



Research Article

GENETIC DISSECTION FOR YIELD ATTRIBUTES IN THE FIVE WHEAT CROSSES UNDER TWO SOWING SEASONS

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Abstract- The study was carried out to analyse gene effects for various yield attributes in wheat at CCS Haryana Agricultural University Hisar during *rabi* 2008-09 and 2009-10. six basic populations (parents, F₁, backcrosses and F₂) of the five wheat crosses namely HS 27 × PBW 502(C-I); HS67 × PBW 502 (C-II); HJP 81 × PBW 502 (C-III) and HG 2 × HD 2009M (C-IV) were grown in the compact family block design in three replications and the morpho-phenological characters such as plant height, Number of spikelet/spike, Number of kernel/spike, Kernel weight/spike (g), Number of spikes per plant, Grain yield per plant (g). By scaling tests the duplicate gene interaction was observed in most of the characters which is difficult to exploit in breeding programs. Some traits shows failure of six parameter model reflected the occurrence of either higher order gene interactions or linkage between the interacting loci or the presence of genotype × environment interaction which may also influence the expression of character(s). Since several important characters are influenced by non-allelic gene interaction.

Keywords- Gene interactions, Epistatic, Gene Effects, Generation Mean Analysis, Yield Attributes.

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Introduction

Wheat is the second most important food crop of the world which required the improvement in productivity enhancement by exploiting the genetic diversity from the germplasm. Further, the phenological traits are responsible for selection of breeding material for wheat improving whereas the yield is considerably affected by sowing date and maturity time. The gene effect knowledge about the phenological traits could lead to the creation of new plant populations in wheat species with a promise to formulating an efficient breeding programme for wheat genetic improvement.

Knowledge of the gene effects of the quantitative characters is useful in the formulation of efficient breeding programme towards tailoring and utilizing efficient plant type. 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 gene effects including epistasis [1-4]. 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 [1-4,6]. 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 [22]. 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 [1,8,11-13,18-

21]. 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 [24]. Although the accomplishments made in wheat breeding are 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 [8,13,18,19]. Genetic analysis of some economic characters showed different pattern of inheritance.

Material and Methods

Seven diverse parents PBW502; HS27; HS67; HJP81; Rm-Ts17; HG2 and HD2009M were selected to develop six generations i.e. P₁, P₂, F₁, F₂, B₁ and B₂ in five cross combinations: HJP81 × Rm-Ts17(C-I); HS27 × PBW502 (C-II); HJP81 × PBW502 (C-III); HS67 × PBW502 (C-IV); HG2 × HD2009M (C-V) [Table-1]. A set of these generations i.e. P₁, P₂, F₁, F₂, B₁ and B₂ of each five crosses were evaluated in Compact Family Block Design with three replications, during two *rabi* seasons viz. WS₁: *Rabi* season 2008-2009; WS₂: *Rabi* season 2009-2010 with different dates of sowing, i.e. 20.11. 2008 (WS₁) and 3.12.2009 (WS₂) respectively at farm of the Department of Genetics and Plant Breeding, CCSHAU, Hisar. Among the treatments, the non segregating generations, viz., parents P₁, P₂, and F₁ were grown in single row of 3m length. The segregating F₂ generation was grown in ten rows of 3m row length and backcrosses B₁ and B₂ were grown in four rows of 3m length. The row to row and plant to plant distance was maintained

23 cm and 10 cm, respectively. All recommended package of practices were followed to raise the healthy crop. Ten plants from each non-segregating P₁, P₂ and F₁ generations were selected. Whereas, 15 plants from each backcross generation and 50 plants from F₂ generation were selected for observing data on plant height (PH) (cm), Number of tillers per plant, number of spikelets per spike (NSS); spike biomass (g) (SB), grain weight per spike (g) (GWS), number of kernels per spike (NKS), grain : spike biomass ratio, grain yield per plant (GY)(g). Generation mean analysis of the six basic generations namely P₁, P₂, F₁, F₂, BC₁ and BC₂ were conducted using a joint scaling test (three-parameter model) based on an additive-dominance model [2, 15, 25]. 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 [9, 25] was used. All statistical analysis was performed by OPSTAT software developed by Dr O P Sheoran, CCS HAU, Hisar, India.

Table-1 Pedigree of parental genotypes involved in five wheat crosses

Genotype	Pedigree
PBW 502	WH485/PBW 343/RAJ/1482
HD 2009 _M	A mutant of HD2009 (ARJUN): LR64A/NAI60
HG2	Advanced line derived from WH 157 x GP 104 ('gigas' spike)
HS27	RILL derived from S 308 : (1154-38-Andes x YT 54-N 103) LB and
HS67	Harrier 's' [(Cno's' - No. 66/C273 x NP 875 - E 853.5.8) 7C] Hock 's'
HJP81	Heritage collection Jai Parkash, a progressive farmer
Rm-Ts17	Advanced line derived from WH 157 x GP 104 ('gigas' spike)

Result and Discussion

Analysis of variance showed that the progenies were highly significant for all the characters in all the crosses [Table-2]. This suggested that the genotypes selected were genetically variable and considerable amount of variability generated in their

filial generations, which facilitate possibility of selection in a breeding programme. Similarly, many scientists also reported high variability in the filial and backcross generations of wheat [14-16]. The significant variation due to year × progenies for plant height (cm), number of spikelets per spike, spike biomass (g), grain weight per spike (g), number of kernels per spike, grain : spike biomass ratio and grain yield per plant (g) revealed that different progenies behaved differently over the different years, for these traits.

