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Gene effects for different traits of spike morphology in wheat (*Triticum aestivum*)

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ABSTRACT

The present investigation was carried out to analyse gene effects for spike morphology under two growing seasons. Six wheat (*Triticum aestivum* L.) genotypes were selected to generate the experimental material comprised six parental and segregating generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of each of the following six crosses: HS 27 × PBW 502(C-I); HS 67 × PBW 502 (C-II); HJP 81 × PBW 502 (C-III) and HG 2 × HD 2009_M (C-IV). The chi square was used to estimate the adequacy of the three parameter model, most of the characters showed the adequacy of the six parameter models indicating the presence of epistasis. Joint scaling tests revealed the presence of epistasis. Some characters like spike length in C-I (S2), C-II (SII); number of spikelets/spike in C-II (S1) and number of fertile spikelets/spike indicates the adequacy of three parameter model, i e no digenic interaction there. The epistatic gene effects were predominant over additive and dominance effects under both growing seasons. Duplicate gene interaction was observed in most of the characters which is difficult to exploit in breeding programs.

Key words: Digenic interactions, Gene effects, Generation mean analysis, Spike morphology

Spike morphology is one of the most widely used criteria for species determination and extensively investigated. Spike is probably most diverse in shape, length, width and density among different genotypes of wheat (*Triticum aestivum* L.); 2n = 6X = 42; genomes AABBDD. It is governed by polygenes mainly, three genes *Q, C* and *SI* which are located on chromosome 5A, 2D, 3D respectively. The effects of these genes are influenced by environmental factors (Sourdille *et al.* 2000, Ma *et al.* 2007 and Feng *et al.* 2009). Systematic attempts for wheat improvements are needed through manipulation of various yield components: spike number/plant, grain number/spike and grain weight. Spike morphology has more benefits of utilizing illumination than the other parts of the plant. The exploitation of genetic information has not been very well demonstrated for this vital yield contributing traits in wheat. Thus, knowledge of the nature, magnitude of gene effects and their contribution to the control of spike traits is important in formulating an efficient breeding program for wheat genetic improvement for grain yield.

There are different analysis methods to estimate genetic basis of quantitative variability of selected plant characters. Among these, generation mean analysis allows breeders to predict epistasis (Falconer 1960). It has been reported that epistatic gene action is a nontrivial factor in the inheritance of investigated plant characters and for morphological traits of the spike showed larger additive than epistatic variance. (Goldringer *et al.* 1997). In different crosses, dominance-epistatic effects and only epistatic effects were found predominant for grain yield. To utilize non-fixable gene effects (non-additive) which were higher in magnitude than fixable (additive), breeding methods involving reciprocal recurrent selection or bi-parental mating were suggested for further improvement in grain yield and tillers/plant in wheat (Shekhawat *et al.* 2006). In the study on durum wheat by Fethi and Mohamed (2010), dominance effects and dominance × dominance epistasis were found to be more important than additive effects and other epistatic components for the number of heads/plant, spikelets/spike and grains/spike.

Geneticists and plant breeders frequently use generation mean analysis to obtain information of gene action controlling the economic traits in wheat (Altinbas and Bilgen 1996, Sheikh *et al.* 2000, 2009, Esmail and Khattab *2002*, Akhtar and Chowdhry 2006, Khaled 2007, Ma *et al.* 2007, Farag 2009 and Khattab *et al*. 2010).

Generation mean analysis is a simple but useful technique for estimating gene effects for a polygenic trait, its greatest merit line in the ability to estimate epistatic gene effects such as additive × additive (aa), dominance × dominance (dd) and additive × dominance (ad) effects (Singh and Singh 1992). Although the accomplishments made in wheat breeding are

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commendable, yet concerted efforts are required to further improve the yield potential to meet the increasing demands of grains. For a systematic and successful hybridization programme a thorough understanding of genetic architecture of plant yield and other important economic characters must be achieved. For genetic studies various workers had used different biometrical methods but amongst them the approach of generation mean analysis is followed to study the gene effects. Genetic analysis of some economic characters showed different pattern of inheritance.

Spike morphology attracts the attention of breeders as it can affect grain yield. Sharma *et al.* (2002), concluded that additive gene action was important for spike length. According to Chaudhry *et al.* (2000) additive type of gene action was prominent in plant traits like flag leaf area, number of spikes/plant, spikelets/spike and grain yield/plant, while non-additive type of gene effect was important in controlling plant height, peduncle length and 1 000-grains weight. While both additive and non-additive gene effects were important in the inheritance of most of the traits like grain yield/plant, spikelets/spike, grains/spike, 1 000-grains weight, fertile tillers/plant and plant height (Shekhawat *et al.* 2000, Shekhawat *et al.* 2006 and Erkul *et al.* 2010).The present study aims to determine the types of gene effects for the different spike morphology traits in wheat.

