

Research Article Generation mean analysis of grain yield and its related traits in barley (*Hordeum vulgare* L.)

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(Received: 12 Aug 2014; Accepted:24 Feb 2015)

Abstract

Generation mean analysis was performed using three crosses namely DL 88 x K 560, K 603 x Azad, RD 2552 x NDB 1020 to study the nature and magnitude of gene effects for yield and its component characters in barley (*Hordeum vulgare* L.). The F_1 , F_2 , BC₁ and BC₂ of these crosses along with P_1 and P_2 were studied for six morphological traits. Additive x additive (i) epistatic effect was more important and higher than the dominance x dominance (l) epistatic effect in the inheritance of no. of effective tillers/plant in DL88 x K560, length of main spike and grain yield/plant in RD 2552 x NDB1020. The length of main spike, weight of grains/main spike, 1000-grain weight and grain yield/plant were significantly higher in RD 2552 x NDB 1020.Thus, these characters were mainly under the control of dominance x dominance (l) type of epistasis. Therefore, selection for these characters would be fruitful, if delayed till dominance and epistasis effects are reduced to minimum. The additive × additive (*i*) type gene interaction and duplicate epistasis also seen in this trait suggest the possibilities of obtaining transgressive segregants in later generations. The study revealed the importance of both additive and non-additive types of gene interaction for all the traits studied.

Key words

Barley, gene effects, generation mean analysis, quantitative trait, recurrent selection

Introduction

Barley (Hordeum vulgare L.), a member of Poaecae family, is an important rabi cereal crop of India, being grown in northern plains of country. It represents the states of Rajasthan, U.P., Haryana, M.P., Punjab, Bihar and Jharkhand belonging in plains and Himachal Pradesh, Uttarakhand and Jammu & Kashmir in the hills. Barley occupies nearly 6.9 lakh ha. area producing nearly 15.52 lakh tones grain, with a per hectare productivity of 22.45 q. Recently, Rajasthan has taken up as number one barley producing state replacing U.P. and the change is mainly because of the shortage of rainfall and irrigation water experienced during past few years during the crop season. Since long, it has been considered as poor man's crop because of its low input requirement and better adaptability to harsh environments, like drought, salinity and alkalinity and marginal lands. Though major production is utilized as cattle feed and food, recent increase in industrial demand of barley as raw material resulted in its consideration as industrial crop. In addition to the use in feed and malt, barley is the main staple food crop in the tribal areas of the plains as well as hills. In the modern time, it is also preferred as medicinal food in urinary as well as cardiac problems. The changing climatic scenario in country for temperature, rainfall and crop duration has made it also a potential crop for near future, when we

Understanding of the genetics underlying these traits is imperative for efficient management of available genetic variability and formulation of systematic breeding programmes. The genetic studies have been conducted to understand the genetic control of grain yield and its component traits in barley. These studies have shown that both additive and non-additive genes control the grain yield in barley. The detection and estimation of epistasis would also enable the breeders to understand the genetic cause of heterosis with greater reliability. The presence or absence of epistasis can be detected by the analysis of generation means using the scaling test, which measures epistasis accurately whether it is complementary (additive x additive) or duplicate (additive x dominance) at the digenic level reported by Sharmila (2005). The present research was aimed to generate information on the nature of gene action in barley to decide selection methods for the improvement of the barley. A lot of information on nature and relative magnitude of genetic components of variation (additive and dominance) have been generated by generation mean analysis. However literature on barley in respect of fixable and non fixable gene effects is meager. Therefore, the present study was planned to investigate genetics of days to ear emergence, days to maturity, no. of effective tillers/plant, weight of grains/main spike (g), no. of

expect reduction in availability of all such resources.



grain/spike and 1000-grain weight (g) by using the data of six-generations of the three crosses under normal and saline sodic soil conditions.

