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Gene Effects on Yield and Quality Traits in Two Bread Wheat (T.

aestivum L.) Crosses

Oğuz Bilgin¹ İmren Kutlu^{*2} Alpay BALKAN¹

¹ Namık Kemal University Agricultural Faculty, Field Crops Department, Tekirdag-Turkey ² Eskisehir Osmangazi University Agricultural Faculty, Field Crops Department, Eskisehir-Turkey

* Corresponding author: *ikutlu@ogu.edu.tr* or *imrenkutlu@hotmail.com*

ABSTRACT

The aim of this study was to investigate gene effects and genetic variability by generation mean analysis for some yield and quality traits in two winter wheat crosses (Pehlivan × Bezostaja and Sana × Krasunia). The parents and F_1 , F_2 , BC₁, and BC₂ populations were grown in a randomized complete block design with three replications during the 2008-2009 crop seasons. A three parameter model was not sufficient to explain variation for most traits in generation means. The additive-dominance model was adequate for plant height, grain number per spike and grain weight per spike in the Pehlivan × Bezostaja-1 cross, and for grain weight per spike and all quality traits in the Sana × Krasunia cross. The scaling test revealed that epistasis had a predominant role in the expression of all traits except grain yield, protein content and gluten index in the Pehlivan × Bezostaja-1 cross, and spike length and grain yield in the Sana × Krasunia cross. Dominance effects and dominance × dominance epistasis were more important than additive effects and other epistatic components. All traits which had significant epistatic gene effects showed duplicate type epistasis. Therefore, early generation selection would fail.

Key words: Epistatisis, generation mean analysis, six parameter model, three parameter model, gene effects, bread wheat.

INTRODUCTION

Bread wheat is the most important and widely consumed food cereal of Turkey as well as the world. Although its acreage and production is high, the low yield of wheat per hectare is a serious problem. To increase the yield of wheat, improvements in high yielding and high quality varieties well as improvements in cultural as techniques are of great importance. High grain yield and grain protein content are basic criterions of selection in wheat breeding (Cho et al., 2001). In addition, the inverse relationship between wheat yield and grain protein content is well known (Entz and Fowler, 1989; Pleijel et al., 1999). However, grain yield and quality in wheat are due to interaction of many genes with environment; thus, direct selection for them will not be successful. To increase yield, it is necessary to improve agronomic traits that affect grain yield but, in order to achieve this, more information on the inheritance patterns of these traits is necessary (Singh et al., 1986). There are

different analysis methods to estimate genetic basis of quantitative variability of selected yield components. Among these, generation mean analysis allows breeders to predict epistasis. It has been reported that epistatic gene action is a nontrivial factor in the inheritance of investigated vield components (Goldringer et al., 1997). 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 \times additive, dominance \times dominance and additive \times dominance effects. Since genetic information obtained from multiple generations is more reliable than that based on one generation, six populations (P_1, P_2, P_3) F_1 , F_2 , BC_1 and BC_2) from different generations were considered sufficient to give detailed genetic information for the employed genotypes (Singh and Singh, 1992).

This study was carried out to investigate heritability of yield and quality components and to determine appropriate selection methods based on gene effects for two populations obtained from crossing four bread wheat cultivars.

MATERIALS AND METHODS

This study was carried out in the experimental area of Faculty of Agriculture, Namık Kemal University, Tekirdag. Turkey. Tekirdag lies at latitude 40° 36'-40° 31' and longitude 26° 43'-28° 08' and altitude 10 m. Total annual precipitation was 369.1 mm and mean temperature 11.7°C, which were more than the long year average (521.2 mm and 11.9 °C) of the site. The soil was loam and non-calcareous, with pH 5.6 and organic matter contents of 0.7%. P₁, P₂, F₁, F₂, BC₁, and BC₂ generations of Pehlivan \times Bezostaja-1 and Sana \times Krasunia crosses were used as genetic materials. Parental cultivars were selected for their differences in end-use quality (Bezostaja-1 and Krasunia) and grain yield (Pehlivan and Sana). The parents and F_1 , F_2 , BC_1 , and BC_2 populations were grown in a randomized complete block design with three replications during the 2008-2009 crop seasons. Plots consisted of 2 rows 5 m long and 400 seeds placed in each row. Fertilization (14 kg N da⁻¹ and, 5 kg $P_2O_5da^{-1}$) and other standard cultural practices were carried out. Ten plants selected randomly from each parent, backcross (BC₁ and BC₂), F_1 and F_2 generation were measured for plant height (cm), spike length (cm), grain number per spike (number), and grain weight per spike (g). In addition, grain yield per plot (g/m^2) and quality components (protein content (%), gluten content (%), gluten index (%), SDS sedimentation (ml), gluten/protein ratio and sedimentation/protein ratio) were analyzed.