MATERIALS AND METHODS

To achieve the objectives of present investigation, the following six wheat genotypes: PBW 502; HS 27; HS 67; HJP 81; HG 2 and HD 2009_M were selected to generate the experimental material. Experimental material comprised six parental and segregating generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of each of following four crosses**:** HS 27 × PBW 502 (C-I); HS 67 × PBW 502 (C-II); HJP 81 × PBW 502 (C-III) and HG 2 × HD 2009_M (C-IV). A set of six basic generations of each of four crosses were grown separately in randomized family block design with three replications during two winter seasons 2008-09 (S_1) and 2009-10(S_2) under two dates of sowing, i e 20.11. 2008(S_1) and 3.12.2009(S_2) respectively. Each replicate consisted of two rows of each of the parents, $F_{1 \cdot S}$ $BC_{\cdot S}$ and 20 rows of F_2 which is a segregating generation/ population. The inter row and intra plant distance was 30 cm and 10 cm respectively. All recommended package and practices to raise good crop in field were followed.

The number of plants evaluated varied depending on the treatment and was larger for the treatments consisting of generations with greater segregation such as the F_2 (with 50 plants per repetition) and the F_1, BC_1 and BC_2 (with 15 plants per repetition each) than for treatments that do not segregate such as the P_1 and P_2 parents generation (with 10 plants per repetition each). At maturity the plants were analyzed for spike morphology, viz. spike length (SPL); number of spikelets per spike (NSS); number of sterile spikelets/spike (SSPN); no. of fertile spikelets/spike (FSPN); spike compactness(SC). Generation mean analysis of the six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) were conducted using a joint scaling test (three-parameter model) based on an additive-dominance model (Cavalli 1952, Mather and Jinks 1971, Singh and Chaudhary 1979). The validity of the additive-dominance model was examined using chi-square analysis. When the three-parameter model was not adequate to explain genetic variation, six-parameter model (Hayman 1958, Singh and Chaudhary 1979) was used. All statistical analysis was performed by *OPSTAT* software developed by Dr O P Sheoran, CCS HAU, Hisar, India.

RESULTS AND DISCUSSION

There were significant variations among six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) for all studied spike morphology traits in all four wheat crosses (Table 1).

These differences for various spike morphology traits between parental genotypes were main aim of this investigation. F1 generation means were more or less closer or higher than that of greater parental genotypes for the traits under study. These results showed that dominance and additive effects were consistent and important for spike morphology. In some cases, viz. the F_1 means of spike length in C-I(S_1), C-II(S_2) and C-IV(S_1); spikelets/spike in C-I(S_2), C-II(S_1, S_2), C-III(S_1, S_2) , C-IV(S_1, S_2); sterile spikelets/spike in C-I(S_2), C-II(S_2) and fertile spikelets/spike in C-I(S_2), C-II(S_1), C-III(S_1, S_2) were more than the parental range indicating considerable heterosis for these plant traits.

In general, for some traits the F1 exceeded the better parent indicating over-dominance in some crosses. The findings of Akhtar and Chowdhry (2006) and Khatab *et al.* (2010) also supported the results of present study regarding heterosis for different plant parameters. Thus spike length and other traits can be used for selection and development of high yielding genotypes from the present material. Genetic variance among F_2 plants was found to be significant for all traits studied. Therefore, other parameters needed were estimated for all traits studied.

In the Tables (2-6), results of the scaling tests (A, B, C and D) and joint scaling test ($\chi 2$) revealed the presence of non-allelic gene interaction for all traits studied in the four crosses except for spike length in C-I (S_2), C-II (S_2); number of spikelets/spike in C-II (S_1); number of fertile spikelets/spike in C-IV(S_2). Mather and Jinks (1982) reported that significant results of scaling tests parameters indicate inadequacy of the additive - dominance model to interpret the gene effects involved in their materials, i e epistatic contributions are important in the inheritance of these traits in the particular materials investigated. Failure of simple additive dominance model in most of the cases for different characteristics revealed that genetic variations which could not be ascribed to additive and dominance effects rather revealed the presence of epistasis. Therefore, the six parameter model was followed to estimate gene effects and digenic

Table 1 Generation means and standard errors for spike morphology traits in the four different wheat cross under two sowing years, 2008-09(S_1) and 2009-10(S_2)