Material and methods

Six barley genotype namely; DL 88, K 560, K 603, Azad, RD 2552 and NDB 1020 were used for generating breeding material which resulted into six basic generations (P $_1$ and P $_2$ parent ,F $_1$ and F $_2$ first and second filial generations, and the BC_1 and BC_2 first and second back crosses) of three cross combinations being DL 88 x K 560, K 603 x Azad, RD 2552 x NDB 102. The parental The parental populations were grown in crossing block. Parents of the respective crosses were used as P_1 and P_2 and the F_1 generations of the particular cross was used as the female parent and back crossed to P1 to produce the BC_1 . F_1 was again backcrossed to P_2 to produce BC_2 and the F_1 hybrids were selfed to obtain F_2 seeds. Six generations of these crosses i.e. P1, P2, F1, F2, BC1 and BC2 were grown separately in Randomized Block Design with three replications in two environments, one sown in normal soil and the other sown in saline sodic soil during the same season. Planting was done in rows of 3 m length. Row to row distance was kept at 25 cm apart. The parents (P_1 and P_2) and F_1 s were sown in 2 rows, while back cross generations and F_2 generations were sown in 5 and 6 rows respectively. The experiment was carried out during rabi, i.e. 2010-11 and 2011- 12 at KVK, Chhatarpur Farm, J.N.K.V.V, Jabalpur, Madhya Pradesh. All the genotypes were grown in row of 3 metre length. However number of rows varied for different generations i.e. three rows, for the nonsegregating generation P_1 , P_2 and F1; 20 rows for the F2; and 15 rows for the BC_1 and BC_2 generations. Since the non- segregating generations represent the homogeneous population while the segregating generations represent the heterogeneous population the sample (i.e. number of plants analysed) varied as follows: 10 plants for the P_1 , P_2 and F_1 generations; 40 plants for the F2 generations; and 30 plants for the BC_1 and BC_2 generations. The traits assessed were days to ear emergence, days to maturity, no. of effective tillers/plant, weight of grains/main spike(g), no. of grain/spike and 1000-grain weight (g).The analysis of variance for RBD was carried out following Panse and Sukhatme (1967). The scaling test was performed to test the estimates of sixparameter model using the digenic epistatic model of Hayman, (1958). The scaling tests 'A', 'B' 'C' and D were used to test the adequacy of the additivedominance model.

Result and discussion

The values of six generations for the joint scaling tests and their interaction effect being presented in Table 1. The additive, dominance and epistatic types of gene interaction in each cross for different traits were found to be different from each other. The dominance \times dominance (l) interaction was larger than the additive \times additive (i) and additive \times dominance (j) effects put together, while for the main effect the dominance component (h) was greater than the additive (d) component. The dominance (h)and dominance \times dominance (l) effects were in opposite direction, suggesting that duplicate-type epistasis occurred in most cases and indicating predominantly dispersed alleles at the interacting loci. Dominance gene effects were found to be relatively more important, as indicated by the fact that in all cases the dominance (h) values were higher than the additive (d) values. Results of the scaling tests revealed that out of four scaling tests one or two scales were found to be significant in all the three crosses for most of the characters. Therefore, the sixparameter model to detect gene effects was applied in all the characters. The estimates of m, d, h, i, j and l of six parameter model for all the characters are presented in Table 1.Mean data and standard error of the six generations with three crosses for six traits were calculated. The earliness in ear emergence and days to maturity along with dwarf stature have been considered as desirable traits in barley as it is mainly grown as a rain fed crop. The Cross found superior to its their respective parents was RD 2552 x NDB 1020 for effective tillers/plant (10.57±0.39).The crosses of DL 88 x K 560, and RD 2552 x NDB 1020, recorded maximum number of grains/main spike (64.43 ± 0.39 and 92.03 ± 0.46 respectively). The cross RD 2552 x NDB 1020 registered maximum 1000 grain weight (40.20±0.36) while DL 88 x K 560 gave maximum grain yield/plant (26.97±0.33 g).