Adequacy of the Genetic Model

Both individual (A, B, C and D) and joint scaling tests were used in all the crosses to determine whether at all the additive-dominance model was adequate for different traits [Table-3]. Further the three parameters m, (d) and (h) were estimated through joint scaling test wherever the additive-dominance model was satisfactory under three parameters. The significant values of scale A, B, C, D in all most all five crosses [Table-4-10] indicated that the non-allelic interactions were present and additive-dominance model was not fit in both the seasons for plant height, Number of spikelet/spike, Number of kernel/spike, Kernel weight/spike (g), Number of spikes per plant, Grain yield per plant (g). It was also substantiated by significant χ^2 -value which suggested that three parameter model was not sufficient. The additive-dominance effects were found significant in joint scaling test for plant height in cross-III (WS₂); Number of spikelet/spike for HJP81 × PBW502 in WS₁; Kernel weight/spike (g) for the cross HS67 × PBW502 in WS₁ and HS67 × PBW502 (WS₁) which is also supported by non-significant χ^2 -value. The joint scaling test also indicated the inadequacy of the 3 parameter for Grain: spike biomass ratio in; Number of spikes per plant and Grain yield per plant (g) all five crosses in WS₁ and both WS₂. The joint scaling test also showed the inadequacy of the 3-parameter for all five crosses in WS₁ and WS₂ and was reflected further by the significant χ^2 -value

Table-2 Mean performances of six basic generations for number of spikelet/spike, number of sterile spikelet/spike and number of fertile spikelet/spike in the five wheat crosses for two growing seasons: 2008-09 (WS₁) and 2009-10 (WS₂)

Generations/Crosses/ Seasons		P ₁	P ₂	F ₁	F ₂	BC ₁	BC ₂
		Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
1. Plant Height (cm)							
Cross-I HJP81 x Rm-Ts 17	WS ₁	117.77±0.339	81.63±0.337	116.77±0.761	103.33±2.022	108.84±2.691	95.02±3.555
	WS ₂	115.23±0.284	81.7±0.382	116.75±0.616	104.86±2.032	110.55±2.403	97.22±3.806
Cross- II HS 27 x PBW502	WS ₁	110.50 ± 0.26	85.93 ± 0.234	114.73±0.186	95.08±2.128	109.26±1.255	98.68±3.482
	WS ₂	109.30 ± 0.26	82.77 ± 0.39	114.40±0.22	87.00±1.65	108.51±0.94	93.80±3.093
Cross-III HJP81xPBW502	WS ₁	114.17 ± 0.236	86.90 ± 0.487	116.31±0.415	104.86±2.032	113.02±0.976	98.55±3.586
	WS ₂	102.47 ± 0.33	81.67 ± 0.44	114.80±0.22	101.35±1.94	108.22±1.68	95.02±3.55
Cross-IV HS67 x PBW 502	WS ₁	111.10 ± 0.292	84.73 ± 0.287	115.75±0.287	102.56±1.966	110.26±1.410	98.02±3.685
	WS ₂	118.10 ± 0.28	82.40 ± 0.19	115.00±0.21	105.17±2.28	111.36±2.55	96.84±3.51
Cross- V (HG2 x HD2009 _M)	WS ₁	88.617 ± 0.354	138.43 ± 0.378	140.33±0.369	115.35±2.331	100.78±3.288	122.84±3.188
	WS ₂	86.03 ± 0.43	136.60 ± 0.91	136.38±0.99	108.76±2.51	103.11±4.67	125.91±2.78
2. Number of Spikelet/Spike							
		P ₁	P ₂	F ₁	F ₂	BC ₁	BC ₂
		Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Cross-I HJP81 x Rm-Ts 17	WS ₁	24.2±0.427	25.8±0.315	24.91±0.381	23.6±0.319	23.26±0.500	24.46±0.472
	WS ₂	24.06±0.431	25.33±0.292	24.64±0.336	23.41±0.400	23.48±0.443	24.73±0.435
Cross-II (HS 27 x PBW502)	WS ₁	23.40±0.257	24.33±0.303	24.15±0.258	23.45±0.356	22.64±0.370	23.35±0.496
	WS ₂	21.53±0.28	22.60±0.26	23.84±0.26	21.35±0.23	22.60±0.32	22.69±0.347
Cross-III (HJP81 x PBW502)	WS ₁	22.26±0.310	23.93±0.321	24.06±0.261	23.22±0.413	23.40±0.512	23.93±0.500
	WS ₂	23.53±0.28	21.67±0.30	23.89±0.26	22.64±0.28	23.09±0.56	23.18±0.51
Cross-IV (HS67 x PBW 502)	WS ₁	25.53±0.284	24.00±0.322	25.75±0.253	23.81±0.368	24.11±0.567	24.42±0.500
	WS ₂	21.93±0.02	23.53±0.28	23.58±0.24	22.19±0.24	23.00±0.40	22.87±0.46
Cross -V (HG2 x HD2009M)	WS ₁	25.86±0.319	27.46±0.319	27.84±0.258	23.28±0.441	25.00±0.550	25.08±0.539
	WS ₂	25.67±0.30	25.80±0.32	25.98±0.26	24.17±0.29	24.42±0.46	25.31±0.48

Gene action and Epistasis Effects

In the present investigation, the failure of three parameter to reveal the presence of epistatic interaction effect has been observed for cross HJP81 x Rm-Ts17 in respect of characters plant height, number of spikelets per spike, under season WS₁ i.e. 2008-09 and for characters plant height, kernel weight/spike, under season WS₂ (2009-10). The absence of epistasis based on six-parameter model has been observed in cross HS27 x PBW502 for kernel weight/spike under WS₁

and spike length in WS₂ whereas for cross HJP81 x PBW502 for plant height under both seasons, for number of spikelets per spike. The cross HS67 x PBW502 indicated the inadequacy of six parameter to detect the epistasis for characters plant height and kernel weight in both the seasons and for spike biomass in WS₂ whereas in cross HG2 x HD2009_M such an inadequacy of six parameter model for detection of any type of epistatic effect i.e. failure of model has been observed for spike biomass under WS₂.