Generation	C-I (HS 27 × PBW 502)		C-II (HJP 81 × PBW 502)		C-III (HS 67 × PBW 502)		C-IV (HG 2 × HD 2009$_M$)´	
	S_1 Mean ± SE	S_2 Mean ± SE	S_1 Mean ± SE	S_2 Mean ± SE	S_1 Mean ± SE	S_2 Mean ± SE	S_1 Mean ± SE	S_2 Mean ± SE
Spike length (cm)(SL)								
P_1	13.517±0.121	13.33±0.14	13.017±0.158	14.26±0.16	15.537±0.159	14.73±0.12	14.920±0.227	15.27±0.16
P_2	12.483±0.128	11.32±0.20	12.387±0.165	10.68±0.12	13.713±0.167	11.38±0.17	15.803±0.142	16.23±0.21
F_1	13.702±0.141	13.29 ±0.23	12.833±0.155	14.70±0.24	14.824±0.141	14.03±0.20	16.876±0.183	15.55±0.21
F_2	13.009±0.251	12.74±0.18	13.409±0.301	13.50±0.24	13.903±0.310	12.52±0.16	15.615±0.297	14.34±0.29
BC_1	13.169±0.227	13.17±0.23	13.802±0.270	14.58±0.25	15.256±0.293	14.01±0.32	15.993±0.451	15.32±0.31
BC_2	12.040±0.325	11.87±0.304	12.558±0.393	12.96±0.49	13.953±0.340	12.60±0.36	15.518±0.482	16.30±.39
No. of spikelets/spike(NSPS)								
P_1	23.400±0.257	21.53±0.28	22.267±0.310	23.53±0.28	25.533±0.284	21.93±0.02	25.867±0.319	25.67±0.30
P_2	24.333±0.303	22.60±0.26	23.933±0.321	21.67±0.30	24.000±0.322	23.53±0.28	27.467±0.319	25.80±0.32
F_1	24.156±0.258	23.84±0.26	24.067±0.261	23.89±0.26	25.756±0.253	23.58±0.24	27.844±0.258	25.98±0.26
F_2	23.453±0.356	21.35±0.23	23.227±0.413	22.64±0.28	23.813±0.368	22.19±0.24	23.280±0.441	24.17±0.29
BC_1	22.644±0.370	22.60±0.32	23.400±0.512	23.09±0.56	24.111±0.567	23.00±0.40	25.000±0.550	24.42±0.46
BC_2	23.356±0.496	22.69±0.347	23.933±0.500	23.18±0.51	24.422±0.500	22.87±0.46	25.089±0.539	25.31±0.48
No. of sterile spikelets/spike(NSS)								
P_1	1.333±0.152	1.50±0.16	1.700±0.169	2.43±0.16	3.467±0.160	1.70±0.15	3.633±0.176	4.00±0.25
P_2	2.300±0.147	1.67±0.15	2.333±0.160	1.67±0.15	1.633±0.155	1.60±0.16	1.767±0.159	2.50±0.16
F_1	2.178±0.158	2.58 ±0.13	2.156±0.174	3.20±0.21	3.267±0.186	1.53±0.13	2.844±0.220	3.64±0.18
F_2	1.213±0.114	1.56±0.13	2.107±0.166	1.77±0.17	2.520±0.188	2.07±0.17	2.587±0.156	1.88±0.18
BC_1	1.289±0.171	1.24±0.16	1.844±0.240	2.58±0.33	2.956±0.330	1.33±0.17	2.222±0.252	2.69±0.41
BC_2	1.600±0.223	1.60±0.223	1.867±0.250	1.87±0.16	1.867±0.161	1.36±0.18	2.000±0.352	2.04±0.39
No. of fertile spikelets/spike(FSNS)								
P_1	22.067±0.184	20.03±0.30	20.5670.396	21.10±0.31	22.0670.248	20.23±0.03	22.233±0.284	21.60±0.31
P_2	22.033±0.269	20.93±0.32	21.400±0.348	20.00±0.33	22.367±0.305	21.93±0.30	25.600±0.317	23.17±0.34
F_1	21.978±0.230	21.27±0.30	21.911±0.320	20.44±0.32	22.489±0.152	22.04±0.04	25.000±0.357	22.33±0.31
F_2	22.240±0.384	20.13±0.24	21.120±0.443	20.87±0.33	21.293±0.359	20.12±0.28	20.693±0.480	22.49±0.33
BC_1	21.356±0.420	21.36±0.39	21.556±0.546	20.51±0.66	21.156±0.454	21.67±0.42	22.778±0.644	21.73±0.62
BC_2	21.756±0.514	21.09±0.389	22.067±0.565	21.31±0.54	22.556±0.518	21.51±0.48	23.089±0.558	23.27±0.68
Spike density(SD)								
P_1	1.731±0.016	1.71±0.03	1.710±0.018	1.65±0.01	1.643±0.007	1.92±0.01	1.857±0.020	1.68±0.01
P_2	1.949±0.016	2.00±0.03	1.934±0.026	2.00±0.03	1.963±0.019	2.11±0.02	1.738±0.012	1.59±0.02
F_1	1.764±0.009	1.68±0.03	1.877±0.022	1.65±0.04	1.736±0.004	1.96±0.01	1.653±0.012	1.68±0.01
F_2	1.820±0.030	1.69±0.03	1.753±0.030	1.70±0.03	1.732±0.024	2.39±0.04	1.519±0.042	1.72±0.04
BC_1	1.728±0.043	1.72±0.03	1.707±0.055	1.59±0.05	1.586±0.041	2.17±0.04	1.576±0.045	1.60±0.04
BC_2	1.962±0.072	1.93±0.06	1.930±0.066	1.83±0.08	1.639±0.080	2.38±0.07	1.640±0.059	1.53±0.07