A simple additive-dominance model was inadequate as inferred from the significance of all traits. The additive, dominance and epistatic types of gene interaction in each cross for different traits were found different from each other (Table 1). Comparison of estimates of gene effect with respect to magnitude as well as significance reveled that additive (d) was of greater importance than to the dominance (h) gene effect for no. of effective tillers/plant, length of main spike and grain yield/plant in the RD 2552 x NDB 1020 cross. Thus, selection for no. of effective tillers/plant and 1000grain weight would be effective in early segregating generations. Both additive (d) and dominance (h)



weight of grains/spike, and grain yield/plant and RD 2552 x NDB 1020 for no. of grains/spike.

The dominance (h) effect was more important than additive gene effects (d) in the inheritance of 1000grain weight in the DL88 x K560 cross. The genetic effect for these characters suggested that selection for these characters would not be effective in segregating generations. Higher magnitude of dominance (h) component than the additive (d) component suggested that the parents involved in the crosses were in dispersion phase and dominance component was more important for these characters. Vimal and Vishwakarma (1999) also reported the predominance of non-additive gene action for yield and yield components in barley.

Estimates of additive x additive (i), additive x dominance (j) and dominance x dominance (l) interactions indicated that the additive x additive (i) was more important in the inheritance of all the characters. Additive x additive (i) epistatic effect was more important and higher than the dominance x dominance (1) epistatic effect in the inheritance of no. of effective tillers/plant in DL88 x K560 and grain yield/plant in RD 2552 x NDB1020. However, dominance x dominance (1) epistatic gene interaction was significant and greater in magnitude than all the gene effects (d, h, i and j) in the inheritance of no of effective tillers/plant, days to maturity and 1000grain weight in DL 88 x K560. The weights of grains/main spike and1000-grain weight were significantly higher in RD 2552 x NDB 1020. These findings are in agreement with those reported earlier Prakash et al. (2005). Thus, these characters were mainly under the control of dominance x dominance (1) type of epistasis. Therefore, selection for these characters would be fruitful if delayed, till dominance and epistatic effects would reduce to the minimum.

In cross, DL88 x K560 for days to maturity and grain yield/plant, cross RD2552 x NDB 1020 for length of main spike were observed with complementary epistasis This suggested the possibility of considerable amount of heterosis in these two crosses for days to maturity, grain yield/plant and 1000-grain weight. On the basis of present study, it could be concluded that grain yield/plant and the component characters like days to ear emergence, no. of effective tillers/plant, days to maturity, weight of grains/main spike, no. of grains/ spike and 1000-grain weight were mainly under the control of non-additive dominance (h) gene action and gene action

dominance x dominance (l) gene interaction which indicated their poor amenability to simple selection procedures and under such a situation, the maximum gain could be achieved by maintaining considerable hetrozygosity through inter-mating of selected plants in early segregating generation or by following some form of recurrent selection method reported by Parlevliet and Van(1988). This would increase the possibility of various recombinants, which might result in accumulation of favorable genes in the ultimate homozygous lines with higher grain yield. Therefore, a few cycles of recurrent selections followed by pedigree breeding would be effective in the improvement of yield in barley.