Analysis of variance was performed using the TARIST statistical program to assess significant differences among genotypes, and the least significant difference test (LSD) was used to compare the generation mean values (Acıkgoz et al., 1994). Differences between parental genotypes were first analysed by applied "t" test for the studied traits before considering the biometrical analysis; the scaling tests (A, B, C and D) were applied to detect the presence of epistasis according to Mather and Jinks (1982). Generation mean analysis was applied to estimate genetic parameters of mean [m], additive [d], dominance [h], and additive-dominance [dh] gene effects for each trait, using the joint scaling test as described by Mather and Jinks (1982). Significance of the differences between expected and realized mean values for each trait of the six generations was compared to test validity of the additive-dominance model using Chi-square $(\chi 2)$ test. Where probability of the Chi-square level was less than 5%, it was accepted that the additivedominance model was inadequate to explain differences of the generation means due to the presence of epistatic effects. The six parameter method, proposed by Hayman (1958) and set out by Singh and Chaudhary (1985), was used to estimate epistatic genetic interactions and main effects. The significance of genetic parameters ([m], [a], [d], [i], [j] and [l]) were tested using a t-test. All statistical analyses were carried out using the TarPopGen Statistical Package Program developed by Ozcan (1999).

RESULTS AND DISCUSSION

Analysis of variance (Table 1) revealed significant differences in the populations for all traits in the two crosses, so the level of differences between generation means is sufficient to allow for statistical genetic analysis. In addition, results of the joint scaling test revealed the presence of nonallelic gene interaction for plant height, grain number per spike and grain weight per spike in the Pehlivan \times Bezostaja-1 cross, and grain weight per spike and all quality traits (protein content, gluten content, gluten index, gluten/protein rate, sedimentation and sedimentation/protein rate) in the Sana x Krasunia cross (Table 1).

Course	Pehlivan x Bezostaja-1											
Source	Df	PH	SL	GNS	GWS	GY	PC	GC	GI	G/P	SED	SED/P
Replication	2	1.31	0.33	19.35	0.05	588.72	0.25	21.50*	6.00	0.09	5.06	0.09
Generation	5	215.27**	1.22**	95.50*	0.26**	2181.96*	1.30*	68.27**	30.80**	0.20**	129.02**	0.42**
Error	10	10.94	0.16	25.39	0.03	548.26	0.26	3.97	2.60	0.03	17.06	0.06
Joint Cooling Test	$\chi^{2}_{(3)}$	16.64	4.20	13.44	20.98	1.11	3.17	6.57	1.75	5.09	6.60	5.09
Joint Scanng Test	Р	0.001	0.24	0.004	0.001	0.78	0.37	0.09	0.63	0.17	0.09	0.16
	А	17.27**	2.32	15.27	0.40	17.00	2.23	15.00*	-3.67	0.75*	21.00*	1.05*
Socie Test	В	10.50	1.11	-0.80	-0.15	8.67	0.27	9.00	-3.67	0.59	10.33	0.63
Scaling Test	С	-2.30	0.040	-14.67	1.54*	79.0	3.27	20.00	0.00	-0.20	24.00	0.97
	D	-15.03	-1.70*	-14.57*	0.65**	26.67	0.50	-2.00	3.67	0.95	-3.67	-0.36
Source	Sana x Krasunia											
	Df	PH	SL	GNS	GWS	GY	PC	GC	GI	G/P	SED	SED/P
Replication	2	27.77	0.18	16.22	0.01	1277.39	0.11	4.50	8.72	0.01	8.39	0.07
Generation	5	197.83**	2.79**	47.73*	0.17*	1797.92*	1.21**	64.53**	117.82**	0.43**	150.32**	0.86**
Error	10	24.53	0.36	9.99	0.04	476.32	0.12	7.03	4.26	0.06	8.26	0.09
Joint Scaling Test	$\chi^{2}_{(3)}$	3.99	2.42	3.90	19.21	2.57	10.79	11.22	30.00	8.54	10.90	8.22
	Р	0.26	0.49	0.27	0.002	0.46	0.01	0.01	0.001	0.04	0.01	0.04
	А	-18.70*	0.29	3.33	0.78	-36.33	0.69*	9.67*	-16.33*	0.65*	1.00	-0.08
Scaling Test	В	-10.67	-1.69	-8.13	-0.80*	86.00	1.63*	11.67*	9.00**	0.61	17.67 *	0.90
	С	11.17	1.48	-17.87*	0.21	-79.67	-2.70*	28.00*	14.67*	3.09*	27.33*	1.26*
	D	20.27*	1.44	-6.53	0.11**	-64.67	-3.08	3.33	20.00**	0.91	4.33	3.34*