S_1, S_2 indicates the sowing year 2008-09 and 2009-10 respectively.

interactions following Jinks and Jones (1958) model.

Six parameter model results are presented in Tables 2-6, which revealed the types of gene effects estimated by generation means for various traits of spike morphology. Mean effects (m) were highly significant for the estimated values which indicated that all the studied characters were quantitatively inherited.

The additive gene effects (d) were significant and either positive or negative for all traits studied except for C-IV(S1); number of spikelets per spike in C-1(S_2), C-II (S_2), C-III(S_1,S_2), C-IV(S_1), number of sterile spikelets/spike in C-I (S_1), C-II (S_1), C-III(S_2), C-IV(S_1); number of fertile spikelets per spike in C-I(S1, S_2) C-II(S_1, S_2), C-III(S_2), C-IV(S_1); spike compactness in C-III(S_1), C-IV(S_1), suggesting the potential for obtaining further improvement of these traits by selection practice of their progenies. The results are in agreement with the findings of Walia (1995) and Sharma *et al.* 2006. They revealed that additive genetic effects (d) were

Table 2 Estimates of different scaling tests, joint scaling tests and genetic components in the best fit model for spike length (cm) in wheat

Parameter	C-I (HS 27 × PBW 502)		C-II (HJP 81 × PBW 502)		C-III (HS 67 × PBW 502)		C-IV (HG 2 × HD 2009$_M$)´	
	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE
Scaling test								
A	0.881**±0.284	0.2867 ±0.3038	–1.754**±0.337	–0.206±0.3289	–0.150±0.360	0.7422± 0.3879	–1.191*±0.548	0.1767±0.3879
B	2.106**±0.39	0.7611±0.3919	0.104±0.472	–0.526±0.5825	0.631±0.412	0.2022± 0.4400	1.643**±0.573	-814±0.4803
C	1.367*±0.611	0.2722± 0.5112	–2.567**±0.730	0.3444± 0.6323	3.288**±0.746	4.1062**±0.4538	1.016±0.734	5.248**±0.726
D	0.810*±0.370	0.4378± 0.3024	0.459±0.443	-0.5378±0.4189	–1.404**±0.44	–0.5809**±0.3336	–0.282±0.513	–2.94**±0.4402
χ2 (df)	39.12**	5.26	36.70**	1.73	21.58**	83.35**	15.42**	59.23**
Joint scaling test (Three parameter)								
m	12.929**±0.049	12.28**±0.067	12.793**±0.063	12.47**±0.05492	14.568**±0.064	12.92**±0.05692	14.860**±0.074	15.67**± .072
d	-0.530**±0.050	–1.037**±0.06	–0.381**±0.064	–1.789**±0.0552	–0.938**±0.063	–1.707**± 0.058	0.897**±0.075	0.487**±0.073
h	0.592**±0.094	0.887**±0.136	0.213**±0.110	2.2514**±0.13619	0.174**±0.010	0.6136**±0.119	1.966**±0.129	–0.34**±0.138
Best fit mode l (Six parameter)								
m	13.0**±0.145	12.74**± 0.104	13.409**±0.174	13.50**±0.1385	13.903**±0.179	12.5173**±0.094	15.615±0.172**	14.336±0.167**
d	1.129**±0.23	1.296**±0.2191	1.244**±0.275	1.6267**±0.3141	1.302**±0.259	1.4067**±0.2758	0.476±0.381	–0.976**±0.287
h	–0.917±0.745	2.091** ± 0.623	–0.786±0.893	3.3078**±0.8514	3.007**±0.890	4.1362**±0.6792	2.577*±1.034	5.683**±0.8918
i	–1.62*±0.739	–0.8756±0.6048	–0.917±0.886	1.0756± 0.8377	2.807**±0.883	3.1618**±0.6671	0.564±1.026	5.886**±0.8804
j	1.224**±0.469	0.5744 ±0.4605	1.859**±0.566	–0.32±0.6384	0.781±0.535	–0.540±0.5644	2.834**±0.778	–0.991±0.5934
l	4.606**±1.101	2.023± 1.2147	-0.733±1.320	–0.8067±1.4065	–2.326±1.277	–0.217±1.1930	–0.111±1.693	–0.524**±1.358
Type of epistasis					Duplicate			Duplicate