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Table 1 Scaling tests estimates of gene effects and type of epistasis for different characters in barley
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	DL 88 x K 560)	K 603 x Azad		RD 2552 x NDB 1020	
	Normal soil	Saline sodic	Normal soil	Saline sodic	Normal soil	Saline sodi
	(N)	soil (S)	(N)	soil (S)	(N)	soil (S)
Scale			Days to ear	· emergence		
А	7.34**	21.00**	26.00**	8.33**	6.34**	8.33**
	+1.56	+1.70	+0.94	+1.63	+1.24	+2.31
В	-3.34**	15.33**	14.00**	7.00**	-6.34*	-7.67**
	<u>+</u> 1.05	+1.70	+1.88	+2.00	+1.63	<u>+</u> 1.15
С	-2.66	26.33**	1.34	8.67	-2.67	12.00
	<u>+</u> 6.30	<u>+</u> 2.87	<u>+</u> 6.20	<u>+</u> 3.80	<u>+</u> 2.30	<u>+</u> 4.14
D	-3.34	-5.00**	-19.34**	-3.33	-1.34	6.33**
2	3.12	+1.50	+3.19	+2.08	+1.00	<u>+</u> 2.00
Gene effects, 6 parameters	<u>5.12</u>	<u>-</u> 1.50	<u></u> 5.17	<u></u> 2.00	1.00	<u></u> 2.00
m	83.00**	87.00**	78.00**	77.33**	77.33**	77.67**
111	+1.52	+0.57	+1.52	+0.89	+0.33	+0.88
(d)	$\frac{-1.52}{2.66**}$	-3.67**	0.00	-1.33	2.66**	1.00
(u)	<u>+</u> 0.66	<u>+</u> 0.94	+0.94	± 1.00	+0.74	+0.94
(h)	<u>+</u> 0.00 5.33	$\frac{+0.94}{11.17**}$	<u>+</u> 0.94 37.99**	$\frac{+}{9.67*}$	<u>+</u> 0.74 7.34**	<u>+</u> 0.94 12.67**
(11)	<u>+</u> 6.30	+3.07	+6.41	+4.20	+2.21	+4.10
(i)	<u>+</u> 0.30 6.66	$\frac{\pm}{10.00}$	$\frac{+0.41}{38.67**}$	<u>+</u> 4.20 6.67	$\frac{+2.21}{2.67}$	$\frac{+}{12.67}$
(1)	+6.25	+2.98	+6.39	+4.16	+2.00	+4.00
	<u>+</u> 0.25 5.33**	$\frac{+2.98}{2.83*}$	<u>+</u> 0.39 6.00**	$\frac{+}{0.67}$	<u>+</u> 2.00 6.34**	$\frac{+4.00}{8.00**}$
(j)						
	± 0.84	<u>+</u> 1.33	± 1.02	<u>+</u> 1.27	± 0.81	± 1.30
(1)	-10.66	-46.33**	-78.67**	-22.00**	-2.67	-13.33**
m (), , , ,	<u>+</u> 6.84	<u>+</u> 4.74	<u>+</u> 7.75	<u>+</u> 5.83	<u>+</u> 3.77	<u>+</u> 5.60
Type of epistasis	-	D	D	D	-	D
Scale	0.04	5 00 th	Da	ays to maturity		
А	8.34**	5.00*	7.00**	7.33	22.00**	7.67**
	<u>+</u> 2.26	<u>+</u> 2.49	<u>+1.24</u>	<u>+4.00</u>	<u>+</u> 3.05	<u>+</u> 2.45
В	6.00	8.00	4.67**	6.67**	17.67**	6.00**
_	± 2.62	<u>+</u> 1.37	± 1.20	± 2.00	<u>+</u> 3.46	<u>+</u> 0.82
С	7.67*	3.00	4.34*	-2.00	53.67**	-3.00
	<u>+</u> 3.16	<u>+</u> 4.20	<u>+</u> 2.42	<u>+</u> 4.94	<u>+</u> 5.65	<u>+</u> 1.56
D	-3.34*	-5.00	-3.67*	-8.00**	7.00**	-8.33*
	<u>+</u> 1.63	<u>+</u> 2.38	<u>+</u> 0.81	<u>+</u> 0.82	<u>+</u> 2.49	<u>+</u> 1.41
Gene effects, 6 parameters						
m	137.33**	146.00**	137.67**	143.33**	146.00**	144.33**
	<u>+</u> 0.33	+1.00	<u>+</u> 0.33	<u>+</u> 0.33	+1.00	<u>+</u> 0.33
(d)	-1.33	-3.00*	0.34	0.00	-1.67	0.33
	<u>+</u> 1.49	<u>+</u> 1.29	<u>+</u> 0.47	<u>+</u> 0.47	<u>+</u> 1.49	<u>+</u> 1.25
(h)	9.83**	12.83**	8.17**	13.67**	-13.83**	19.17**
	<u>+</u> 3.56	<u>+</u> 4.78	<u>+</u> 1.92	<u>+</u> 2.21	<u>+</u> 5.37	<u>+</u> 2.85
(i)	6.66*	10.00*	7.34**	16.00**	-14.00**	16.67
- *	<u>+</u> 3.26	<u>+</u> 4.76	<u>+</u> 1.63	<u>+</u> 1.63	<u>+</u> 4.98	<u>+</u> 2.83
(j)	1.16	-1.50	1.16*	0.33	2.17	0.83
U/	<u>+</u> 1.81	<u>+</u> 1.40	<u>+</u> 0.50	<u>+</u> 2.03	<u>+</u> 2.10	<u>+</u> 1.27
Type of epistasis	С	С	D	D	С	D