Table 1. Mean squares and scaling test for yield and quality traits

Df: Degree of freedom, PH: plant height, SL: spike length, GNS: Grain number per spike, GWS: grain weight per spike, GY: grain yield, PC: protein content, GC: gluten content, GI: gleten index, G/P: Gluten/protein rate, SED: sedimentation, SED/P: sedimentation/protein rate.

The expectation of A, B, C and D scaling tests tend towards zero in the absence of interactions. According to some researchers, if there is a significant deviation from zero, then it is assumed that epistasis may play an important role (Mather and Jinks, 1982; Singh et al., 2014). Significance of parameters A and B indicate all non-allelic gen interactions, while significance of parameters C and D indicate dominance × dominance and additive \times additive genetic interactions, respectively (Mather and Jinks, 1982). It can be visualized from Table 1 that, for most of the characters, the additivedominance model was found inadequate. The scaling test revealed that epistasis had a predominant role in the expression of all traits except grain yield, protein content and gluten index in the Pehlivan \times Bezostaja-1 cross, and except in spike length and grain yield in the Sana \times Krasunia cross (Table 1).

The results of generation means and standard errors of the Pehlivan \times Bezostaja-1 cross showed that the Pehlivan parent had smaller values with respect to all traits studied except grain yield per parcel; the Sana parent was observed to have smaller values in terms of all traits studied except grain number per spike and grain yield per plot (g/m^2) (Table 2). Mean values of the F_1 generation lower than parental values were observed for grain number per spike and grain weight per spike in both crosses and for gluten content and gluten/protein rate in the Sana × Krasunia cross. These results indicate that there is a dominance direction of reducing these traits in these crosses (Ozberk, 1997). Because F₁ values were between the male and female parents' values, heterosis cannot be claimed for other traits except sedimentation and sedimentation/protein rate in both crosses. Mean values of the F₂ generation, compared with their parents, were higher than the highest parent for grain weight per spike, protein content. sedimentation and sedimentation/gluten rate in the Pehlivan \times Bezostaja-1 cross and for plant height, gluten index, gluten/protein rate, sedimentation and sedimentation/gluten rate in the Sana \times Krasunia cross. High mean values of the F₂ generation indicated that superior parental lines can be selected depending on transgressive segregation. When backcross generations are considered, in both crosses, values of almost all traits are between the two parents (Table 2).

