Research Article

Quantitative inheritance of some wheat plant traits

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Abstract

The objective of this study was to estimate gene effects and genetic variability for some quantitative traits of two winter wheat crosses (Soissons/Zitarka and Soissons/Sana) by generation mean analysis. In most cases a digenic epistatic model was sufficient to explain variation in generation means. The additive-dominance model was adequate for plant height and grain weight per spike of the longest culm. In two cases (grain yield per plant and single grain weight) these models failed to explain variation in generation means, implying the presence of higher order interactions or interactions between linked loci. Dominance effects and additive x additive epistasis were more important than additive effects and other epistatic components. Only complementary type epistasis was observed. The estimated values of narrow-sense heritability (h^2_n) varied for plant height (54-81%), number of heads per plant (9-76%), number of grains per spike (11-99.8%), grain weight per spike (23-73%), grain yield per plant (21-78%) and single grain weight (49.7-72%). The adequacy of certain modes of inheritance as well as the importance and significance of gene effects and genetic components of variance for analyzed traits were dependent upon the particular crossing combination and experimental site.

Key words: wheat, quantitative traits, joint scaling test, gene effects, heritability.

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Introduction

Grain yield is a complex trait made up of the interaction between different yield components and environmental effects. Because of these complex interactions it is difficult to improve yield through breeding (especially in the early generations) if yield is the only factor recorded, suggesting that component traits should also be used as selection criteria for yield improvement. This is the reason why it is necessary to know the genetic architecture of yield components (Misra *et al*., 1994). Generation mean analysis is a simple but useful technique for estimating gene effects for a polygenic trait, its greatest merit lying in the ability to estimate epistatic gene effects such as additive x additive (aa), dominance x dominance (dd) and additive x dominance (ad) effects (Singh and Singh, 1992).

Besides gene effects, breeders would also like to know how much of the variation in a crop is genetic and to what extent this variation is heritable, because efficiency of selection mainly depends on additive genetic variance, influence of the environment and interaction between genotype and environment.

The research reported in this paper was carried out to provide information about gene effects and available genetic variability for the most important quantitative traits of winter wheat (*Triticum aestivum L.*).

Material and Methods

We used winter wheat (*Triticum aestivum L.*), the female parent used in the crosses being cultivar (cv.) Soissons (bred by Desprez, Veuve et Fils, France) and the male parent cv. Sana (bred by the Bc Institute for Plant Breeding and Seed Production, Zagreb, Croatia) and cv. Zitarka (bred by the Agricultural Institute, Osijek, Croatia).

The six basic generations (parent cultivars (P_1, P_2), first and second filial generations (F_1, F_2), first and second backcrosses (BC_1, BC_2)) of two combinations of crossings (Soissons/Zitarka and Soissons/Sana) were planted in a randomized block design in two replicate plots at two sites (Osijek and Nova Gradiska, Croatia) during the autumn season of 1999/2000. The experimental field layout was rectangular at the Osijek site and square at the Nova Gradiska site. The plots were 1 m long with a between-row spacing of 20 cm and a within-row spacing of 10 cm. The number of rows per plot and the number of analyzed plants per plot varied depending on the generation.

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The traits assessed were: plant height (cm); number of heads per plant; number of grains per spike of the longest culm; grain weight per spike of the longest culm (g); grain yield per plant (g) and single grain weight (mg), *i.e.* grain weight per spike of the longest culm divided by the number of grains on that particular spike.

The mean values, standard errors and variances of the different generations were subjected to weighted least squares analysis using the joint scaling test (Mather and Jinks, 1982) to estimate gene effects and the maximum likelihood method (Hayman, 1960) to estimate variance components to fit models of increasing complexity until an adequate description of the observed means were found as shown by non-significance in the χ^2 test. The significance of genetic parameters was tested by t-test.

The type of epistasis was determined only when dominance (d) and dominance x dominance (dd) effects were significant, when these effects had the same sign the effects were complementary while different signs indicated duplicate epistasis (Kearsey and Pooni, 1996).