Table 3 Estimates of different scaling tests, joint scaling tests and genetic components in the best fit model for no. of spikelets/spike in wheat

Parameter	C-I (HS 27 × PBW 502)		C-II (HJP 81 × PBW 502)		C-III (HS 67 × PBW 502)		C-IV (HG 2 × HD 2009$_M$)´	
	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE
Scaling test								
A	2.267**±0.476	0.1778±0.4338	–0.467±0.635	1.245±0.685	3.067**±0.691	–0.489±0.513	3.711**±0.678	2.80**±0.5815
B	1.778**±0.617	1.0667 *±0.4529	0.133±0.624	–0.80 ± 0.637	0.911±0.624	1.378*±0.572	5.133**±0.666	1.1556±0.602
C	2.231*±0.904	6.436**± 0.646	1.427±1.032	2.4178**± 0.75	5.791**±0.932	3.875**±0.668	15.902**±1.092	6.73** ±0.7835
D	0.907±0.545	–2.596**± 0.3805	–0.880±0.630	–0.987± 0.5456	–0.907±0.609	–1.493**±0.4475	–3.529**±0.676	–3.387** ±0.512
χ2 (df)	31.16**	104.23**	2.73	15.58**	53.19**	40.91**	263.99**	85.65**
Joint scaling test (Three parameter)								
m	23.664**±0.108	21.73**±0.10	23.073**±0.121	22.490**±0.1115	24.490**±0.116	22.5**± 0.11130	26.000**± 0.123	25.31**±0.1161
d	0.502**±0.109	0.5**±0.10	0.806**±0.123	–0.870**±0.1157	–0.730**±0.119	0.71945**±0.11634	0.739**± 0.125	0.1353**± 0.120
h	0.131**±0.186	1.5**±0.18	0.958**±0.197	1.220**±0.19035	0.868**±0.191	0.77677**±0.18397	0.971**± 0.197	0.059**±0.1955
Best fit mode l (Six parameter)								
m	23.45**±0.206	21.3467**±0.1321	23.227**±0.238	22.64**±0.1617	23.813**±0.212	22.187**±0.1392	23.280**±0.255	24.174**±0.17
d	–0.711*±0.357	–0.0889±0.2738	–0.533**±0.213	–0.089±0.4394	–0.311±0.437	0.134 ±0.35	–0.089±0.445	–0.89*±0.3844
h	–1.524±1.106	6.969**±0.7833	2.727*±1.276	3.263**±1.1079	2.802**±1.233	3.83**±0.9139	8.236**±1.366	3.018**±1.0436
i	–1.813±1.089	5.191**±0.761	1.760±1.261	1.9734±1.0912	1.813±1.218	2.987**±0.8951	7.058**±1.352	2.774**±1.0249
j	–0.489±0.70	0.8889±0.5907	0.600±0.865	–2.045**±0.911	–2.156*±0.908	1.867*±0.7434	1.422±0.927	–1.645*±0.809
l	5.858**±1.69	–3.9467±1.2714**	–2.093±1.948	–1.5289±1.9117	2.164±1.980	–0.098±1.5528	1.787±2.088	1.1822±1.726
Type of epistasis								

Table 4 Estimates of different scaling tests, joint scaling tests and genetic components in the best fit model for no. of sterile spikelet/spike in wheat

