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Assessment of Genetic Architecture of Grain Yield and its Component Traits in Barley (*Hordeum vulgare* L.) through Generation Mean Analysis

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The suitable breeding procedure for crop improvement mainly depends on knowledge of the genetic make-up of the character to be selected. Unique architectural phenotypes have the vast potential for increasing the yield of the crop. Therefore, the investigation was carried out during three successive seasons *Rabi* 2009-10, 2010-11 and 2011-12 at Agriculture Research Farm, Banaras Hindu University, U.P. India with objective to estimate the main genetic effects including digenic non-allelic interactions controlling yield and yield component traits as-well-as to determine the yield component that affects yield to a greater extent. The generation mean analysis was carried out on six generations (P_1, P_2, F_1, F_2, B_1 and B_2) in six crosses involving two tester (LAKHAN and BH-902) and three exotic lines (MOROC-9-75, BEECHER and HARMAL) of barley. Duplicate type of epistasis was found for most of the traits in certain cross combinations, whose effect can be wiped out by following sophisticated selection procedure such as reciprocal recurrent selection and/or biparental mating in early segregating generations for the development of high yielding barley varieties with desirable yield contributing traits.

Key Words: Barley, Epistasis, Generation mean analysis, *Hordeum vulgare*, Yield traits

Introduction

Barley (*Hordeum vulgare* L.) is one of the principal crop species grown in the world (Eshghi and Akhundova, 2010), ranking fourth after wheat, rice and maize (Bengtsson, 1992; FAO, 2005; Kakani *et al.,* 2007; Raikwar, 2013) with a great adaptation potential. It has been widely used for different purposes such as staple food for mankind in few countries, cheap ingredient in whisky and beer production, and feed for animals. It can grow on wide range of environmental conditions compared to any other cereal and spreads in tropical to sub-tropical areas. With the economic development, more and more barley will be needed for beer processing and animal feed. Hence, improvement of yield potential of the crop has been a major objective in barley breeding programmes (Xue *et al.,* 2008).

Progress in yield improvement or even for quality traits of a crop requires information about the nature of combining ability of parents to be involved in the hybridization programme along with the nature of gene effects operative in the inheritance of different traits (Singh *et al*., 2013). The generation mean analysis is one of the most appropriate methods for genetic analysis of quantitative traits (Eshghi and Akhundova, 2010). In this method, epistatic effects as-well-as additive and dominance effects can be estimated.

The present study was undertaken to estimate the main genetic effects including digenic non-allelic interactions controlling yield and yield components in six cross combinations comprising two indigenous and three exotic barley genotypes. The other aim was to determine the yield component that affects yield to a greater extent in order to define efficient selection strategy for increasing the yielding ability in barley crop.

Materials and Methods

Experimental material consisted of six generations *viz.,* P_1, P_2, F_1, F_2 and two backcrosses (B_1 and B_2) relating to six crosses involving two tester (LAKHAN and BH-902) and three exotic lines (MOROC-9-75, BEECHER and HARMAL) (Table 1). The genotypes were intercrossed in Line x Tester design during the *Rabi* season of 2009-10 in order to produce F_1 hybrids. In the next year by selfing of F_1, the F_2 generation was obtained and also the backcrosses (B_1 and B_2) were made. Comparative field trial involving six generations of each of the six crosses were grown during *Rabi* 2011-2012 in Randomized Block Design with three replications at Agriculture Research Farm, Banaras Hindu University.

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The row-length was 2.5 metre and distance between two rows was 0.25 metre. The plants were spaced at 10 cm from each other. Each parent and F_1 had 3 rows/plot, while, 10 and 7 rows/plot, respectively, were for each F_2 and backcross populations. Data on yield and other five traits on 10 randomly selected plants in parents and their F_1s were recorded. In each F_2 population data was recorded on 50 plants and in the backcross population data on 20 plants were recorded.

The type of interactions in crosses was sorted out with the help of scaling test (Mather, 1949) as well as joint scaling tests by Cavalli (1952) and the gene effects were estimated using the model as suggested by Hayman (1958) and Jinks and Jones (1958).