Homogeneity of variances of non-segregating generations was tested for using Bartlett's test (Bartlett, 1937), and when the variances were heterogeneous the environmental variance (V_E) was replaced by an adequate number of separate parameters in the model fitting and pooled to produce a single environmental variance. Additive, dominance and environmental variance components were estimated using the maximum likelihood method with the observed variances of the six basic generations being used as the initial weights ($df/2*s^2 + 2$) until the χ^2 test values reached a minimum (Lynch and Walsh, 1998).

Narrow-sense heritability (h^2_n) was calculated as follows:

$h^2_n = V*_A/V*_A + V*_D + V_E$, where $V*_A = 0.5*a^2_A$ is the additive genetic component of variance, $V*_D = 0.25*d^2_A$ the dominance or non-additive genetic component of variance and V_E the environmental variance (Kearsey and Pooni, 1996). The $V*_D$ value was set to zero when estimated variance turned out to be a negative.

All statistical analyses were carried out using the STAT module and PROC REG procedure of the SAS software (SAS Institute, 1996).

Results

The mean values, their standard errors and variances for the analyzed traits of the two crosses at the two sites are presented in Tables 1 and 2. The parents of the Soissons/Zitarka cross differed in respect to the number of heads per plant, grain yield per plant and single grain weight at both sites, although for the F_1 generation only the means for the number of grains and grain weight per spike of the longest culm and single grain weight were greater than the better parent, and this occurred only at the Nova Gradiska site. For the other traits, differences were not so conspicuous

Table 1 - Quantitative trait data for the Soissons/Zitarka cross at the Osijek and Nova Gradiska sites.

Generation[1]	Osijek site Mean ± SE[2]	Variance	Nova Gradiska site Mean ± SE	Variance
Plant height (cm)				
P_1	64.3 ± 0.69	30.47	75.3 ± 0.29	5.80
P_2	65.0 ± 0.58	22.88	68.4 ± 0.36	8.68
F_1	63.9 ± 0.78	42.59	70.7 ± 0.54	28.58
F_2	70.0 ± 0.44	75.31	73.6 ± 0.38	48.95
BC_1	64.0 ± 0.88	49.28	72.1 ± 0.52	23.79
BC_2	67.1 ± 0.60	31.32	71.6 ± 0.50	23.25
Number of heads per plant				
P_1	11.0 ± 0.34	7.39	9.0 ± 0.25	4.31
P_2	7.6 ± 0.23	3.59	6.9 ± 0.21	2.95
F_1	8.6 ± 0.35	8.58	6.8 ± 0.23	5.18
F_2	10.8 ± 0.21	17.15	7.0 ± 0.11	4.10
BC_1	9.0 ± 0.28	6.04	7.6 ± 0.19	3.18
BC_2	8.5 ± 0.24	5.01	7.9 ± 0.24	5.36
Number of grains per spike of the longest culm				
P_1	58.5 ± 1.23	96.83	53.8 ± 0.89	54.65
P_2	58.3 ± 0.92	57.56	52.1 ± 0.91	55.48
F_1	55.4 ± 1.09	83.17	55.9 ± 1.05	108.05
F_2	58.7 ± 0.70	190.61	52.5 ± 0.59	118.00
BC_1	61.1 ± 1.31	132.14	53.1 ± 1.12	110.39
BC_2	60.4 ± 0.93	75.25	53.6 ± 0.96	85.71
Grain weight per spike of the longest culm (g)				
P_1	2.55 ± 0.06	36.97	2.18 ± 0.04	0.11
P_2	2.72 ± 0.05	6.54	2.20 ± 0.04	0.11
F_1	2.47 ± 0.06	24.37	2.42 ± 0.05	0.25
F_2	2.61 ± 0.04	130.86	2.26 ± 0.03	0.31
BC_1	2.61 ± 0.06	43.31	2.23 ± 0.05	0.22
BC_2	2.80 ± 0.05	29.27	2.22 ± 0.04	0.15
Grain yield per plant (g)				
P_1	20.37 ± 0.83	44.09	17.88 ± 0.60	24.84
P_2	14.36 ± 0.53	19.10	10.97 ± 0.39	10.19
F_1	16.76 ± 0.83	48.22	13.57 ± 0.54	28.58
F_2	20.96 ± 0.52	105.19	13.42 ± 0.26	22.92
BC_1	15.89 ± 0.66	33.54	14.37 ± 0.51	22.89
BC_2	17.68 ± 0.63	34.53	13.75 ± 0.44	18.00
Single grain weight (mg)				
P_1	43.55 ± 0.49	15.37	40.56 ± 0.35	8.45
P_2	46.63 ± 0.43	12.57	42.23 ± 0.34	7.75
F_1	44.51 ± 0.52	18.93	43.25 ± 0.33	10.67
F_2	44.16 ± 0.30	35.01	43.12 ± 0.23	17.93
BC_1	42.68 ± 0.46	16.29	42.15 ± 0.41	14.79
BC_2	46.26 ± 0.40	13.92	41.53 ± 0.38	13.43