Table 1 Contd..

	DL 88 x K 560		K 603 x Azad		RD 2552 x NDB 1020	
	Normal soil (N)	Saline sodic soil (S)	Normal soil (N)	Saline sodic soil (S)	Normal soil (N)	Saline sodi soil (S)
~ -						
Scale	1 644	2.02**		tive tillers/plant	0.70**	2.07**
А	1.6**	-3.03**	-0.36	-2.33**	2.73**	3.07**
Л	<u>+</u> 0.68	<u>+</u> 0.57	<u>+0.47</u>	± 1.11	<u>+0.79</u>	± 0.70
В	1.47**	5.75**	-1.17**	0.73	-14.10**	
C	<u>+0.28</u>	± 0.62	± 0.52	± 1.05	<u>+</u> 0.47	<u>+</u> 0.58
С	1.43**	13.63**	1.87	-8.80**	-17.10**	8.70*
	± 0.33	<u>+1.04</u>	± 1.82	± 1.09	± 0.47	+1.26
D	-1.00**	5.47**	1.70	-3.60**	-2.87**	3.47*
	<u>+</u> 0.33	<u>+</u> 0.55	<u>+</u> 0.91	<u>+</u> 0.71	<u>+</u> 0.74	<u>+</u> 5.88
Gene effect 6-parameters						
m	11.70	10.70**	12.33**	11.07	8.09**	12.07
	<u>+</u> 0.33	<u>+</u> 0.21	<u>+</u> 0.43	<u>+</u> 0.09	<u>+</u> 0.32	<u>+</u> 0.24
(d)	0.53	-3.47**	1.23**	-2.77**	6.67**	2.80*
	<u>+</u> 0.31	<u>+</u> 0.35	<u>+</u> 0.27	<u>+</u> 0.28	<u>+</u> 0.36	<u>+</u> 0.34
(h)	4.58**	10.72**	-2.53	-3.75**	7.12**	-5.58*
	<u>+</u> 0.68	<u>+</u> 1.13	<u>+</u> 1.86	<u>+</u> 0.69	<u>+</u> 1.52	<u>+</u> 1.25
(i)	2.00**	-10.93**	-3.39	-4.73**	5.73**	6.93*
	<u>+</u> 0.66	<u>+</u> 1.09	<u>+</u> 1.81	<u>+</u> 0.66	<u>+</u> 1.48	<u>+</u> 1.18
(j)	0.25	-4.38**	0.40	-4.25**	8.42**	2.18*
<u>,</u>	<u>+</u> 0.37	<u>+</u> 0.36	<u>+</u> 0.30	<u>+</u> 0.30	<u>+</u> 0.41	<u>+</u> 0.36
(1)	-5.43*	8.23**	4.93*	2.83*	3.63**	5.17*
	<u>+</u> 1.33	<u>+</u> 1.75	<u>+</u> 2.12	<u>+</u> 1.27	<u>+</u> 2.06	<u>+</u> 1.86
Type of epistasis	D	D	-	D	С	D
Scale			Weight of gra	ains/main spike (g	()	
A	-0.17	0.67**	-0.67**	0.96**	0.17	1.30*
	<u>+0.35</u>	<u>+0.14</u>	<u>+</u> 0.16	<u>+0.13</u>	<u>+</u> 0.19	<u>+0.19</u>
В	0.73**	0.27	0.90**	0.73**	0.20	-0.30
2	<u>+</u> 0.19	+0.16	+0.19	+0.22	+0.16	+0.23
С	-0.57	0.00	-0.63*	-1.70**	0.57*	-4.27*
-	<u>+0.40</u>	<u>+</u> 0.34	<u>+</u> 0.27	<u>+0.41</u>	<u>+0.23</u>	<u>+0.44</u>
D	-0.57**	-0.47**	-0.43*	-1.70^{**}	0.10	-2.77
_	<u>+</u> 0.19	<u>+</u> 0.15	<u>+</u> 0.16	<u>+</u> 0.20	<u>+</u> 0.24	<u>+</u> 0.21
Gene effects, 6 parameters						
m	2.80**	2.03**	0.22**	2.67**	3.17**	1.63*
111	<u>+</u> 0.06	<u>+</u> 0.07	<u>+</u> 0.06	± 0.08	<u>+0.03</u>	1.05 +0.08
(d)	0.57	0.13*	-0.50**	0.09	-0.16	0.03
(u)	<u>+</u> 0.15	<u>+</u> 0.07	± 0.11	± 0.09	<u>+</u> 0.08	<u>+0.12</u>
(h)	1.92**	0.73*	1.75**	2.95**	0.15	$\frac{-0.12}{4.67*}$
(11)	± 0.41	± 0.32	± 0.33	± 0.41	<u>+</u> 0.24	<u>+0.4</u>
(i)	1.13^{**}	0.93**	0.87**	3.40**	$\frac{-0.24}{0.19}$	<u></u> 0 5.53*
(1)	+0.37	+0.30	+0.32	± 0.40	+0.22	+0.04
(j)	-0.45**	<u></u> 0.50 0.19*	-0.78**	0.12	-1.67**	<u>-1</u> 0.0- 0.67*
U/	<u>+0.17</u>	<u>+</u> 0.08	± 0.12	± 0.12	± 0.12	<u>+</u> 0.13
(1)	-1.70^{*}	<u>+</u> 0.08 1.86**	-1.09*	-5.10^{**}	$\frac{+}{-0.12}$	-6.80^{*}
(1)	± 0.71	± 0.43	± 0.52	± 0.56	+0.42	<u>+0.05</u>