Parameter	C-I (HS 27 × PBW 502)		C-II (HJP 81 × PBW 502)		C-III (HS 67 × PBW 502)		C-IV (HG 2 × HD 2009$_M$)´	
	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE
Scaling test								
A	0.933**±0.234	1.5889**±0.2171	0.167±0.310	0.478±0.408	0.822*±0.407	0.5667*±0.2219	2.033**±0.333	2.2667**±0.506
B	1.278**±0.286	1.0444**±0.2819	0.956**±0.319	1.133 ** ±0.2391	1.167**±0.233	0.4222±0.2429	0.611±0.436	2.055**±0.465
C	3.136**±0.343	2.082**±0.35	0.118±0.452	3.407**±0.475	1.553**±0.501	–1.90**±0.429	0.742±0.462	6.269**±0.487
D	–0.462*±0.209	0.2756 ±0.2155	0.502±0.277	–0.898**±0.287	0.218±0.304	1.45**±0.24	0.951**±0.308	–0.973** ±0.384
χ2 (3)	89.99**	76.44**	9.17*	58.08**	29.88**	37.45**	37.88**	178.37**
Joint scaling test (Three parameter)								
m	1.590**±1.590	1.34**± 0.057	2.079**±0.063	1.9**±0.05986	2.433**±0.060	1.65**±0.05668	2.603**±0.064	2.81**±0.07845
d	0.479**±0.479	0.18**± 0.05	0.380**±0.064	–0.4268**±0.060	–0.978**±0.061	–0.0295**±0.0571	–0.847**±0.066	–0.578**±0.0818
h	0.077**±0.077	0.91279**±0.097	–0.011**±0.117	0.7505**± 0.125	0.502**±0.118	–0.1168**±0.0969	–0.066**±0.133	0.214**±0.1316
Best fit mode l (Six parameter)								
m	1.213**±0.066	1.560**±0.0736	2.107**±0.096	1.7733**±0.0970	2.520**±0.109	2.0667**±0.0954	2.58**7±0.090	1.88**± 0.1023
d	–0.311±0.162	–0.3556*±0.1575	–0.022±0.200	0.7111**±0.2110	1.089**±0.212	–0.0222±0.143	0.222±0.250	0.65*±0.3253
h	1.286**±0.432	0.4433±0.4421	–0.966±0.566	2.9456**±0.5895	0.281±0.620	–3.006**±0.4863	–1.76**±0.634	2.3411**±0.780
i	0.924*±0.418	–0.5511±0.43	–1.004±0.553	1.7956**±0.5733	–0.436±0.607	–2.889**±0.4764	–1.90**±0.617	1.9467**±0.769
j	0.344±0.346	–0.5444±0.3398	0.789±0.422	0.6556±0.4408	0.344±0.443	–0.145±0.3114	–1.42**±0.518	–0.21±0.6728
l	1.287±0.734	3.1844**±0.7224	2.127*±0.919	–0.185±0.9686	2.424*±0.986	3.878**±0.7138	4.547**±1.102	2.3756±1.389
Type of epistasis						Duplicate	Duplicate	

Table 5 Estimates of different scaling tests, joint scaling tests and genetic components in the best fit model for no. of fertile spikelets/spike in wheat

Parameter	C-I (HS 27 × PBW 502)		C-II (HJP 81 × PBW 502)		C-III (HS 67 × PBW 502)		C-IV (HG 2 × HD 2009$_M$)´	
	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE
Scaling test								
A	1.333**±0.514	–1.411±0.5132**	–0.633±0.696	0.5222±0.8095	2.244±0.550**	–1.056±0.5409**	1.678±0.789*	0.4667±0.757
B	0.500±0.628	0.0222± 0.5151	–0.822±0.707	–2.1778±0.674**	–0.256±0.630	0.9556±0.5979	4.422±0.701**	–1.034±0.826
C	–0.904±0.945	2.9667±0.701**	1.309±1.130	–1.4778±0.896	4.238±0.877**	5.7756± 0.7616**	15.060±1.209**	–0.51±0.8837
D	1.369*±0.586	–2.178±0.4217**	–1.382±0.684*	–0.0889±0.626	–1.124±0.574**	–2.9378±0.485**	–4.480±0.742**	–0.027±0.653
χ2 (3)	8.80*	34.23**	8.19*	12.67**	38.023**	71.11**	176.63**	2.28
Joint scaling test (Three parameter)								
m	22.030**±0.090	20.38±0.1155	20.998**±0.141	20.66**± 0.1236	22.032**±0.106	20.84**±0.11709	23.505**±0.118	22.42**±0.12446
d	0.007**±0.091	0.3464**±0.11	0.422**±0.144	–0.443**±0.127	0.214**±0.109	0.7488**±0.12070	1.546**±0.119	0.8301**± 0.129
h	–0.118**±0.160	0.70815**±0.21	0.936**±0.238	–0.0103**±0.223	0.334**±0.142	0.7971**±0.20422	0.368**±0.232	–0.0324**±0.218
Best fit mode l (Six parameter)								
m	22.24**±0.222	20.133**±0.1386	21.120**±0.256	20.8667**±0.193	21.293**±0.207	20.120**±0.160	20.693±0.277**	22.4867**±0.19
d	–0.400±0.383	0.2667±0.3178	–0.511±0.454	–0.800±0.4928	–1.400**±0.398	0.1556±0.3646	–0.311±0.492	–1.5333**±0.53
h	–2.810*±1.183	5.1389**±0.8702	3.692**±1.389	0.0722±1.2731	2.521*±1.157	6.8367**±0.9919	10.043±1.502**	1.325±0.0033
i	–2.738*±1.172	4.3556**±0.8434	2.764*±1.368	0.1778±1.2528	2.249*±1.148	5.8756**±0.9701	8.960±1.483**	0.0533±1.307
j	–0.833±0.789	1.4333*± 0.6850	–0.189±0.957	–2.70**±1.0204	–2.500**±0.827	2.0111**±0.7730	2.744±1.014**	–1.50±1.092
l	4.571*±1.800	–5.75**±1.4516	–4.220*±2.139	–1.8333± .1655	–0.260±1.816	–5.9756**±1.645	–2.860±2.310	–0.620±2.296
Type of epistasis	Duplicate	Duplicate	Duplicate			Duplicate		