[1]P_1, P_2 = parent cultivars; F_1, F_2 = first and second filial generations; BC_1, BC_2 = first and second backcrosses.
[2]SE = standard error.

Table 2 - Quantitative trait data for the Soissons/Sana cross at the Osijek and Nova Gradiska sites.

Generation[1]	Osijek site Mean ± SE[2]	Variance	Nova Gradiska site Mean ± SE	Variance
Plant height (cm)				
P_1	73.1 ± 0.55	22.69	73.8 ± 0.33	8.28
P_2	67.0 ± 0.54	15.45	65.1 ± 0.50	15.50
F_1	73.0 ± 1.13	79.17	75.3 ± 0.60	28.80
F_2	78.1 ± 0.41	57.99	73.3 ± 0.45	66.62
BC_1	76.0 ± 0.46	19.04	75.1 ± 0.46	13.75
BC_2	70.9 ± 0.62	30.37	71.2 ± 0.61	29.39
Number of heads per plant				
P_1	9.5 ± 0.27	5.47	7.9 ± 0.24	4.38
P_2	8.4 ± 0.27	3.86	7.5 ± 0.26	4.19
F_1	10.4 ± 0.46	13.12	7.9 ± 0.21	3.53
F_2	8.8 ± 0.14	6.76	7.4 ± 0.15	7.40
BC_1	9.4 ± 0.23	4.76	7.9 ± 0.26	4.39
BC_2	8.3 ± 0.25	4.94	8.1 ± 0.23	4.18
Number of grains per spike of the longest culm				
P_1	58.8 ± 0.98	72.03	55.8 ± 1.11	93.64
P_2	61.5 ± 1.37	99.48	58.1 ± 1.51	141.37
F_1	60.9 ± 1.30	104.78	55.7 ± 1.05	88.20
F_2	54.2 ± 0.75	194.06	50.8 ± 0.76	190.03
BC_1	58.5 ± 0.95	81.23	54.7 ± 1.09	77.23
BC_2	61.0 ± 1.15	104.48	57.8 ± 1.34	141.85
Grain weight per spike of the longest culm (g)				
P_1	2.48 ± 0.05	0.19	2.29 ± 0.05	0.19
P_2	2.88 ± 0.08	0.34	2.18 ± 0.06	0.22
F_1	2.88 ± 0.09	0.50	2.40 ± 0.04	0.13
F_2	2.38 ± 0.04	0.55	2.14 ± 0.04	0.53
BC_1	2.58 ± 0.05	0.23	2.45 ± 0.05	0.16
BC_2	2.64 ± 0.06	0.28	2.35 ± 0.05	0.20
Grain yield per plant (g)				
P_1	16.92 ± 0.62	28.83	15.24 ± 0.58	25.57
P_2	19.19 ± 0.77	31.42	12.99 ± 0.48	14.28
F_1	23.01 ± 1.44	128.56	16.53 ± 0.57	25.99
F_2	16.90 ± 0.38	49.82	13.78 ± 0.32	33.69
BC_1	18.62 ± 0.57	29.24	15.42 ± 0.60	23.40
BC_2	17.66 ± 0.60	28.44	15.49 ± 0.52	21.36
Single grain weight (mg)				
P_1	42.09 ± 0.38	10.83	41.14 ± 0.29	6.39
P_2	46.69 ± 0.45	10.73	37.60 ± 0.43	11.46
F_1	47.04 ± 0.72	32.14	43.14 ± 0.30	7.20
F_2	43.63 ± 0.33	37.57	42.0 ± 0.28	25.79
BC_1	43.96 ± 0.36	11.66	44.91 ± 0.44	12.58
BC_2	43.38 ± 0.58	26.58	40.99 ± 0.46	16.72

