F_1$), $Bc_{1.2}$, ($P_2 \times F_1$), $Rbc_{1.1}$, ($F_1 \times P_1$) and $Rbc_{1.2}$, ($F_1 \times P_2$)) were raised and subjected to generation mean analysis for detecting the nature of gene effects responsible for inheritance of the number of grains, grain weight and single grain weight per spike of the longest culm.

Results: Digenic epistatic model was adequate to explain variation in generation means for single grain weight in Divana/Srpanjka and for grain weight per spike of the longest culm in Soissons/Žitarka crossing combinations. Additive gene effects were more important for grain weight per spike of the longest culm in Soissons/Žitarka cross, while dominance and epistatic gene effects were predominant in controlling inheritance of single grain weight in Divana/Srpanjka cross. For the number of grains in both crosses, single grain weight in Soissons/Žitarka and grain weight per spike in Divana/Srpanjka crossing combinations, digenic epistatic model failed to explain variation in generation means.

Conclusions: These data suggest that in crosses where digenic epistatic model was adequate with predominant positive influence of additive gene effects accompanied with high narrow-sense heritability, it is possible to expect advance for traits studied in further segregation generations. Crosses where digenic epistatic model were insufficient to explain all variation in generation means along with low heritability imply more complex nature of inheritance and/or influence of the environment on the expression of these traits.

INTRODUCTION

Grain yield is a complex polygenic trait resulting from interaction among a number of inherent characters and environment. Wheat grain yield can be improved through indirect selection on the basis of yield components (1). Increase in one component might have positive or negative effect on other components. This occurrence is direct consequence of their interdependence during ontogenetic development of plants which is reflected through genetic correlations and compensation abilities (2, 3). Favourable combinations of yield contributing characters may improve yielding capacity (4). Sufficient understanding of the inheritance of quantitative traits and information about heri-

tability of grain yield and their components is essential to develop an efficient breeding strategy (5, 6). Generation mean analysis belongs to the quantitative biometric methods based on measurements of phenotypic performances of certain quantitative traits on as many as possible plant individuals in basic experimental breeding generations (parental, filial, backcross and segregation generations). As it was outlined by Kearsley and Pooni (8), generation mean analysis is a useful technique in plant breeding for estimating main gene effects (additive and dominance) and their digenic (additive x additive, additive x dominance, and dominance x dominance) interactions responsible for inheritance of quantitative traits. It helps us in understanding the performance of the parents used in crosses and potential of crosses to be used either for heterosis exploitation or pedigree selection (7). Considering the fact that grain yield and quality of winter wheat are the most important complex traits and that their improvement is the most frequent goal of wheat breeding programs in the world, selection of parental components in this study was done in attempt to fulfil these requirements. Cultivar Srpanjka is a leading cultivar in Croatian production with high grain yield as well as cultivar Soissons, while cultivars Divana and Žitarka possess excellent bread making quality, but are coupled with significantly lower yield potential. Expectation is that crossings between these cultivars may result in high and exploitable genetic variability either for grain yield and/or quality improvement. Considering these facts we undertook, the present study to estimate genetic effects and heritability for three important quantitative traits (grain yield components) in order to improve breeding efficiency in two promising winter wheat crosses.

MATERIALS AND METHODS

Materials: In this study, we used winter wheat (*Triticum aestivum* L.) cultivars Divana (bred by Jošt sjeme, Croatia), Soissons (bred by Desprez, Veuve et Fils, France), Srpanjka and Žitarka (bred by the Agricultural Institute Osijek, Croatia). Eight basic generations involved in these studies were two parents (P_1 , P_2), first and second filial generations (F_1 , F_2), first and second backcross $Bc_{1.1}$ ($P_1 \times F_1$), $Bc_{1.2}$ ($P_2 \times F_1$) and first and second reciprocal backcross $RBc_{1.1}$ ($F_1 \times P_1$), $RBc_{1.2}$ ($F_1 \times P_2$) of two crossing combinations (Divana/Srpanjka and Soissons/Žitarka).