The results of the three and six parameter analyses are listed in Table 3. Significant gene effects based on the joint scaling test with three parameters and six parameter models were partially different for the same traits (Table 3). This may be due to genotype × environment interaction or linkage (Sheikh et al., 2009; Tonk et al., 2011). The mean effects were highly significant for all studied traits in the two crosses. indicating these that traits are quantitatively inherited. According to the three parameter model, additive gene effect (d) was positive and significant for plant height, spike length, protein content, gluten index, and gluten/protein rate in the Pehlivan \times Bezostaja-1 cross and for plant height, spike length and gluten index in the Sana \times Krasunia cross. The magnitude of additive gene effects was small relative to the corresponding dominance effects in all cases, suggesting that pedigree selection method is a useful breeding program for improving these populations (ZaaZaa et al., 2012; Snape, 1987). Dominance gene effects were significant for gluten content in the Pehlivan \times Bezostaja-1 cross and for grain weight per spike in the Sana \times Krasunia cross. Both additive and dominance gene effects were significant for protein content, gluten content, sedimentation and sedimentation/protein rate in the Sana × Krasunia cross.

According to the six parameter model in the Pehlivan \times Bezostaja-1 cross, additive, dominance, additive \times additive

Generations	Pehlivan x Bezostaja-1											
	PH	SL	GNS	GWS	GY	PC	GC	GI	G/P	SED	SED/P	
P ₁	100.03 ± 0.50	8.83±0.22	28.87 ± 4.38	1.88 ± 0.11	246.00±19.09	11.90 ± 0.15	25.00 ± 0.58	86.67 ± 0.88	2.10 ± 0.06	33.67±2.73	2.83 ± 0.25	
P ₂	122.20 ± 2.10	10.30 ± 0.21	37.40 ± 3.81	1.90 ± 0.08	179.67±13.69	13.50 ± 0.20	36.33 ± 1.20	95.33±0.88	2.69 ± 0.12	43.67 ± 0.89	3.24 ± 0.09	
F_1	102.83 ± 2.26	9.41±0.23	22.20 ± 2.31	1.19 ± 0.21	183.67±15.34	12.87 ± 0.32	28.67 ± 1.20	91.67±0.88	2.23 ± 0.05	47.33±2.33	3.67 ± 0.09	
F ₂	106.40 ± 1.10	9.50±0.17	24.00 ± 0.46	1.93 ± 0.01	218.00 ± 7.37	13.60 ± 0.26	34.67 ± 1.86	91.33±0.88	2.55 ± 0.15	49.00±3.21	3.60 ± 0.17	
BC_1	110.07 ± 1.02	10.28 ± 0.41	33.17 ± 1.41	1.74 ± 0.08	223.33 ± 15.88	13.50 ± 0.51	34.33 ± 2.19	87.33±1.67	2.54 ± 0.11	51.00 ± 1.73	3.78 ± 0.10	
BC_2	117.77 ± 1.24	10.41 ± 0.18	29.40 ± 2.74	1.47 ± 0.06	186.00 ± 4.04	13.43 ± 0.12	37.00 ± 1.53	91.67±0.67	2.76±0.13	50.67±1.76	3.77 ± 0.10	
LSD (0.05)	8.56	1.03	9.17	0.48	42.59	0.92	5.15	4.17	0.42	10.69	0.63	
Generations	Sana x Krasunia											
	PH	SL	GNS	GWS	GY	PC	GC	GI	G/P	SED	SED/P	
P ₁	77.53±1.27	8.23±0.18	51.27 ± 1.68	2.04 ± 0.11	236.00±9.07	11.71±0.11	28.33 ± 1.20	85.67±1.20	2.42 ± 0.11	32.00 ± 1.15	2.73 ± 0.08	
P ₂	92.30±2.70	11.12 ± 0.23	46.87 ± 0.84	2.32 ± 0.06	176.33±15.43	12.57±0.29	34.33 ± 2.73	97.00 ± 0.58	$2.73{\pm}0.19$	42.67±0.33	3.40 ± 0.06	
F_1	95.90±2.61	9.57±0.27	44.07 ± 1.91	1.98 ± 0.14	199.67±4.70	12.20 ± 0.15	22.67 ± 0.33	96.00 ± 0.58	1.86 ± 0.05	44.33±3.18	3.64 ± 0.30	
F ₂	93.20±2.20	9.99±0.21	42.10 ± 1.04	2.13 ± 0.04	183.00 ± 18.58	11.40 ± 0.31	34.00 ± 1.53	97.33±0.67	2.99 ± 0.18	47.67±1.45	4.19 ± 0.19	
BC_1	77.37 ± 3.00	9.05 ± 0.54	49.33±3.17	2.40 ± 0.17	199.67±14.68	12.30 ± 0.06	30.33 ± 1.20	82.67 ± 2.67	$2.47{\pm}0.09$	38.67 ± 0.89	3.14 ± 0.06	
BC_2	88.77±4.53	9.50 ± 0.40	41.40 ± 1.94	1.75 ± 0.04	231.00±17.79	13.20 ± 0.15	34.33±0.67	92.00 ± 0.58	$2.60{\pm}~0.07$	52.33 ± 1.45	3.97 ± 0.16	
LSD (0.05)	12.81	1.54	5.75	0.36	39.70	0.90	6.86	5.34	0.61	7.43	0.75	