Results and Discussion

The incorporation of derived traits from the donor parent in the background of cultivated varieties is often not profuse direction owing interaction at genetic level. This requires the need to understand the gene effects controlling yield and its component traits. The scaling test (A, B, C and D) were applied to detect the presence or absence of non-allelic gene interaction for the eight quantitative traits (Table 2). Presence of gene action and inter-allelic interaction varied cross-wise as-well-as trait-wise. Most of the crosses revealed presence of duplicate type of inter-allelic interaction.

Two crosses namely LAKHAN × MOROC-9-75 and BH-902 × BEECHER showed absence of non-allelic interactions, revealing additive (d) and dominance gene effect (h) for plant height (Table 2). The dominance gene effect for plant height was in agreement with findings of Taleei *et al*., 2004. Crosses *i.e.,* LAKHAN × BEECHER and LAKHAN × HARMAL exhibited duplicate type of epistasis while, cross BH-902 × MOROC-9-75 showed complementary gene effects. In cross BH-902 × HARMAL additive x dominance (j) and dominance × dominance (l) interaction was found significant.

The LAKHAN × HARMAL and BH-902 × BEECHER revealed absence of non allelic interaction for peduncle length. In the cross LAKHAN × HARMAL dominance gene effect (h) was significant, whereas, in BH-902 × BEECHER cross, both additive as well as dominance gene effects were significant. In cross, BH-902 × MOROC-9-75 peduncle length revealed duplicate type of gene action while BH-902 × HARMAL revealed complementary type of gene action.

The crosses such as LAKHAN × MOROC-9-75, BH-902 × MOROC-9-75 and BH-902 × HARMAL indicated absence of non-allelic interactions for number of tiller/plant. The dominance gene effect (h) was significant in all these three crosses. Duplicate type of gene action was revealed significant for LAKHAN × BEECHER and LAKHAN × HARMAL, whereas, dominance × dominance (l) was significant for BH-902 × BEECHER.

Complement type of gene action was significant in BH-902 × MOROC-9-75 and BH-902 × HARMAL for number of grain/ear, whereas, duplicate gene action was revealed in LAKHAN × Moroc-9-75 and BH-902 × BEECHER. In crosses LAKHAN × BEECHER and LAKHAN × HARMAL both additive gene effect (d) and dominance (h) gene effects were found significant.

1000-grain weight was under the control of duplicate type of gene action in LAKHAN × BEECHER, whereas, LAKHAN × HARMAL, BH-902 × BEECHER and BH-902 × HARMAL revealed both additive (d) and dominance (h) gene effect. The cross BH-902 × MOROC-9-75 showed dominance gene effect (h)

Table 1. Experimental material (genotypes) used in the study with their special feature

Lines	Special Features
MOROC-9-75	2-rowed, rainfed, prostrate, vigour- medium, spread bushy, sensitive to drought stress (exotic)
BEECHER	6-rowed, cross between Atlas and Vaughn received in Kansas in 1934 from Aberdeen, Idaho, tolerant to spot blotch, erect ear, prostrate, earlier maturity, long awn (exotic)
HARMAL	2-rowed, irrigated, prostrate, improved cultivar from Syria (exotic)
Testers	
LAKHAN	Spike 6-rowed, parentage: K-12/IB-226, plant semi erect, medium tall, good tillering, rachis non-fragile, non-shattering, seed medium bold, ear medium long, mid-lax awns, long serate semi-spreading at top and seed semi uniform well developed medium bold light blue in colour.
BH-902	Spike 6-rowed, parentage: BH-495/RD-2552, medium plant height, erect growth habit, green leaf sheath, dark green foliage colour (boot stage) and medium leaf width (boot stage).

Table 2. Scaling test, estimate of gene effects from analysis of generation mean for various traits studied in six crosses of barley