Table 1 Contd..

	DL 88 x K 56	DL 88 x K 560		K 603 x Azad		RD 2552 x NDB 1020	
	Normal soil	Saline sodic			Normal soil	Saline sodi	
	(N)	soil (S)	(N)	soil (S)	(N)	soil (S)	
Scale	No. of grain/spi	ke					
А	3.87	-2.20	0.47	-19.90**	12.87**	11.43**	
	<u>+</u> 2.65	<u>+</u> 1.58	<u>+</u> 2.08	<u>+</u> 1.93	<u>+</u> 2.11	<u>+</u> 3.31	
В	20.87**	-22.37**	24.57**	32.97	11.57**	-34.33**	
	<u>+1.08</u>	<u>+</u> 1.20	<u>+0.81</u>	<u>+</u> 3.14	<u>+</u> 2.24	<u>+</u> 2.79	
С	-27.33** 1.79	-46.77**	40.76**	37.07**	-25.17**	-37.56**	
		+2.20	<u>+</u> 2.58	+4.12	<u>+3.62</u>	+5.57	
D	-26.03**	-11.10**	7.87**	12.00**	-24.80**	-7.33**	
	+1.46	+1.35	+1.35	<u>+</u> 2.72	<u>+</u> 1.93	<u>+</u> 1.89	
Gene effects, 6 parame	eters	—	-	—	_	_	
m	83.13**	50.27**	72.57**	100.67**	80.73**	63.67**	
	<u>+</u> 0.29	<u>+</u> 0.49	<u>+</u> 0.49	<u>+</u> 1.06	<u>+</u> 0.75	<u>+</u> 0.67	
(d)	1.89	8.57	13.00**	20.73**	1.40	5.46**	
	<u>+</u> 1.32	<u>+</u> 0.92	<u>+0.91</u>	+1.81	<u>+1.21</u>	<u>+</u> 1.29	
(h)	68.86	27.15	-24.75**	40.53**	59.62**	15.08**	
	<u>+</u> 2.97	<u>+</u> 2.75	<u>+</u> 2.82	<u>+</u> 5.44	+3.99	+4.44	
(i)	52.07	22.20**	15.73**	-23.99**	49.59**	14.67**	
	± 2.89	<u>+</u> 2.71	<u>+</u> 2.69	<u>+</u> 5.42	<u>+</u> 3.86	<u>+</u> 3.72	
(j)	-8.50**	10.08	-12.05**	26.43**	0.65	22.88**	
0/	<u>+</u> 1.37	<u>+</u> 0.95	<u>+</u> 0.99	+1.83	<u>+</u> 1.50	<u>+</u> 1.34	
(1)	-76.80**	2.36	-9.30*	10.93	-74.03**	8.23	
(-)	<u>+</u> 5.9	<u>+</u> 4.28	+4.45	<u>+</u> 8.34	<u>+</u> 6.04	<u>+</u> 7.57	