3. Spike Biomass(g)							
Cross-I HJP81 x Rm-Ts 17	WS ₁	3.34±0.047	3.99±0.103	5.19±0.107	4.75±0.122	5.23±0.110	4.51±0.208
	WS ₂	3.48±0.049	3.96±0.075	4.32±0.081	4.74±0.124	5.25±0.132	4.35±0.218
Cross- II HS 27 x PBW502	WS ₁	2.60±0.011	2.35±0.017	4.23±0.016	3.69±0.145	2.73±0.146	2.97±0.198
	WS ₂	2.44±0.01	2.32±0.02	2.43±0.03	2.42±0.10	2.55±0.09	2.52±0.15
Cross-III HJP81xPBW502	WS ₁	2.45±0.020	2.32±0.016	2.85±0.019	3.03±0.073	2.77±0.070	2.79±0.126
	WS ₂	2.75±0.01	2.21±0.02	2.62±0.01	2.39±0.08	2.55±0.07	2.44±0.08
Cross-IV HS67 x PBW 502	WS ₁	2.74±0.007	2.31±0.012	3.61±0.011	3.21±0.100	3.65±0.260	2.98±0.182
	WS ₂	3.00±0.02	2.96±0.02	2.99±0.03	2.02±0.47	2.87±0.13	2.09±0.14
Cross -V (HG2 x HD2009 _M)	WS ₁	3.05±0.021	4.80±0.025	5.85±0.019	4.66±0.153	4.10±0.189	4.89±0.183
	WS ₂	3.04±0.02	3.99±0.02	3.90±0.03	3.28±0.47	3.31±0.13	3.82±0.14
4. Number of Kernels/Spike							
Cross-I HJP81 x Rm-Ts 17	WS ₁	59.56±0.378	69.3±0.558	68.42±0.636	59.55±1.732	55.55±1.957	63.80±1.610
	WS ₂	55.83±0.381	65.9±0.303	68.97±0.645	58.88±1.415	56.57±1.771	60.17±2.325
Cross- II HS 27 x PBW502	WS ₁	52.76±0.307	41.43±0.404	56.53±0.342	50.54±1.254	49.42±1.932	46.91±2.049
	WS ₂	50.87±0.66	39.77±0.46	57.49±0.27	53.05±1.40	49.42±1.93	46.91.049
Cross-III HJP81xPBW502	WS ₁	52.53±0.396	40.46±0.523	60.51±0.384	55.38±1.659	53.53±1.289	49.93±2.403
	WS ₂	56.03±0.44	40.97±0.56	59.84±0.60	47.27±1.42	50.98±1.72	45.82±2.25
Cross-IV HS67 x PBW 502	WS ₁	55.900±0.254	43.63±0.357	67.75±0.378	55.67±1.468	53.46±2.091	54.26±2.556
	WS ₂	51.17±0.48	40.33±0.41	67.82±0.57	53.53±2.06	51.80±2.25	48.04±2.40
Cross -V (HG2 x HD2009 _M)	WS ₁	52.66±0.434	66.80±0.435	66.75±0.405	52.01±1.781	57.64±2.001	61.53±2.164
	WS ₂	50.07±0.48	67.90±0.41	68.49±0.57	56.23±2.06	54.98±2.25	59.22±2.40

5. Weight of Kernel/Spike(g)							
Cross-I HJP81 x Rm-Ts17		P ₁	P ₂	F ₁	F ₂	BC ₁	BC ₂
		Mean ± SE	Mean ±SE	Mean ±SE	Mean ±SE	Mean ±SE	Mean ±SE
	WS ₁	2.40±0.043	3.33±0.090	3.96±0.091	3.41±0.129	3.78±0.186	3.08±0.171
	WS ₂	2.63±0.047	3.47±0.074	3.63±0.070	3.40±0.131	3.87±0.191	3.12±0.178
Cross- II HS 27 x PBW502	WS ₁	2.16±0.012	1.78±0.015	3.47±0.015	2.93±.145	2.20±0.147	2.17±0.222
	WS ₂	1.86±0.01	1.55±0.01	2.01±0.03	1.77±0.08	1.90±0.09	1.97±0.521
Cross-III HJP81xPBW502	WS ₁	2.11±0.023	1.75±0.02	2.39±0.023	2.14±0.067	2.33±0.042	2.10±0.102
	WS ₂	2.27±0.01	1.51±0.02	1.99±0.02	1.38±0.06	2.01±0.08	1.72±0.09
Cross-IV HS67 x PBW 502	WS ₁	2.28±0.009	1.66±0.011	2.94±0.012	2.52±0.098	2.66±0.140	2.18±0.139
	WS ₂	1.01±0.01	1.54±0.01	1.45±0.01	1.71±0.09	1.37±0.10	1.53±0.15
Cross -V (HG2 x HD2009 _M)	WS ₁	2.62±0.024	3.62±0.023	4.37±0.031	3.34±0.134	3.12±0.178	3.96±0.173
	WS ₂	2.59±0.01	3.24±0.01	3.28±0.01	2.17±0.09	2.49±0.10	2.93±0.15
6. Grain: Spike Biomass Ratio (%)							
Cross-I HJP81 x Rm-Ts 17	WS ₁	72.00±0.57	83.57±0.57	76.59±0.545	72.48±2.169	72.87±3.604	68.67±2.378
	WS ₂	75.87±0.41	87.17±0.51	84.32±0.524	71.99±2.08	74.12±3.151	72.11±2.121
Cross- II HS 27 x PBW502	WS ₁	82.96±0.39	75.90±0.57	81.92±0.493	78.52±1.50	80.52±2.606	72.10±3.869
	WS ₂	77.03±0.43	66.77±0.48	83.64±0.75	73.16±1.59	75.74±2.85	67.88±4.50
Cross-III HJP81xPBW502	WS ₁	85.85±0.37	76.97±0.37	85.45±0.352	70.95±1.79	84.83±2.038	76.18±2.958
	WS ₂	82.70±0.45	68.50±0.81	75.98±0.60	60.92±1.52	78.77±2.36	70.05±3.17
Cross-IV HS67 x PBW 502	WS ₁	83.32±0.48	72.01±0.5	81.34±0.4	78.26±1.51	75.15±3.141	73.61±2.338
	WS ₂	55.73±0.39	74.48±0.4	76.18±0.5	65.29±1.58	63.30±3.44	64.13±2.36
Cross -V (HG2 x HD2009 _M)	WS ₁	83.70±0.4	75.4±0.52	74.7±0.55	71.89±1.76	76.38±2.717	81.01±1.719
	WS ₂	84.51±0.39	81.15±0.4	84.09±0.5	72.99±1.58	76.60±3.44	76.62±2.36