[1]P_1, P_2 = parent cultivars; F_1, F_2 = first and second filial generations; BC_1, BC_2 = first and second backcrosses.
[2]SE = standard error.

and consistent. The observed variances were lower at the Nova Gradiska site for all analyzed traits (Table 1). For the Soissons/Sana cross, at both sites, parents differed in respect of plant height and number of grains per spike of the longest culm but, depending on the site, differences between these parents were inconsistent for grain weight per spike of the longest culm, grain yield per plant and single grain weight. For the number of heads per plant differences were not so conspicuous at either site. At both sites the mean grain yield per plant and single grain weight of the F_1 generation of this cross was greater than that of the better parent, but the means for plant height and grain weight per spike of the longest culm of the F_1 generation were greater than the corresponding means for the parents only at the Nova Gradiska site, while the mean number of heads per plant was greater for the F_1 generation only at the Osijek site. The variances were lower at the Nova Gradiska site for all the analyzed traits except number of grains per spike of the longest culm where the differences were not so consistent (Table 2).

The estimates of the main and first order interaction gene effects and χ^2 values are presented in Table 3.

For plant height, an additive-dominance model was adequate only for the Soissons/Sana cross at the Nova Gradiska site, while a digenic epistatic model was adequate for the Soissons/Sana cross at the Osijek site and the Soissons/Zitarka cross at both sites (non-significant χ^2 test), with dominance effects and additive x additive epistasis being more important than other genetic effects and complementary epistasis being found only in the Soissons/Sana cross at the Osijek site. For the number of heads per plant and the number of grains per spike of the longest culm the digenic epistatic model was adequate for both crosses and for both sites, with dominance effects and dominance x dominance epistasis, when present, being more important as compared to other genetic effects. Except for the Soissons/Sana cross at the Osijek site, both crosses showed complementary epistasis for the number of heads per plant. For the number of grains per spike of the longest culm complementary epistasis was only found in the cross Soissons/Sana at the Osijek site. For grain weight per spike of the longest culm, an additive-dominance model adequately explained variation between generations of the Soissons/Zitarka cross, while a digenic epistatic model was applicable to the Soissons/Sana cross at both sites, although complementary epistasis was found only in the Soissons/Sana cross at the Nova Gradiska site. For grain yield per plant, both models failed to explain variation between generations (significant χ^2 test) for the Soissons/Zitarka cross at the Osijek site, with all three epistasis components being significant and both negative and complementary epistasis also being found. However, at the Nova Gradiska site a digenic epistatic model adequately explained variation between the Soissons/Zitarka cross generations regarding

grain yield per plant, although only additive effects were significant.

For the Soissons/Sana cross, grain yield per plant was adequately explained by a digenic epistatic model with dominance effects and additive x additive epistasis being most important. For single grain weight, the digenic epistatic model was satisfactory for the Soissons/Zitarka and Soissons/Sana crosses at the Osijek site, although both the additive-dominance model and the digenic epistatic model failed to explain variation in single grain weight in the Soissons/Sana cross at the Nova Gradiska site where all three epistasis components were significant and positive. Complementary type of epistasis was only found in the Soissons/Zitarka cross at the Nova Gradiska site (Table 3).