Methods: These eight generations of two crosses were raised and planted in a randomized block design in three replications at Osijek location during the autumn season of 2001/2002. Each generation was planted in 1.2 m long plot with a between-row spacing of 20 cm and within-row spacing of 10 cm, while the number of rows per plot and the number of analyzed plants per plot varied with generation. Grain yield components, namely the number of grains per spike, grain weight per spike (g) and single grain weight per spike (mg) of the longest culm were analyzed. According to the methodology of Kearsley and Pooni (8) the following notation for gene effects were used: [m]-mean, [a]-additive, [d]-dominance, [aa]-ad-

ditive*additive, [ad]-additive*dominance, [dd]-dominance*dominance effect. The type of epistasis was determined only when dominance [d] and dominance*dominance [dd] effects were significant. When these effects had the same sign, the type of epistasis was complementary, while different signs indicated duplicate epistasis (8).

Data analysis: The mean values, standard errors and variances of different generations were subjected to weighted least squares analysis using the joint scaling test (9) to fit models of increasing complexity until an adequate description of the observed means was found as non-significant χ^2 test. The significance of gene effects was tested by t-test. Additive (V_A), dominance (V_D), additive*dominance (V_{AD}) and environmental variance (V_E) components were estimated according to Kearsley and Pooni (8):

$$V_P = V_G + V_E, \text{ where } V_P \text{ is phenotypic variance and } V_G \text{ represents genotypic variance.}$$

$$V_G = V_A + V_D + V_{AD}$$

$$V_A = (2 * \text{variance of } F_{2 \text{ generation}} - \text{variance of } Bc_{1.1 \text{ generation}} - \text{variance of } Bc_{1.2 \text{ generation}})$$

$$V_D = (\text{variance of } Bc_{1.1 \text{ generation}} + \text{variance of } Bc_{1.2 \text{ generation}} - \text{variance of } F_{2 \text{ generation}} - V_E)$$

$$V_{AD} = 0,5 * (\text{variance of } Bc_{1.2 \text{ generation}} - \text{variance of } Bc_{1.1 \text{ generation}})$$

Heritability in broad (h^2_b) and narrow sense (h^2_n) was calculated as follows:

$$h^2_b = V_G / (V_G + V_E); h^2_n = V_A / (V_G + V_E)$$

The V_D and V_{AD} values were set to zero when estimated variance turned out to be negative.

Statistical analyses were carried out using the PROC REG procedure (10).

RESULTS

Mean values and their standard errors for the analyzed traits of the two crosses are presented in Table 1. Parents used in this research showed difference in all the characters studied in both crosses, except for the grain weight per spike of the longest culm in Soissons/Žitarka cross. Mean value of the first filial generation F_1 was between parental values for the number of grains and single grain weight in cross Soissons/Žitarka and for grain weight in cross Divana/Srpanjka. Mean values of F_1 generation lower than the parental ones were observed for the number of grains in Divana/Srpanjka and for grain weight in Soissons/Žitarka crossing combinations, while F_1 generation for single grain weight in Divana/Srpanjka cross was better than the one for both parents. Mean values of the second filial generations F_2 was between parental values for the number of grains and single grain weight in Divana/Srpanjka and for the number of grains in Soissons/Žitarka crossing combinations. For grain

TABLE 1

Generation means and standard errors for quantitative traits in two winter wheat crosses.

Generation	Trait ¹					
	NG		GW (g)		SGW (mg)	
	Crossing combinations ²					
	D/S	S/Ž	D/S	S/Ž	D/S	S/Ž
Parameter ³						
	Mean±SE	Mean±SE	Mean±SE	Mean±SE	Mean±SE	Mean±SE
P ₁	40.7±0.77	65.0±1.34	1.97±0.050	1.95±0.043	48.31±0.528	30.18±0.542
P ₂	57.7±1.74	52.0±0.97	1.60±0.049	1.96±0.050	27.92±0.488	37.63±0.626
F ₁	28.0±0.62	53.2±1.19	1.66±0.035	1.81±0.066	59.71±0.680	33.64±0.892
F ₂	46.0±0.49	62.3±0.47	2.13±0.023	2.36±0.024	46.93±0.302	37.92±0.266
Bc _{1.1} . (P ₁ xP ₁)	37.8±0.60	62.7±0.67	1.91±0.032	2.11±0.034	50.93±0.511	33.52±0.366
Bc _{1.2} . (P ₂ xP ₁)	46.7±0.82	54.9±0.79	1.90±0.031	2.07±0.043	41.63±0.650	37.70±0.450
RBc _{1.1} . (F ₁ xP ₁)	41.0±0.63	64.1±0.81	2.01±0.032	2.11±0.037	49.40±0.480	32.99±0.366
RBc _{1.2} . (F ₁ xP ₂)	40.3±0.75	57.9±0.75	1.71±0.035	2.10±0.037	43.03±0.751	36.25±0.405