Table 2. Mean values of generations for yield and quality traits

PH: plant height, SL: spike length, GNS: Grain number per spike, GWS: grain weight per spike, GY: grain yield, PC: protein content, GC: gluten content, GI: gleten index, G/P: Gluten/protein rate, SED: sedimentation, SED/P: sedimentation/protein rate.

Pabliyan v Razastaja_1												
Parameter	PH	SL	GNS	GWS	GY	PC	GC	GI	G/P	SED	SED/P	
m	110.96±1.54**	9.69±0.24**	30.39±3.24**	1.99±0.11**	220.62±17.27**	12.77±0.20**	6.11±1.09**	90.59±0.98**	2.48±0.11**	41.72±2.10**	3.35±0.16**	
d	10.53±1.50**	0.78±0.24*	-4.23±3.31	-0.16±0.09	-40.05 ± 14.60	$0.78 \pm 0.20 *$	-0.27±2.28	3.97±0.98*	0.33±0.11*	2.22 ± 2.06	-0.03±0.16	
h	-1.07±3.23	0.001 ± 0.45	-10.72±6.26	-0.20±0.22	-26.34±31.56	0.58 ± 0.48	31.41±1.09**	0.26±1.82	-0.21±0.14	11.77±4.26	0.47±0.25	
m	106.40±1.10**	9.50±0.17**	24.00±0.46**	1.93±0.01**	218.00±7.37**	13.60±0.26**	34.67±1.86**	91.33±0.88**	2.55±0.15**	49.00±3.22**	3.60±0.17**	
d	-7.70±1.61**	-0.13±0.45	3.77±3.09	0.27 ± 0.10	37.33±16.38	0.07 ± 0.53	-2.67 ± 2.67	-4.33±1.79	-0.22±0.17	0.33 ± 2.47	0.01 ± 0.14	
h	21.78±6.00*	3.24±1.17	18.20 ± 7.43	-1.99±0.31**	-82.50±48.13	-0.37±1.53	2.00 ± 9.24	-6.67±5.15	0.22 ± 0.69	$16.00{\pm}14.05$	1.35 ± 0.76	
i	30.07±5.45**	3.39±11.14*	29.13±6.44*	-1.29±0.21**	-53.33±44.08	-0.53±1.49	4.00 ± 9.14	-7.33±5.03	0.39±0.69	7.33±13.78	0.71±0.74	
j	3.38 ± 1.94	0.60 ± 0.47	8.03 ± 4.24	$0.28 \pm 0.12*$	4.17±20.16	0.87 ± 0.54	3.00 ± 2.75	0.00 ± 1.90	0.08 ± 0.18	5.33 ± 2.86	0.21±0.20	