Table 6 Estimates of different scaling tests, joint scaling tests and genetic components in the best fit model for spike density in wheat

Parameter	C-I (HS 27 × PBW 502)		C-II (HJP 81 × PBW 502)		C-III (HS 67 × PBW 502)		C-IV (HG 2 × HD 2009_{M})´	
	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE	S_1 Estimate ± SE	S_2 Estimate ± SE
Scaling test								
A	0.038±0.050	–0.1484**±0.043	0.174**±0.066	0.124± 0.0578*	0.207**±0.048	–0.138**±0.049	0.357**±0.053	0.16±0.0508
B	–0.21*±0.084	–0.1788*± 0.072	–0.048±0.079	0.0018± 0.0970	0.420**±0.093	0.078± 0.074	0.112±0.069	0.218± 0.081
C	–0.073±0.070	0.217**± 0.0751	0.389**±0.076	0.1708*±0.0817	0.150**±0.057	–0.226**±0.066	0.827**±0.098	–0.218**±0.086
D	–0.051±0.059	–0.272**± 0.050	–0.132*±0.060	–0.0226±0.063	0.239**±0.059	0.083±0.0511	–0.179**±0.064	0.2978**±0.063
$\chi2$ (3)	8.00*	32.79**	32.69**	7.62*	45.12**	19.94**	112.97**	24.03**
Joint scaling test (Three parameter)								
m	1.842**±0.006	1.81**±0.008	1.811**±0.009	1.82**± 0.00967	1.796**±0.006	1.78**±0.00827	1.781**±0.007	1.64**±0.00491
d	0.111**±0.006	0.1897**± 0.007	0.112**±0.009	0.1731**±0.0097	0.156**±0.006	0.29223**±0.00840	–0.048**±0.007	–0.0461**±0.0049
h	–0.077**±0.008	–0.12138**±0.018	0.042**±0.015	–0.1995**±0.021	–0.062**±0.006	–0.0839**±0.016	–0.142**±0.010	0.04717**±0.00788
Best fit mode l (Six parameter)								
m	1.82**±0.017	1.6905**±0.0159	1.753±0.017**	1.697±0.0166**	1.732±0.014*	1.784**± 0.0143	1.519**±0.024	1.7151**±0.021
d	–0.23**±0.05	–0.207**±0.0391	–0.223**±0.05	–0.236**±0.053	–0.053±0.052	–0.184**±0.042	–0.063±0.043	0.075**±0.128
h	0.025±0.119	0.415**±0.1027	0.319**±0.122	–0.126±0.1280	–0.545**±0.1	–0.268**±0.103	0.213±0.129	–0.547**±0.127
i	0.101±0.118	0.545**±0.1008	0.264*±0.121	0.0452±0.1258	–0.48**±0.118	–0.166±0.102	0.357**±0.129	–0.596**±0.127
j	–0.25*±0.097	–0.03±0.0799	–0.222*±0.101	–0.122±0.1087	0.213*±0.105	0.216*±0.0864	–0.245**±0.087	0.0579±0.095
l	–0.275±0.205	–0.872±0.1735	–0.138±0.213	0.0805± 0.2287	1.104**±0.216	0.1066±0.182	0.112±0.197	0.973**±0.208
Type of epistasis					Duplicate			Duplicate

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

*, ** indicates that the value was significant by the t-test at the 5% and 1% probability level respectively.

S_1, S_2 indicates the sowing year 2008-09 and 2009-10 respectively.

more important than dominance effects (h) for spike length, spikelets/spike in wheat. While Chowdhry *et al*. (1999) reported that spike length was controlled by partial dominance with additive gene action in wheat.