7. Number of Tillers/Plant							
Cross-I HJP81 x Rm-Ts17		P ₁	P ₂	F ₁	F ₂	BC ₁	BC ₂
		Mean ± SE	Mean ±SE	Mean ±SE	Mean ±SE	Mean ±SE	Mean ±SE
	WS ₁	7.9±0.287	13.66±0.410	13.68±0.630	9.48±0.418	9.71±0.700	11.20±0.978
	WS ₂	8.16±0.26	13.56±0.318	13.88±0.336	10.44±0.506	9.64±0.701	10.89±0.878
Cross- II HS 27 x PBW502	WS ₁	8.53±0.16	15.43±0.29	15.84±0.25	12.83±0.64	11.17±0.87	13.88±0.75
	WS ₂	8.17±0.26	13.97±0.24	14.76±0.24	10.44±0.51	13.44±0.41	13.02±0.532
Cross-III HJP81xPBW502	WS ₁	8.16±0.26	13.56±0.318	13.88±0.336	10.44±0.506	13.44±0.410	13.02±0.53
	WS ₂	7.93±0.29	14.20±0.33	14.76±0.36	9.48±0.42	9.71±0.70	13.80±0.54
Cross-IV HS67 x PBW 502	WS ₁	10.4±0.16	18.80±0.326	16.37±0.266	13.72±0.567	7.42±0.859	9.57±1.051
	WS ₂	7.93±0.26	14.07±0.24	14.84±0.32	12.22±0.42	9.96±0.40	11.47±0.84
Cross -V (HG2 x HD2009 _M)	WS ₁	8.46±0.21	12.53±0.160	13.62±0.313	9.93±0.445	8.33±0.777	10.13±0.999
	WS ₂	12.70±0.26	8.20±0.24	13.82±0.32	9.75±0.42	12.29±0.40	10.22±0.84
8. Grain Yield/Plant(g)							
Cross-I HJP81 x Rm-Ts 17	WS ₁	22.24±0.22	17.80±0.129	18.44±0.231	16.44±0.572	16.75±0.931	16.18±0.469
	WS ₂	22.14±0.23	17.36±0.201	17.46±0.210	16.96±0.526	17.13±0.910	15.30±0.72
Cross- II HS 27 x PBW502	WS ₁	8.13±0.04	15.42±0.038	16.76±0.182	15.25±0.623	12.26±1.028	12.61±0.97
	WS ₂	7.11±0.06	12.90±0.16	14.17±0.12	10.93±0.57	11.74±0.75	10.56±0.873
Cross-III HJP81xPBW502	WS ₁	9.44±0.175	15.94±0.119	16.47±0.200	11.64±0.553	13.16±0.854	14.27±0.89
	WS ₂	16.95±0.2	12.10±0.103	16.72±0.274	11.79.649	13.52±0.686	15.93±0.51
Cross-IV HS67 x PBW 502	WS ₁	15.66±0.15	15.14±0.072	16.64±0.251	15.20±0.725	12.77±0.776	15.28±0.778
	WS ₂	12.93±0.1	12.33±0.16	15.63±0.15	13.28±0.63	9.88±1.25	13.38±0.52
Cross -V (HG2 x HD2009 _M)	WS ₁	15.37±0.02	14.23±0.291	15.38±0.315	10.56±0.480	11.80±1.113	13.55±0.804
	WS ₂	15.30±0.06	13.89±0.16	14.81±0.15	9.25±0.63	10.61±1.25	14.16±0.52

The inconsistency of non-allelic interactions over the environments for majority of traits reveals that expression of non-allelic interaction is influenced by the genotype x environment interaction to large extent. Therefore, experiments should be conducted over environments to have valid estimates of non-allelic interactions. Contrary, the goodness of fit for three parameter model may not show the significance of any of the gene effects as observed and described for above crosses. This situation may be attributed either to sampling error leading to high standard error as visualized in most cases for the estimates of gene effects or to the cancellation of gene effects. The inconsistency of findings being apparent may also be attributed to the differences in the material and the genotype x environment interactions. However, it need to be borne in mind that inconsistency of results should be interpreted cautiously and more detailed investigations over

the larger environments are required to have a definite and concrete conclusion. In general, there has been close agreement between the results of joint scaling test and that of six-parameter model. However, the epistasis predicted by the joint scaling test may not be detected in six parameter model in few cases as described above. However, the frequency of such disagreement is quite low when we take into consideration the fifteen characters studied in five crosses under two growing seasons i.e. leading to a total of 150 cases or combinations out of which merely 27 cases have been in discordant based on the information obtained for the estimates under joint scaling test and six parameter model. Further, the non-significance of the genetic components of gene effects might be due to high standard error of estimates or cancelling effect of contribution of individual loci in towards the net effect in such cases of non-conformity.