The estimates of the different variance components and narrow-sense heritability (h^2_n) are presented in Table 4. Maximum likelihood estimates of environmental variance were higher at the Osijek site than the Nova Gradiska site for all traits and crosses except the number of grains per spike of the longest culm for the Soissons/Zitarka cross.

Table 3 - The estimates of gene effects for six quantitative traits in two crossing combinations and sites.

Trait	Cross	Site	m	a	d	aa	dd	ad	χ^2 (df)[1]	Type of epistasis
Plant height (cm)	Soissons/ Zitarka	Osijek	76.0***	0.39	-12.7***	-11.5***	-5.3	-	3.76 (1)	-
		Nova Gradiska	78.7***	3.2	-8.0***	-6.8***	-4.2	-	3.64 (1)	-
	Soissons/ Sana	Osijek	87.5***	3.5	-14.5***	-17.5***	-8.8*	-	1.72 (1)	Complementary
		Nova Gradiska	69.7***	4.3	6.4***	-	-	-	3.59 (3)	-
Number of heads per plant	Soissons/ Zitarka	Osijek	17.2***	1.43***	-8.6***	-8.0***	-8.4***	-	0.63 (1)	Complementary
		Nova Gradiska	5.0***	0.73***	1.8*	2.9***	4.3**	-	0.77 (1)	Complementary
	Soissons/ Sana	Osijek	7.5***	0.65***	2.5**	1.4*	-	-	5.33 (2)	-
		Nova Gradiska	5.0***	0.13	2.87**	2.67**	3.62*	-	0.06 (1)	Complementary
Number of grains per spike of the longest culm	Soissons/ Zitarka	Osijek	50.6***	0.19	4.8	7.8	22.5**	-	0.17 (1)	-
		Nova Gradiska	49.1***	0.62	6.75***	3.81*	-	-	0.67 (2)	-
	Soissons/ Sana	Osijek	47.9***	1.6*	14.2***	12.8***	10.9***	-	6.98 (2)	Complementary
		Nova Gradiska	46.7***	1.6	9.7***	10.9***	-	-	7.13 (2)	-
Grain weight per spike of the longest culm	Soissons/ Zitarka	Osijek	2.7***	0.11**	-0.11	-	-	-	9.9 (3)	-
		Nova Gradiska	2.2***	0.01	0.19***	-	-	-	3.72 (3)	-
	Soissons/ Sana	Osijek	1.9***	0.17***	1.04***	0.81***	-	-	3.16 (2)	-
		Nova Gradiska	1.2***	0.07*	1.2***	1.1***	1.4***	-	0.001 (1)	Complementary
Grain yield per plant (g)	Soissons/ Zitarka	Osijek	34.1***	3.0***	-7.7	-16.7***	-37.0***	-9.6***	(0) **	Complementary
		Nova Gradiska	11.0***	2.8***	2.6	3.2	4.6	-	3.39 (1)	-
	Soissons/ Sana	Osijek	11.3***	0.58	10.9***	6.5***	-	-	5.44 (2)	-
		Nova Gradiska	11.2***	0.89**	5.8***	3.1**	-	-	6.33 (2)	-
Single grain weight (mg)	Soissons/ Zitarka	Osijek	43.8***	1.99***	0.74	1.2	-	-	8.71 (2)	-
		Nova Gradiska	46.8***	0.6**	-3.5*	-5.4***	-7.6**	-	0.86 (1)	Complementary
	Soissons/ Sana	Osijek	42.0***	1.8***	5.0*	2.3	-3.6	-	3.97 (1)	-
		Nova Gradiska	35.6***	1.8**	3.3	3.8*	19.2**	4.3*	(0) **	-

[1]df = degrees of freedom, calculated as the number of generations minus the number of estimated genetic parameters.
* = statistically significant at p = 0.95.
** = statistically significant at p = 0.99.
*** = statistically significant at p = 0.999.