Cross/trait	A	B	C	D	[m]	[d]	[h]	[i]	[j]	[l]	Epistasis
LAKHAN × MOROC-9-75											
Plant height	-1.23	1.11	1.37	1.54	110.20**	3.66**	1.96	-	-	-	-
Peduncle length	-2.20*	1.50	-0.29	-0.09	12.26**	-0.33	7.86**	0.66	-3.73**	0.53	-
Ear length with awn	-1.83	0.54	0.93	0.98	33.60**	0.33	-50.70**	-	-	-	-
Ear length without awn	-2.76**	-0.98	0.57	1.76	10.00**	0.19	-6.06**	-7.60**	-0.86	12.66**	D
Number of tiller/plant	-1.70	-0.86	0.06	1.51	10.33**	-0.39	-5.16**	-	-	-	-
Number of grain/ear	-0.09	0.82	-5.03**	-1.38	27.60**	7.20**	32.93**	45.60**	-9.66**	-60.00**	D
1000-grain weight	-2.07*	2.23*	-0.46	-0.18	48.76**	-8.15**	19.38**	3.38**	-13.03**	1.10	-
Grain yield/plant	-2.09*	-1.64	-2.39*	-1.27	9.02**	5.27**	14.87**	13.43**	0.38	-0.80	-
LAKHAN × BEECHER											
Plant height	2.69*	1.99	1.41	-3.17**	108.26**	5.53**	16.06**	14.26**	0.66	-45.20**	D
Peduncle length	0.01	2.47*	-0.05	-1.41	10.00**	-0.39	5.70**	6.40**	-2.96**	-12.46**	D
Ear length with awn	2.22*	0.82	1.71	-0.58	20.66**	0.40	0.66	2.40*	0.53	-9.33**	-
Ear length without awn	0.36	1.25	-0.47	-1.26	7.26**	-0.66	2.76**	-	-	-	-
Number of tiller/plant	0.67	3.34**	0.20	-1.32	7.66**	-2.00	7.13**	7.20**	-1.73	-15.33**	D
Number of grain/ear	0.63	0.91	1.43	1.35	87.26**	-2.20*	-108.03**	-	-	-	-
1000-grain weight	-0.00	2.73**	-1.03	-2.89**	39.45**	3.27**	20.71**	16.86**	-5.20**	-27.22**	D
Grain yield/plant	0.87	1.39	-0.50	-1.25	10.67**	1.84	16.68**	-	-	-	-
LAKHAN × HARMAL											
Plant height	2.50*	0.03	-0.85	-1.10	101.13**	5.26**	34.86**	31.33**	2.79**	-37.46**	D
Peduncle length	0.48	0.77	-0.36	-0.80	10.13**	0.66	7.53**	-	-	-	-
Ear length with awn	1.13	1.22	0.84	-0.08	20.53**	1.40	0.96	-	-	-	-
Ear length without awn	0.71	0.44	0.51	-0.14	8.93**	0.80	1.59	-	-	-	-
Number of tiller/plant	-0.53	-3.34**	0.64	1.70	9.06**	1.20	-5.56**	-7.20**	1.43	11.66**	D
Number of grain/ear	-0.87	0.73	0.51	0.41	51.13**	-6.80**	-42.26**	-	-	-	-
1000-grain weight	0.66	0.86	0.32	-0.87	49.54**	-12.67**	34.31**	-	-	-	-
Grain yield/plant	-0.78	-1.20	-1.97	-0.45	11.91**	2.80**	0.30	-	-	-	-
BH-902 × MOROC-9-75											
Plant height	3.94**	0.88	2.87**	1.15	97.06**	10.26**	-14.63**	-20.80**	3.76**	-5.39**	C
Peduncle length	-0.21	-0.51	3.81**	4.07**	12.80**	1.46	-18.76**	-20.26**	0.23	21.80**	D
Ear length with awn	3.25**	-0.34	-0.03	-1.32	18.06**	-0.13	-1.63	5.06**	5.90**	-9.80**	-
Ear length without awn	0.73	0.43	0.00	-0.69	7.80**	-6.66**	3.20**	-	-	-	-
Number of tiller/plant	-1.02	0.09	0.59	0.76	9.00**	0.19	-6.09**	-	-	-	-
Number of grain/ear	-2.00	-5.45**	-22.22**	0.15	28.26**	15.60**	14.49**	-2.66*	-0.16	67.54**	C
1000-grain weight	-1.30	2.57*	1.54	0.78	48.18**	-4.65**	3.55**	-6.98	-12.57**	-1.22	-
Grain yield/plant	-1.98	-0.41	0.67	1.31	11.84**	-84.66**	-12.72**	-	-	-	-
BH-902 × BEECHER											
Plant height	1.49	0.04	0.75	0.11	95.2**0	1.33	4.66**	-	-	-	-
Peduncle length	0.93	-0.16	0.27	-0.80	8.93**	14.90**	28.16**	-	-	-	-
Ear length with awn	1.85	0.39	-0.96	-1.89	16.73**	1.13	10.31**	-	-	-	-
Ear length without awn	0.92	0.68	0.65	-0.48	7.46**	0.46	1.30	-	-	-	-
Number of tiller/plant	3.59**	1.97	2.20*	0.21	10.86**	0.00	-0.29	-1.59	-0.10	-11.13**	-
Number of grain/ear	3.11**	2.29*	0.30	-1.72	54.00**	-1.63	19.86**	26.46**	4.16**	-58.13**	D
1000-grain weight	0.15	-0.72	-1.37	-1.32	33.61**	7.54**	38.70**	-	-	-	-
Grain yield/plant	-2.52*	-0.62	-0.64	0.10	11.08**	-0.49	-5.35**	-1.29	-3.17**	10.59**	D
BH-902 × HARMAL											
Plant height	2.04*	3.60**	2.06*	-0.09	98.86**	-3.80**	1.40	1.20	3.73**	-25.46**	-
Peduncle length	23.72**	3.80**	9.66**	2.70**	12.06**	1.33	-5.76**	-6.13**	1.16	-7.66**	C
Ear length with awn	1.78	2.14*	2.45*	0.04	17.60**	-0.33	-0.83	-0.13	3.33**	-6.33**	-
Ear length without awn	0.11	0.14	2.64*	2.96**	9.40**	-0.73	-6.73**	-6.80**	0.00	6.53**	D
Number of tiller/plant	-0.14	-0.02	0.85	0.92	14.06**	-0.40	-10.86**	-	-	-	-
Number of grain/ear	-1.73	-1.04	-2.46*	-0.63	32.80**	5.00**	12.86**	10.53**	-6.26**	19.33**	C
1000-grain weight	0.06	0.20	0.38	0.33	47.67**	-4.21**	-13.29**	-	-	-	-
Grain yield/plant	1.12	3.46**	1.27	-1.25	13.55**	-6.85**	1.45	10.53**	-7.02**	-31.91**	-