Table-3 Estimates of different scaling tests and genetic effects for plant height (cm) in the five wheat crosses for two sowing years: 2008-09(WS₁) and 2009-10(WS₂)

Cross	Cross-I (HJP81 x Rm-Ts 17)		Cross-II HS 27 x PBW 502		Cross-III HJP81 x PBW 502		Cross-IV HS67 x PBW 502		Cross-V HG2 x HD 2009M	
	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂
Parameter	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
Scaling test										
A	16.86**±3.14	10.88**±2.8	6.70**±1.46	6.68** ±1.105	4.43**±1.16	0.822 ±1.950	6.32**±1.646	10.39**±2.96	27.39**±3.809	16.19**±5.43
B	8.37**±4.133	4.01±4.414	3.29±4.025	9.57** ±3.58	6.10±4.157	6.42±4.1149	4.44±4.262	3.71±4.060	33.07**±3.694	21.6 **±3.30
C	19.62**±4.76	11.04**±4.75	45.55**±4.92	72.87**±3.825	14.25**±4.727	8.32±4.490	17.10**±4.559	9.46 ±5.2793	46.95**±5.409	60.35**±5.935
D	2.80±3.475	1.94±3.501	-17.78**±3.26	-8.31**±2.666	-1.86±3.179	-0.54±3.1858	-3.17±3.216	2.32 ±3.6354	7.08±3.774	-11.5**±4.2713
Joint scaling test(Three Parameter)										
m	99.63**±0.138	98.43**±0.137	98.15**±0.1	95.77** ±.134	100.46**±0.15	92.03**±0.158	97.86**±0.12	100.22**±0.14	113.36**±0.15	110.77**±0.286
d	-18.04**±0.138	-16.76**±0.137	-12.25**±0.10	-13.29**±0.13	-13.63**±0.16	-10.46**±0.16	-13.15**±0.12	-7.84**±0.1396	24.89**±0.149	24.87**±0.2872
h	16.43**±0.45	18.01**±0.376	16.51**±0.147	18.36**±0.18	15.58**±0.28	22.75**±0.205	17.78**±0.203	14.76**±0.183	26.64**±0.260	23.77**±0.634
χ ² (df=3)	47.986**	20.7596**	106.79**	402.71**	25.078**	N.S.	29.54**	16.33**	202.87**	145.52**
Six Parameter										
m	103.33**±1.17	104.86**±1.173	95.09**±1.228	87**±0.9518	104.86**±1.173	101.35**±1.118	102.56**±1.135	105.26**±1.317	115.36**±1.346	108.76**±1.449
d	13.82**±2.574	13.34**±2.599	10.58**±2.137	14.71**±1.867	14.47**±2.146	13.20**±2.27	12.24**±2.278	14.51±2.5064	-22.07**±2.644	-2.80**±3.1386
h	11.48±6.966	14.41**±7.013	52.08**±6.514	74.99**±5.335	19.49**±6.375	23.81**±6.375	24.18**±6.436	10.11±7.2731	12.64±7.552	48.07**±8.567
i	-5.60±6.951	-3.88±7.002	35.56**±6.512	56.63**±5.332	3.77±6.359	1.07±6.3716	6.34±6.433	-4.64±7.2708	-14.17±7.547	23.00**±8.542
j	-8.49±5.155	-6.87±5.205	-13.41**±4.279	2.89 ±3.7429	1.67±4.303	5.60±4.5498	-1.88±4.562	-6.78±5.0205	5.68±5.297	4.97±6.304
l	30.82**±11.34	18.77±11.43	-25.58**±9.86	-20.38**±8.389	6.82±9.799	6.17±10.127	4.43±10.189	18.74±11.33	74.63**±11.881	14.34±13.886
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

Table 4 Estimates of different scaling tests and genetic effects for number of spikelet/spike the five wheat crosses for two sowing years: 2008-09(WS₁) and 2009-10(WS₂)

Crosses	Cross-I (HJP81 x Rm-Ts 17)		Cross-II HS 27 x PBW 502		Cross-III HJP81 x PBW 502		Cross-IV HS67 x PBW 502		Cross-V HG2 x HD 2009M	
	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂
Parameter	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
Scaling test										
A	2.58**±0.665	1.73**±0.600	2.27**±0.476	0.18±0.4338	-0.47±0.635	1.24±0.685	3.07**±0.691	-0.49±0.513	3.71**±0.678	2.80**±0.5815
B	1.78**±0.615	0.51±0.564	1.78**±0.617	1.07 *±0.4529	0.13±0.624	-0.80 ± 0.637	0.91±0.624	1.38**±0.572	5.13**±0.666	1.15±0.602
C	5.42**±0.911	5.04**±1.047	2.23**±0.904	6.44**± 0.646	1.43±1.032	2.42**± 0.75	5.79**±0.932	3.87**±0.668	15.90**±1.092	6.73** ±0.7835
D	-0.53±0.542	-1.39**±0.585	0.91±0.545	-2.59**±0.3805	-0.88±0.630	-0.98±0.5456	-0.90±0.609	-1.49**±0.4475	-3.53**±0.676	-3.38** ±0.512
Joint scaling test(Three Parameter)										
m	24.59**±0.140	24.41**±0.136	23.66**±0.108	21.73**±0.10	23.07**±0.121	22.49**±0.1115	24.49**±0.116	22.5**±0.11130	26.00**±0.123	25.31**±0.1161
d	0.95**±0.142	0.81**±0.137	0.50**±0.109	0.5**±0.10	0.81**±0.123	-0.87**±0.1157	-0.73**±0.119	0.72**±0.11634	0.74**±0.125	0.13**±0.120
h	-0.50**±0.259	-0.19**±0.241	0.13**±0.186	1.50**±0.18	0.96**±0.197	1.22**±0.19035	0.87**±0.191	0.77**±0.18397	0.97**±0.197	0.06**±0.1955
χ ² (df=3)	43.2447**	26.701**	31.16**	104.23**	N.S.	15.58**	53.19**	40.91**	263.99**	85.65**
Six Parameter										
m	23.60**±0.184	23.41**±0.231	23.45**±0.206	21.35**±0.1321	23.22**±0.238	22.64**±0.1617	23.81**±0.212	22.19**±0.1392	23.28**±0.255	24.17**±0.17
d	-1.20**±0.397	-1.24**±0.358	-0.71**±0.357	-0.09±0.2738	-0.53**±0.213	-0.09±0.4394	-0.31±0.437	0.13 ±0.35	-0.89±0.445	-0.89**±0.3844
h	0.98±1.116	2.74**±1.195	-1.53±1.106	6.97**±0.7833	2.73**±1.276	3.26**±1.1079	2.80**±1.233	3.83**±0.9139	8.24**±1.366	3.02**±1.0436
i	1.07±1.083	2.79**±1.170	-1.81±1.089	5.19**±0.761	1.76±1.261	1.97±1.0912	1.81±1.218	2.99**±0.8951	7.06**±1.352	2.77**±1.0249
j	-0.80±0.851	-1.22±0.777	-0.49±0.70	0.89±0.5907	0.60±0.865	-2.04**±0.911	1.87**±0.7434	1.42±0.927	-1.64**±0.809	
l	3.29±1.831	-0.55±1.774	5.86**±1.69	-3.95±1.2714**	-2.09±1.948	-1.52±1.9117	2.16±1.980	-0.98±1.5528	1.78±2.088	1.18±1.726
Type of gene interaction	---	---	---	---	---	---	---	---	---	---