Table 4 - Estimation of variance components and narrow-sense heritability (h^2_n) for some quantitative traits of the Soissons/Zitarka and Soissons/Sana crosses at the Osijek and Nova Gradiska sites.

	Quantitative trait data			
	Soissons/Zitarka cross		Soissons/Sana cross	
Variance components	Osijek site	Nova Gradiska site	Osijek site	Nova Gradiska site
Plant height (cm)				
Phenotypic variance	93.67	66.09	107.83	108.5
Environmental variance	36.47	18.06	49.53	20.1
Additive variance	57.2*	48.03	58.3	88.4
Dominance variance	-17.8	-16.6	-49.1	-42.7
χ^2 (df) [1]	0.075 (3) ns [2]	2.89 (3) ns	1.828 (3) ns	15.47 (3) s [3]
Heritability (h^2_n) (%)	61	73	54	81
Number of heads per plant				
Phenotypic variance	28.4	5.24	11.43	9.38
Environmental variance	6.78	4.76	9.29	3.962
Additive variance	21.6	0.48	2.137	5.42
Dominance variance	-12.6	-0.494	-3.91	-2.437
χ^2 (df)	0.296 (3) ns	0.0684 (3) ns	1.518 (3) ns	1.344 (3) ns
Heritability (h^2_n) (%)	76	9	19	58
Number of grains per spike of the longest culm				
Phenotypic variance	258.8	118.73	288.5	165.05
Environmental variance	79.43	81.65	90.5	0.252
Additive variance	179.4*	13.22	198.1*	164.8
Dominance variance	-65.6	23.88*	-96.7	-78.9
χ^2 (df)	0.147 (3) ns	0.0058 (3) ns	2.703 (3) ns	1.9395 (3) ns
Heritability (h^2_n) (%)	69	11	69	99.8
Grain weight per spike of the longest culm (g)				
Phenotypic variance	0.843	0.2465	1.11	0.642
Environmental variance	0.232	0.1843	0.564	0.172
Additive variance	0.611	0.056	0.55*	0.47*
Dominance variance	-0.264	0.006	-0.372	-0.218
χ^2 (df)	2.534 (3) ns	0.117 (3) ns	0.0274 (3) ns	1.096 (3) ns
Heritability (h^2_n) (%)	72	23	49	73
Grain yield per plant (g)				
Phenotypic variance	179.7	28.7	103.28	45
Environmental variance	39.36	22.92	78.67	20.12
Additive variance	140.3*	5.79	24.61	24.88*
Dominance variance	-75.3*	-5.72	-54.48	-13.19*
χ^2 (df)	0.1689 (3) ns	0.569 (3) ns	0.127 (3) ns	0.01 (3) ns
Heritability (h^2_n) (%)	78	21	24	55
Single grain weight (mg)				
Phenotypic variance	55.25	18.71	54.85	39.15
Environmental variance	15.66	9.11	21.45	16.66
Additive variance	39.59*	9.3	33.4*	22.49
Dominance variance	-20.1	0.3	-16.6*	-4.492
χ^2 (df)	2.934 (3) ns	1.863 (3) ns	0.0125 (3) ns	0.1398 (3) ns
Heritability (h^2_n) (%)	72	49.7	61	57

[1]df = degrees of freedom, calculated as the number of generations minus the number of estimated variance parameters.
[2]ns = non-significant χ^2 test.
[3]s = significant χ^2 test.
* = statistically significant at p = 0.95.

The additive and dominance variance components estimates were inconsistent between crosses and across the testing sites. The values of narrow-sense heritability (h^2_n) varied depending on the testing site, crossing combination and trait analyzed. For the Soissons/Sana cross higher h^2_n values were observed for all traits (except for single grain weight) at the Nova Gradiska site, while for the Soissons/Zitarka cross higher values were found for all traits (except for plant height) at the Osijek site. The h^2_n values for the Soissons/Zitarka cross were highest for plant height, single grain weight and grain yield per plant, whilst for the Soissons/Sana cross the h^2_n values were highest for the

number of grains per spike of the longest culm, plant height and grain weight per spike of the longest culm.