1	-57.83±9.26**	-6.83±2.01*	-43.60±14.52*	1.04 ± 0.61	27.67 ± 81.60	-2.20 ± 2.46	-28.00 ± 13.28	14.67 ± 8.29	-1.74 ± 0.92	-38.67±17.12	-2.39 ± 0.95	
Domonator	Sana x Krasunia											
Parameter	PH	SL	GNS	GWS	GY	PC	GC	GI	G/P	SED	SED/P	
m	84.9233±2.43**	• 9.69±0.24**	48.37±1.53**	2.28±0.10**	209.28±14.09**	12.43±0.21**	37.37±1.38**	91.84±1.03**	2.89±0.13**	36.75±0.97**	3.06±0.08**	
d	7.8479±2.46*	1.39±0.24**	-2.03 ± 1.55	-0.0798±0.09	-22.40±14.31	$0.60 \pm 0.19*$	6.70±1.40**	$4.05 \pm 1.06*$	0.24±0.13	6.10±0.96**	0.38±0.08**	
h	9.4897±4.82	-0.04±0.49	-8.15±3.20	-0.52±0.19*	-9.79±16.81	0.15±0.33*	-14.38±1.61**	3.54±1.50	-0.96±0.18**	14.45±2.96**	0.78±0.24*	
m	93.20±2.20**	9.99±2.21**	42.10±1.04**	2.13±0.04**	183.00±18.58**	11.40±0.31**	34.00±1.53**	97.33±0.67**	2.99±0.18**	47.67±1.45**	4.19±0.19**	
d	-11.40±5.44	-0.45±0.67	7.93±3.72	0.65 ± 0.18 *	-31.33±23.06	-0.90± 0.16**	$-4.00\pm1.37*$	-9.33±2.73*	-0.13±0.11	-13.67±1.70**	-0.82±0.16**	
h	-29.55±14.32	-2.99±1.61	8.07 ± 8.78	-0.43 ± 0.41	122.83 ± 88.06	5.46±1.28*	-15.33±6.87	$-35.33 \pm 6.14 **$	$-2.54\pm0.78*$	-1.67±7.47	-1.95±0.89	
i	$-40.53 \pm 14.00*$	-2.88 ± 1.59	13.07 ± 8.52	-0.23±0.38	129.33 ± 87.48	5.40±1.27*	-6.67±6.70	$-40.00 \pm 6.07 **$	-1.83 ± 0.77	-8.67±6.73	$-2.53\pm0.83*$	
j	-4.02 ± 5.64	0.99 ± 0.69	5.73 ± 3.83	$0.79 \pm 0.19 *$	-61.17±24.74	-0.47 ± 0.23	-1.00 ± 2.03	-3.67 ± 2.81	0.02 ± 0.15	$-8.33 \pm 1.80*$	-0.49±0.17*	
1	69.90±24.22*	4.28 ± 2.88	-8.27±16.01	0.25 ± 0.78	-179.00±120.18	-7.72±1.45 **	-14.67±8.77	65.33±11.37**	0.56 ± 0.89	-10.00 ± 11.04	1.71 ± 1.18	