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

For those characters, where digenic model has been found as adequate, largely the characters have been observed where there has been preponderance of both 'additive' and 'dominance' components and among epistatic components mostly 'i'

type (additive x additive) and 'l' type (dominance x dominance) epistasis contributed significantly towards the gene effects. Moreover, in some other situations either 'i-type' epistasis alone or 'i-type' epistasis in combination with 'j-type' epistasis or all

the three types of epistasis were found significantly contributing to the gene effects. It is interesting to note that 'j' type of epistasis alone has been reported only in few cases viz. spike biomass in cross HS67 x PBW502 in WS₂ and WS₁, respectively, for kernel weight/spike in cross HJP81 x Rm-TS17 under both seasons and for days to heading in cross HS27 x PBW502 under WS₂ whereas for cross HS67 x PBW502 under WS₁. The lesser frequency of 'j-type' of interaction has also been reported by Kumar *et al.*, 2013; Pawar *et al.*, 2015 in wheat crosses. Preponderance of additive x additive (i-type) epistasis or gene interaction suggested that such traits in the population maybe improved through random mating of the selected desirable plants followed by selection. This approach will lead to the exploitation of additive (d); additive x additive (i-type) of gene effects and interactions in the populations. The high frequency of occurrence

of dominance (h) and dominance x dominance (l-type) gene effects and interactions may paradoxically suggest the exploitation of heterosis in wheat. However, a close examination for the sign of 'h' and 'l' type of epistasis reveal that magnitude of the two if found in opposite direction than contribution to the phenotypic mean imply thereby antagonistic effects in heterosis expression and it has been termed as 'duplicate' type of epistasis which may be explained on the basis of fact that majority of the parents involved in the cross were selections towards a single optimum phenotype and as such it is this selection for optimum type that has favoured the duplicate but not the complementary interaction. Hence, it is difficult to improve the populations in the presence of duplicate type of epistasis.

Table-5 Estimates of different scaling tests and genetic effects for spike biomass in the five wheat crosses for two sowing years: 2008-09(WS₁) and 2009-10(WS₂)

Crosses	Cross-I (HJP81 x Rm-Ts 17)		Cross-II HS 27 x PBW 502		Cross-III HJP81 x PBW 502		Cross-IV HS67 x PBW 502		Cross-V HG2 x HD 2009 _M	
Parameter	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂
Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
Scaling test										
A	-1.94**±0.14	-2.69**±0.16	1.37**±0.169	-0.23*±0.1097	-0.23**±0.083	0.26**±0.0784	-0.94**±0.30	-0.45**±0.132	0.21**±0.698	0.323*±0.1492
B	0.15±0.254	-0.39±0.260	0.64**±0.229	-0.28±0.1705	-0.41**±0.147	-0.05±0.095	-0.03±0.210	-0.68**±0.1468	0.21**±0.864	0.2537±0.161
C	-1.28**±0.31	-2.86**±0.30	-1.35**±0.33	0.04±0.2283	-1.63**±0.17	0.63**±0.18	-0.58*±0.232	-1.61**±0.186	0.35*±0.897	1.719±1.0794
D	-0.24±0.195	-0.11±0.205	1.68**±0.220	-0.24±0.1511	0.49**±0.118	-0.21**±0.108	-0.19±0.217	0.23±0.1334	0.23±0.333	-0.57±0.55
Joint scaling test(Three Parameter)										
m	3.70**±0.031	3.81**±0.025	2.47**±0.006	2.38**±0.00552	2.4**±0.007	2.48**±0.00670	2.53**±0.004	2.02**±0.0055	3.92**±0.009	3.51**±0.00952
d	0.28**±0.031	0.23**±0.025	-0.12**±0.01	-0.05**±0.005	-0.0**±0.007	-0.26**±0.0067	-0.21**±0.004	0.09**±0.0055	0.87**±0.009	0.47627**±0.00952
h	1.85**±0.064	0.83**±0.051	1.75**±0.011	0.06**±0.017	0.47**±0.013	0.13**±0.0067	1.08**±0.008	-0.008**±0.019	1.92**±0.014	0.38803**±0.01868
χ ² (df=3)	189.09**	336.38**	90.30**	7.45*	105.81**	23.79**	16.15**	103.07**	32.94**	9.58*
Six Parameter										
m	4.75**±0.070	4.74**±0.072	3.69**±0.084	2.41**±0.0564	3.03**±0.042	2.39**±0.045	3.21**±0.058	2.39**±0.0455	4.66**±0.088	3.279**±0.2697
d	0.72**±0.136	0.89**±0.147	-0.23±0.142	0.03±0.1006	-0.02±0.084	0.11±0.0608	0.67**±0.183	-0.20*±0.0976	-0.79**±0.152	-0.51**±0.1088
h	2.01**±0.397	0.80*±0.404	-1.61**±0.43	0.53±0.3028	-0.52*±0.237	0.57**±0.217	1.48**±0.433	-0.53*±0.2676	1.25**±0.466	1.535±1.1006
i	0.49±0.391	0.21±0.411	-3.37**±0.43	0.48±0.3023	-0.99**±0.237	0.42*±0.2164	0.39±0.433	-0.47±0.2668	-0.66±0.466	1.142±1.1004
j	2.09**±0.279	2.30**±0.299	-0.73**±0.28	-0.05±0.2014	-0.17±0.168	-0.31*±0.1224	0.90*±0.367	-0.22±0.195	0.16±0.304	-0.069±0.218
l	-2.27**±0.62	-3.30**±0.66	5.38**±0.660	-1.0*±0.4625	0.35±0.375	-0.22±0.303	-1.37*±0.769	-0.66±0.4327	2.22*±0.703	-0.565±1.164
Type of gene interaction	Duplicate	Duplicate	Duplicate	---	---	---	---	---	Complementary	---