The magnitude of additive gene effects (d) were small relative to the corresponding dominance effects (h) in most cases, suggesting that pedigree selection method is a useful breeding program for improving these populations. However, the negative value of (h) observed in most cases indicated that the alleles responsible for less value of the trait were dominant over the alleles controlling high value. These results are in harmony with those obtained by Srivastava *et al.* (1992), Esmail and Khattab (2002), Seikh *et al*. (2009) and Erkul *et al*. (2010).

The inheritance of quantitative traits become complex as the contribution of (h) to their inheritance becomes more. Also, sign of (h) has enhancing effects on expression in that particular direction. The negative dominance effects were noticed for almost all characters. The digenic, interactions, i, j and l were found important for most of the characters. But the type and magnitude of epistatic effects varied from character to character and cross to cross. These results are in agreement with Singh and Singh (1992) and Yadava *et al.* (1995), Novoselovic *et al*. (2004) and Sheikh *et al.* (2009).

Considering individual digenic epistatic effects, additive × additive type of gene effects [i] was significant and detected for spike length in C-I(S_1, S_2), C-III(S_2); C-IV(S_2); number of spikelets/spike in C-1(S_2), C-III (S_2), C-IV(S_1,S_2), number of sterile spikelets/spike in C-I (S_1), C-II (S_2), C-III(S_2), C-IV($S_{1,}$ S_2); number of fertile spikelets per spike in C-I(S_1, S_2) C-II(S_1, S_2), C-III(S_2), C-IV(S_1); spike compactness/ density in C-I(S_2), C-II(S_1) C-III(S_1), C-IV(S_1, S_2). Additive × dominance [j] epistatic type of gene effects was found to be significant detected for spike length in C-I(S_1), C-II(S_1); C-IV(S_1); number of spikelets/spike in C-II(S_2), C-III (S_1, S_2), C-IV(S_2), number of sterile spikelets/spike in C-IV(S_1); number of fertile spikelets/spike in C-I(S_2) C-II(S_2), C-III(S_1, S_2), C-IV(S_1); spike compactness in C-I(S_1), C-II(S_1), C-III(S_1, S_2), C-IV(S_1). The negative sign of additive × dominance [j] interaction in most cases also suggested dispersion of genes in the parents. Concerning the third type of epistatic effect, i e dominance × dominance [l], highly significant effects were detected spike length in C-I(S_1), C-IV(S_2); number of spikelets/spike in C-I(S_1, S_2); number of sterile spikelets/spike in C-I(S_2), C-II(S_1), C-III(S_1, S_2) C-IV(S_1); number of fertile spikelets/spike in C-I(S_1, S_2), C-II(S_1) C-III(S_2); spike compactness in C-III(S_1), C-IV(S_2). These results are in agreement with those obtained by Khattab *et al*. (2001), Esmail and Khattab (2002), Mahgoub and Hamed (2006), Khaled (2007) and Farag (2009).

The traits which controlled by complementary type epistasis (i) are easy to exploit for the crop improvement, whereas those controlled by duplicate epistasis are difficult to exploit since in case of former type the association between the two parameters h and l is positive. In present investigation, the estimate (h) and (l) had opposite sign in majority of all crosses for different characters which suggesting duplicate type of non-allelic interaction in these traits, while complementary epitasis type of gene effects gave similar signs of (h) and (l) for all other traits in the four crosses.

In cases of spike length in C-III(S_1); number of fertile spikelets/spike in C-IV(S_2); spike density in C-II(S_2), the additive–additive model was found to be inadequate, when it was subjected to six parameter model and failed to show any of the significant gene effects. This may be due to the presence of higher order interaction (trigenic etc.) or G × E interaction or linkage.

Results obtained here revealed the importance of epistatic types of gene effects in the inheritance of all traits studied, and cannot be ignored when establish a new breeding program to improve wheat populations for spike traits. The inheritance of all traits studied was controlled by additive and non-additive genetic effects, with greater values of dominance gene effect than the additive one in most cases. When additive effects are larger than the non-additive, it is suggested that selection in early segregating generations would be effective, while, if the non-additive portion are larger than additive, the improvement of the characters needs intensive selection through later generation. These findings correspond with the results published by other authors (Singh *et al.* 1986, Singh and Singh 1992, Singh *et al*. 1998, Sheikh *et al.* 2009, Khattab *et al.* 2010 and Erkul *et al.* 2010). This information is of importance for wheat breeders to improve yield potential, release new wheat genotypes and enhancement of wheat germplasm.

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