Table 3. Gene action for yield and quality components according to three and six parameter analyses

PH: plant height, SL: spike length, GNS: Grain number per spike, GWS: grain weight per spike, GY: grain yield, PC: protein content, GC: gluten content, GI: gleten index, G/P: Gluten/protein rate, SED: sedimentation, SED/P: sedimentation/protein rate.

m: mean gene effects, d: additive gene effects, h: dominance gene effects, i: additive x additive gene interaction, j: dominance x dominance gene interaction, l: additive x dominance gene interaction

and dominance \times dominance gene effects were significant for plant height. Although both additive and dominance gene effects are significant, the dominance gene effects were greater than additive gene effects. This situation may arise from overdominance or unidirectional dominance or dispersion of genes in parents.

Because dominance and epistatic gene effects are significant in inheritance of these traits, selection for these traits should be delayed to later generations when the dominance effect is diminished. In the Sana \times Krasunia cross, additive \times additive and dominance \times dominance gene effects were significant for plant height. Similarly, selection should be continuous for next generations in this cross, too. The results for plant height are in accordance with the previous findings of Fatehi et al. (2008), Ilker (2010), Khattab et al. (2010), Tonk et al. (2011), Golestani et al., (2012), Hassan and El-Said (2014).

Additive \times additive and dominance \times dominance type epistatic gene effects were significant for spike length and grain number per spike in Pehlivan \times Bezostaja-1, although no gene effects were significant for these traits in the Sana × Krasunia cross. Novoselovic et al. (2004), Erkul et al. (2010), Tonk et al. (2011), Koumber and El-Gammaal (2012) found that additive, dominance and epistatic gene effects were significant for these traits. For grain weight per spike, dominance, dominance \times dominance, additive \times dominance gene additive effects and dominance. Х dominance gene effects were statistically significant in Pehlivan \times Bezostaja-1 and Sana \times Krasunia crosses, respectively. Owing to the fact that additive \times dominance interactions have a positive value; it is expected to obtain high grain weight per spike in infinity generations. No gene effect for the grain yield trait in either cross was significant. For quality traits, all parameters were found non-significant in the Pehlivan \times Bezostaja-1 cross. If none of the parameters were described by genetic variation, this indicates a more complex

mechanism of genetic control. Such a situation is the least favourable from a breeder's point of view, suggesting that a revised breeding strategy is needed due to complexity of gene effects occurring in these generations (Chatrtah et al., 1986; Srivestava et al., 1992; Amawate and Behl, 1995; Duvojkovic et al., 2010). In the Sana × Krasunia cross, all gene effects were significant except additive × dominance for protein content and gluten index; additive gene effects for gluten content, dominance gene effects for gluten/protein rate, additive and additive × dominance gene effects for sedimentation, additive, additive \times additive and additive \times dominance gene effects for sedimentation/protein rate were found significant. Coskun et al. (2010) found that SDS sedimentation was controlled only by environmental variance, but Bnejdi and El-Gazzah (2010), El-Bok et al. (2013), Singh et al. (2014) found that all types of gene effects were significant for quality characters.

The traits that were found inadequate with the three parameter model according to joint scaling test ($\chi^2 < 0.05$) were different in the two crosses (Table 1). Altinbas and Bilgen (1996) explained that inheritance of epistasis can change according to population. Traits that were found adequate with the three parameter model had significant values of scaling test parameters (A, B, C or D). It is possible that there is a linkage that causes deviations from the model (Mather and Jinks, 1971).

Hayman (1958) asserted that if the additivedominant model is inadequate, additivedominant parameters may include unknown epistatic factors. extended Although epistatic parameters estimated with the six parameter model are simple values, d and h parameters gained from the three parameter model are more dependable. It can be said that additive gene effects play a significant role in inheritance of plant height, spike length, protein content, gluten index and gluten/protein rate in the Pehlivan \times Bezostaja cross and inheritance of plant height, spike length, gluten index in the

Sana × Krasunia cross (Table 3). However, there are duplicate type epistatic gene effects for plant height and spike length for the Pehlivan \times Bezostaja-1 cross and for plant height and gluten index in the Sana Krasunia cross. Further generations of selection should be done for these traits. In addition, dominance gene effects play a significant role in the inheritance of gluten content in the Pehlivan \times Bezostaja-1 cross, and in grain weight per spike and gluten/protein rate in the Sana \times Krasunia cross. Also, both additive and dominance gene effects play a significant role in inheritance of protein and gluten content, sedimentation and sedimentation/protein rate in the Sana \times Krasunia cross (Table 3). Kaur and Singh (2004) stated that the nature and magnitude of gene effects vary within the different crosses for different characters, necessitating that a specific breeding strategy be adopted for particular crosses to obtain improvement (ZaaZaa et al., 2012). All traits that had significant epistatic gene effects showed duplicate type Therefore, early generation epistasis. selection would have failed.

CONCLUSION

Additive, dominance and epistatic effects seemed to have played roles in the inheritance of all studied traits for the two crosses. However, in the Pehlivan x Bezostaja-1 cross, due to the similarities of both parents for the traits (especially quality traits) under study, actual genetic variation could not be defined. It is recommended that selection be delayed due to the presence of epistatic gene interactions for many traits. The epistasis has been expressed through influencing yield and quality traits and it is suggested that breeders should be aware of this as a source of variation that might influence predicted gain in a selection programme. The information on genetics of various contributing traits will further support plant breeders in the selection of breeding programs.

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