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

Table 6 Estimates of different scaling tests and genetic effects for number of kernels/spike in the five wheat crosses for two sowing years: 2008-09(WS₁) and 2009-10(WS₂)

Crosses	Cross-I (HJP81 x Rm-Ts 17)		Cross-II HS 27 x PBW 502		Cross-III HJP81 x PBW 502		Cross-IV HS67 x PBW 502		Cross-V HG2 x HD 2009 _M	
Parameter	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂
Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
Scaling test										
A	16.87**±2.299	11.65**±2.091	10.45**±2.246	9.51**±2.2476	5.97**±1.522	13.92**±2.031	16.72**±2.429	15.38**±2.028	4.13±2.336	8.60**±2.6385
B	10.12**±1.922	14.52**±2.716	4.14±2.386	3.33±2.3816	1.11±2.800	9.16**±2.6417	2.86±2.966	12.06**±3.061	10.48**±2.522	17.95**±2.7953
C	27.49**±4.086	24.16**±3.364	5.10±2.938	-6.43*±3.2324	-7.52±3.874	27.62**±3.3721	12.35**±3.427	13.03**±3.35	44.92**±4.155	30.03**±4.806
D	-0.24±2.478	1.00±2.349	4.74*±2.178	9.64**±2.2818	7.30**±2.479	-2.26±2.3133	3.61±2.551	7.20**±2.453	-15.15**±2.67	-1.74±3.039
Joint scaling test(Three Parameter)										
m	64.11**±0.192	60.69**±0.140	47.02**±0.145	45.24**±0.16	46.46**±0.187	48.14**±0.20324	49.69**±0.126	45.57**±0.16533	59.50**±0.176	58.79**±0.18
d	4.76**±0.192	5.08**±0.140	-5.66**±0.146	-5.56**±0.16	-5.96**±0.188	-7.534**±0.204	-6.12**±0.126	-5.40**±0.166	7.03**±0.176	8.91**±0.18212
h	3.14**±0.408	7.12**±0.386	9.35**±0.245	12.22**±0.22178	13.96**±0.291	10.62**±0.39904	17.81**±0.251	21.81**±0.29645	6.85**±0.293	9.04**±0.37515
χ ² (df=3)	118.462**	104.014**	27.22**	24.08**	19.74**	118.38**	60.47**	85.83**	135.10**	87.79**
Six Parameter										
m	59.55**±1.000	58.88**±0.817	50.54**±0.724	52.98**±0.80	55.38**±0.958	47.26**±0.818	55.67**±0.847	53.52**±0.823	52.01**±1.028	56.22**±1.187
d	-8.24**±1.463	-3.60*±1.688	2.51±1.626	2.51±1.6260	3.60*±1.574	5.15**±1.6348	-0.80±1.906	3.75*±1.8201	-3.89**±1.702	-4.25*±1.8988
h	4.48±4.974	6.10±4.716	-0.06±4.362	-7.05±4.569	-0.60±4.967	15.87**±4.65	10.76*±5.108	7.65±4.9158	37.32**±5.347	12.99*±6.090
i	0.49±4.957	-2.00±4.699	-9.49*±4.355	-19.28**±4.5636	-14.61±4.958	4.54±4.6267	-7.22±5.102	-14.41**±4.907	30.30**±5.339	3.49±6.0788
j	-6.75*±2.952	2.86±3.387	-6.31±3.265	-6.17±3.2675	-4.86±3.172	-4.75±3.2955	-13.86**±3.821	-3.33±3.6554	6.35±3.422	9.35*±3.8152
l	26.50**±7.138	28.18**±7.543	24.09**±7.137	32.12**±7.2628	21.70**±7.394	18.55*±7.3574	26.80**±8.360	41.87**±8.0114	-15.68**±7.97	23.05*±8.988
Type of gene interaction	---	---	---	---	Duplicate	Complementary	Complementary	---	Duplicate	Complementary

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

Further in this situation of presence of duplicate epistasis, the positive sign of “h” indicate that dominance was contributed by higher scoring parent i.e. the parent which express to higher manifestation for the trait under consideration and vice-versa. Opposite sign of ‘h’ and ‘i’ components of gene effect and interaction indicate the presence of duplicate type of epistasis. The complementary type of epistasis interaction has been observed for cross HG2 x HD2009_M for plant height, and number of kernels per spike under season 2009-10 (WS₂) and for spike biomass under season 2008-09 (WS₁). The cross HS27 x PBW502 indicated the complementary type of interaction for number of tillers per plant under WS₁ whereas the cross HJP81 x PBW502 exhibited this kind of epistasis under both the seasons i.e. WS₁ and WS₂ for number of kernels per spike under WS₂ only. The cross HS67 x PBW502 hold good for complementary type of interaction in respect of number of kernels per spike under WS₁ only.

The duplicate type of epistasis has been observed in larger number of cases where the negative value of “h” (dominance effect) as observed for certain characters indicate the lower scoring or manifesting parent has the pre-dominant contribution for the expression of the characters and it is considered important for the trait number. The cross HS67 x PBW502 has exhibited negative value of ‘h’ for number of tillers per plant and grain spike biomass ratio. The cross HG2 x HD2009_M has revealed the presence of duplicate type of epistasis with sign of ‘h’ as positive for characters namely grain: spike biomass ratio, number of kernels per spike under WS₁ and for grain yield under both seasons. The cross HS27 x PBW502 exhibited duplicate type of epistasis with positive sign of ‘h’ component for plant height (both seasons), number of tillers per plant and number of fertile spikelets/spike under WS₂ and with having negative sign of ‘h’ for grain yield per plant, kernel weight per spike, spike biomass under WS₁.