Type of epistasis	D	-	C	-	D	-	
Scale			1000-grain v	veight (g)			
А	-8.93**	-13.67**	19.47**	-0.67	-6.17**	7.67**	
	<u>+</u> 1.33	<u>+</u> 1.58	<u>+</u> 1.17	<u>+</u> 1.31	<u>+</u> 1.32	<u>+</u> 1.12	
В	2.60**	-23.80**	21.13**	-4.30**	13.97**	4.73**	
2	+1.06	<u>+1.95</u>	<u>+</u> 1.28	<u>+1.21</u>	<u>+0.52</u>	<u>+</u> 1.04	
С	19.07**	-30.87**	-20.13**	-12.63*	-26.40**	-2.47**	
-	+2.44	<u>+</u> 1.97	<u>+2.44</u>	<u>+</u> 5.49	<u>+2.08</u>	+0.74	
D	12.70**	3.30**	-30.36**	-3.83	-17.10**	30.50**	
	<u>+0.92</u>	<u>+</u> 0.73	+1.41	<u>+</u> 2.76	+1.19	<u>+0.21</u>	
Gene effect 6-paramete		<u></u>	<u>_</u>	<u> </u>	<u> </u>	<u></u>	
m	37.47**	30.50**	26.13**	32.76**	28.77**	30.50**	
	<u>+</u> 0.41	<u>+</u> 0.06	<u>+</u> 0.58	<u>+</u> 1.33	<u>+</u> 0.49	<u>+2.21</u>	
(d)	-1.83	5.23**	-0.17	0.89	-5.29**	-2.80**	
	+0.41	<u>+</u> 0.72	<u>+</u> 0.80	<u>+</u> 0.70	<u>+</u> 0.67	<u>+</u> 0.61	
(h)	-22.07**	-10.43	58.99**	11.15	43.86**	4.33**	
(/	+2.04	+1.75	+2.84	<u>+</u> 5.56	+2.39	+1.59	
(i)	-25.40**	-6.60**	60.73**	7.67	34.20	4.93**	
(-)	+1.83	+1.45	+2.81	<u>+</u> 5.52	<u>+</u> 2.37	+1.48	
(j)	-5.76**	5.07**	-0.83	1.83	-10.07**	6.19**	
V/	<u>+0.68</u>	<u>+</u> 0.74	<u>+0.85</u>	<u>+0.83</u>	+0.67	+0.72	
(1)	31.73**	44.07**	-101.33**	-2.69	-41.99**	-2.00	
(*)	<u>+2.94</u>	<u>+</u> 3.48	<u>+4.03</u>	<u>+</u> 6.17	<u>+</u> 3.37	<u>+</u> 2.86	
Type of epistasis	<u> </u>	D	D	-	<u>D</u>	-	

*, ** = 0.05 and 0.01 respectively; D = Duplicate; C = Complementary