* Significant at 5% and ** significant at 1% level of significance; A, B, C and D are scaling test; C and D are complementary and duplicate type of epistasis, respectively.

as well as additive × dominance (j) type of interaction. The cross LAKHAN × MOROC-9-75 revealed dominance gene effect (h), additive × dominance (j) and dominance × dominance (l) type of interaction. These results corroborate the findings of Soyhu *et al*. (2002).

Duplicate type of gene action was significant in BH-902 × BEECHER for grain yield/plant while, LAKHAN × MOROC-9-75 showed dominance gene effect (h) as well as additive × dominance (j) type of interaction. BH-902 × HARMAL revealed significant effect for three types of interactions *viz.,* additive × additive (i), additive × dominance (j) and dominance × dominance (l). The crosses LAKHAN × BEECHER, LAKHAN × HARMAL and BH-902 × MOROC-9-75 showed absence of non-allelic interaction; additive gene effect (d), dominance gene effect (h) and both additive gene effect (d) and dominance gene effect (h). These results were similar with the findings of Verma *et al*. (1981). The generation mean analysis for most of the traits showed the importance of both additive and dominant type of gene effects. In presence of epistasis, almost all the crosses revealed duplicate type of gene interaction. Only four crosses showed complementary type; in such situation additive component is often underestimated, while dominance effect tends to be overestimated (Pathak and Singh, 1970).

The present investigation revealed that epistasis as basic mechanism cannot be ignored and epistasis must be included in a model for the unprejudiced estimation of genetic components. Thus, formulating breeding policies on the basis of only main effects *i.e.* additive and dominance could be ambiguous. The results showed presence of gene action, and inter-allelic interaction varied cross-wise as well as trait-wise. Hence, specific breeding strategy has to be adopted for a particular cross to get improvement in grain yield along with desirable yield contributing traits. Most of the traits revealed presence of duplicate type of inter-allelic interaction, as a consequence of higher magnitude of interactions; the non-fixable gene effects were higher than the fixable. Moreover, duplicate type of epistasis was also found in majority of traits in one or the other cross combinations. In such crosses, the selection intensity should be more intense in the later generations because it marks the progress through selection. Hence, selection procedure such as reciprocal recurrent selection and/or biparental mating in early segregating generations for the development of high yielding barley varieties with desirable yield contributing traits would be rewarding.

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