¹Quantitative traits (per spike of the longest culm)-NG=number of grains, GW=grain weight, SGW=single grain weight.

²Crossing combinations-D/S=Divana/Srpanjka, S/Ž=Soissons/Žitarka

³Mean±SE (standard error)

weight in both crosses, the value of F₂ generation was better than the parental one. First and second backcrosses and reciprocal backcrosses showed differences due to parental participation in particular cross. The differences among analyzed generations were sufficient to perform generation mean analysis.

The results of generation mean analysis provide estimates of the main and first order interaction gene effects (Table 2). Digenic epistatic model was adequate to ex-

plain variation in generation means for single grain weight in Divana/Srpanjka and for grain weight per spike of the longest culm in Soissons/Žitarka crossing combinations. Additive and dominance gene effects were more important for grain weight per spike of the longest culm in Soissons/Žitarka cross, while dominance and epistatic gene effects were predominant in controlling inheritance of single grain weight in Divana/Srpanjka cross. Regarding the number of grains in both crosses, single grain

TABLE 2

The estimates of gene effects for quantitative traits in two winter wheat crosses.

Gene effects	Trait ¹					
	NG		GW (g)		SGW (mg)	
	Crossing combinations ²					
	D/S	S/Ž	D/S	S/Ž	D/S	S/Ž
Parameter ³						
	Mean±SE	Mean±SE	Mean±SE	Mean±SE	Mean±SE	Mean±SE
m	31.07±3.39**	65.48±9.47**	3.075±0.401**	2.80±0.41**	59.56±5.56**	44.55±4.68**
a	-8.49±0.95**	6.51±0.82**	0.187±0.035**	1.02±0.28**	10.19±0.36**	-3.73±0.41**
d	25.81±17.99 ^{ns}	-3.85±3.10 ^{ns}	-2.029±0.820*	0.98±0.17**	-32.25±11.18**	-16.34±9.49 ^{ns}
aa	18.15±9.63 ^{ns}	-7.27±9.21 ^{ns}	-1.287±0.399**	0.65±0.23**	-21.44±5.53**	-10.64±4.70*
ad	9.24±2.38**	0.64±2.24 ^{ns}	-0.076±0.096 ^{ns}	0.05±0.11 ^{ns}	-4.61±1.41**	0.19±1.15 ^{ns}
dd	-28.78±8.98**	-8.70±9.16 ^{ns}	0.620±0.426 ^{ns}	0.02±0.16 ^{ns}	32.40±5.82**	5.43±5.13 ^{ns}
χ ² (df) ⁴	45.28** (2)	39.83** (2)	21.34** (2)	5.34 ^{ns} (2)	4.68 ^{ns} (2)	22.79** (2)
Type of epistasis	-	-	-	-	duplicate	-

¹Quantitative traits (per spike of the longest culm)-NG=number of grains, GW=grain weight, SGW=single grain weight.

²Crossing combinations-D/S=Divana/Srpanjka, S/Ž=Soissons/Žitarka

³Mean±SE (standard error)

⁴df=degrees of freedom, calculated as the number of generations minus the number of estimated genetic parameters.

*, ** – significant at the levels of probability p=0.95 and p=0.99.

TABLE 3

The estimates of variance components and heritability for quantitative traits in two winter wheat crosses.