Discussion

Although varying depending on the cross, experimental site and trait, in most cases the variation in the generation means fitted a digenic epistatic model which indicated that improvement of the traits studied would be moderately difficulty as compared to the situation pertaining had an additive-dominance model (best from a breeders point of view) provided the best fit. These findings correspond with the results published by some other authors (Pawar *et al*., 1988; Singh and Singh, 1992; Misra *et al*., 1994; Singh *et al*., 1998) but not with those reported by Sawant and Jain (1985). This situation is even more complicated when dominance effects are more important than additive effects, as was the case in this experiment.

For grain yield per plant in the Soissons/Zitarka cross at the Osijek site and single grain weight in the Soissons/Sana cross at the Nova Gradiska site none of the models explained variation between generations, indicating more complex mechanisms of genetic control. Such a situation is the least favorable from a breeders point of view, suggesting that a revised selection strategy is needed for the early generations due to complexity of the gene effects occurring in these generations. These results are in accordance with reports published by other authors (*e.g.* Chatrtah *et al*., 1986; Srivastava *et al*., 1992; Amawate and Behl, 1995, Kathiria and Sharma, 1996).

To identify whether a cause of the model failure is the presence of higher order interactions or linkage effects there further analyses needs to be carried out with enough generations to fit a full trigenic interaction and linkage model. In respect of epistatic effects, additive x additive effects were more important than dominant x dominant effects and only complementary epistasis was observed.

This situation is more favorable than the presence of dominant x dominant effects and/or duplicate epistasis due to a greater chance of breeding success, and partially explains why heterosis was not as frequent as might be expected from the fact that dominance effects were more important than additive effects. Snape (1987) pointed out that a very common situation, especially when analyzing yield and yield components, is to find that the additive effect is small and non-significant while the dominance estimate is large and highly significant. Estimates of additive effects can be small due to a high degree of dispersion of increasing alleles between parents, and dominance can be small due to its bi-directional nature. This might explain why additive genetic component of variance (V_A^*) varied greatly, although a clear-cut relationship between additive effects and additive genetic variance could not be detected. On the other hand, the negative and non-significant estimates of dominance variance (V_D^*) seen in our study could have been due to sampling errors and/or the fact that basic

generations are inefficient when used for determining dominance variance.

The estimated values of narrow-sense heritability (h_n^2) varied for plant height (54-81%), number of heads per plant (9-76%), number of grains per spike of the longest culm (11-99.8%), grain weight per spike of the longest culm (23-73%), grain yield per plant (21-78%) and single grain weight (49.7-72%) depending on the crossing combination and testing site. These heritability values are in accordance with those reported by other authors (Sidwell, 1978; Baric, 1996 and Drezner, 1996).

From a breeders point of view, the heritability estimates from both sites show that the Soissons/Zitarka cross has the greatest chance of genetic improvement in the number of heads per plant, grain yield per plant and single grain weight, while the Soissons/Sana cross has the greatest chance of increase in the number of grains per spike and grain weight per spike of the longest culm. The higher h_n^2 values found at the Osijek site can be partially explained by the fact that the experimental field layout was rectangular at the Osijek site and square at the Nova Gradiska site. The estimates of heritability suggest that it would be better to breed the Soissons/Zitarka cross at the Osijek site and the Soissons/Sana cross at the Nova Gradiska site, suggesting that success in a breeding program could be under the influence of environment, even as regards specific genetic effects. These results show that both the adequacy of certain modes of inheritance as well as the importance and significance of gene effects for a certain trait were dependent upon the particular cross and experimental site, stressing the importance of the appropriate selection of both parents and breeding site for the success of a program.

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