Generation	Trait ¹					
	NG		GW (g)		SGW (mg)	
	Crossing combinations ²					
	D/S	S/Ž	D/S	S/Ž	D/S	S/Ž
V _E	70.613	70.071	0.110	0.138	19.660	23.015
V _A	102.396	43.457	0.195	0.194	17.491	26.742
V _D	59.553	4.019	0.062	0.036	0	15.139
V _{AD}	10.685	5.266	0.017	0	21.548	0
V _G	172.636	52.741	0.274	0.230	39.039	41.881
V _P	243.250	122.812	0.385	0.369	58.699	64.896
h ² _b	0.709	0.429	0.712	0.624	0.665	0.645
h ² _n	0.420	0.353	0.507	0.526	0.297	0.412

¹Quantitative traits (per spike of the longest culm)-NG=number of grains, GW=grain weight, SGW=single grain weight.

²Crossing combinations-D/S=Divana/Srpanjka, S/Ž=Soissons/Žitarka

weight in Soissons/Žitarka and grain weight per spike in Divana/Srpanjka crossing combinations, digenic epistatic model failed to explain variation in generation means.

The estimation of genetic variance component (V_G) vs. environmental variance component (V_E) yielded higher values for all the analyzed traits except for the number of grains in Soissons/Žitarka cross. Higher additive variance component (V_A) was estimated for grain weight in both crosses, for single grain weight in Soissons/Žitarka and for the number of grains in Divana/Srpanjka crossing combinations. In accordance with these results, estimated values of narrow-sense heritability (h²_n) for grain weight in both crosses (0.507–0.526), for the number of grains in cross Divana/Srpanjka (0.42) and single grain weight in Soissons/Žitarka crossing combinations (0.412) were higher than those for single grain weight in Divana/Srpanjka (0.297) and the number of grains in Soissons/Žitarka (0.353) crosses.

DISCUSSION

Although varying depending on the cross and a trait, in most cases the variation in the generation means did not fit a simple epistatic model, which indicated that improvement of traits studied would be more difficult as compared to the situation pertaining to more simple models of inheritance (additive-dominance and digenic epistatic model). These results are in accordance with reports published by other authors (11, 12). For the number of grains per spike in both crosses, for grain number per spike in the cross Divana/Srpanjka, and single grain weight in the cross Soissons/Žitarka none of the models explained variation between generations, thus indicating more complex mechanisms of genetic control. Such a situation is the least favorable from a breeder's point of view, suggesting that revised breeding strategy is needed due to complexity of gene effects occurring in these generations (13, 14, 15, 16). To identify whether a cause of

the model failure is presence of higher order interactions or linkage, effects there should be enough generations to fit full trigenic interaction and linkage model.

Variation in generation means fitted a digenic epistatic model for single grain weight in the cross Divana/Srpanjka and grain weight per spike in the cross Soissons/Žitarka, which indicated that improvement of these traits would be moderately difficult.

In respect to epistatic effects, additive*additive effects were more important as compared to others and only duplicate epistasis was observed for single grain weight in the cross Divana/Srpanjka.

Snape (17) pointed out that a very common situation, when analyzing yield and yield components, is to find that the additive effect is slight and non-significant while the dominance estimate is large and highly significant. Estimates of slight additive effects are possible due to high degree of dispersion of increasing alleles between parents. Similarly, dominance could be small due to its ambidirectional nature. This might explain why additive genetic component of variance (V_A) varied to a great extent. On the other hand, negative and non-significant estimates of dominance variance (V_D) could be due to micro-environmental variation, sampling errors and/or the fact that basic generations are inefficient for determining dominance variance.

The estimated values of narrow-sense heritability (h²_n) varied for the number of grains per spike (0.353–0.42), grain weight per spike (0.507–0.526) and single grain weight (0.297–0.412) depending on crossing combination. These heritability values are in accordance with those reported by other authors (18, 19).

In accordance with initial expectations of this research, in their future phases the best populations in segregation generations according to analyzed grain yield components and other important agronomic traits will

be selected and included in comparative field trials. The high yielding breeding lines then will be subjected to quality analysis according to indirect and rheological quality parameters as well as through determination and quantification of high-molecular-weight glutenin subunits in their genetic composition.

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