Table-7 Estimates of different scaling tests and genetic effects for kernel weight/spike in the five wheat crosses for two sowing years: 2008-09(WS₁) and 2009-10(WS₂)

Crosses	Cross-I (HJP81 x Rm-Ts 17)		Cross-II HS 27 x PBW 502		Cross-III HJP81 x PBW 502		Cross-IV HS67 x PBW 502		Cross-V HG2 x HD 2009 _M	
	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂
Parameter	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
Scaling test										
A	-1.21**±0.22	-1.48**±0.226	1.22**±0.170	0.08±0.1005	-0.16**±0.05	0.24**±0.0931	-0.10±0.162	-0.28**±0.10	0.74**±0.206	0.88**±0.1112
B	1.13**±0.211	0.85**±0.213	0.91**±0.256	-0.37±0.602	-0.06±0.119	0.07±0.1067	0.23±0.161	-0.08±0.132	0.06±0.201	0.65**±0.168
C	-0.01±0.321	-0.23±0.317	-0.87**±0.335	0.37±0.291	0.10±0.158	2.24**±0.1442	-0.27±0.228	-1.37**±0.531	1.61**±0.313	3.70**±0.204
D	-0.03±0.208	-0.19±0.214	1.50**±0.227	-0.33±0.319	-0.16±0.100	-0.96**±0.0998	0.20±0.161	0.50±0.277	-0.40±0.211	-1.08**±0.14
Joint scaling test(Three Parameter)										
m	2.83**±0.028	3.04**±0.024	1.97**±0.005	1.77**±0.0040	1.93**±0.009	1.88**±0.00557	1.97**±0.004	1.28**±0.00645	3.11**±0.010	2.91**±0.00422
d	0.42**±0.028	0.39**±0.024	-0.19**±0.005	-0.15**±0.004	-0.18**±0.009	-0.38**±0.00558	-0.31**±0.004	0.26**±0.00645	0.50**±0.010	0.32**±0.0042
h	1.12**±0.058	0.61**±0.046	1.49**±0.010	0.304**±0.016	0.46**±0.016	0.07**±0.01239	0.96**±0.008	0.18**±0.01667	1.23**±0.020	0.35**±0.00866
χ ² (df=3)	62.32**	61.7**	71.17**	N.S.	11.38**	246.85**	N.S.	14.76**	39.06**	404.12**
Six Parameter										
m	3.41**±0.074	3.40**±0.076	2.93**±0.084	1.76**±0.047	2.14**±0.039	1.38**±0.035	2.52**±0.057	1.70**±0.132	3.34**±0.078	2.17**±0.0509
d	0.70**±0.146	0.75**±0.151	0.03±0.153	-0.07±0.305	0.23**±0.064	0.29**±0.070	0.48**±0.114	-0.16**±0.082	-0.84**±0.143	-0.43**±0.100
h	1.17**±0.421	0.97**±0.430	-1.51**±0.454	0.98±0.6386	0.79**±0.202	2.02**±0.1999	0.55**±0.222	-0.84±0.554	2.05**±0.423	2.52**±0.286
i	0.07±0.417	0.39±0.427	-3.03**±0.45	0.66±0.6384	0.33±0.201	1.92**±0.20	-0.41±0.322	-1.01±0.554	0.80±0.422	2.16**±0.286
j	2.34**±0.297	2.34**±0.305	-0.30±0.307	-0.45±0.61	0.10±0.129	-0.16±0.1407	0.33±0.228	0.19±0.164	-0.68**±0.287	-2.22±0.201
l	-0.15±0.666	-1.02±0.681	5.13**±0.700	-0.96±1.235	-0.56±0.301	-1.61**±0.315	0.54±0.510	0.65±0.623	0.01±0.653	-0.61±0.45
Type of gene interaction	--	--	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

N.S. = Non-significant

Table-8 Estimates of different scaling tests and genetic effects for grain: spike biomass ratio in the five wheat crosses for two sowing years: 2008-09(WS₁) and 2009-10(WS₂)

Crosses	Cross-I (HJP81 x Rm-Ts 17)		Cross-II HS 27 x PBW 502		Cross-III HJP81 x PBW 502		Cross-IV HS67 x PBW 502		Cross-V HG2 x HD 2009 _M	
	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂
Parameter	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
Scaling test										
A	2.85±4.186	11.95**±3.659	3.85±3.032	9.17**±3.324	1.64±2.371	1.13±2.7571	14.35**±3.646	5.30±2.9954	5.63±3.162	15.38**±3.992
B	22.81**±2.783	27.26**±2.485	13.63**±4.489	14.62**±5.218	10.06**±3.429	4.38±3.7083	6.12**±2.728	22.39**±3.246	-11.92**±2.032	11.99**±2.756
C	18.84**±5.069	43.71**±4.852	8.64**±3.540	18.42**±3.788	49.92**±4.166	59.48**±3.615	4.96±3.536	21.42**±4.055	20.95**±4.125	41.87**±3.707
D	3.41±3.533	-2.24±3.251	4.41±3.204	2.69±3.5789	-19.11**±2.928	-6.97**±2.8778	7.75**±2.852	3.13±2.9663	-13.62**±2.750	-7.24**±3.02
Joint scaling test(Three Parameter)										
m	77.54**±0.232	81.18**±0.189	79.33**±0.198	71.77**±0.18	81.25**±0.152	74.93**±0.26317	77.55**±0.203	64.87**±0.200	79.57**±0.188	82.58**±0.17118
d	5.63**±0.233	5.45**±0.190	-3.57**±0.199	-5.13**±0.18	-4.45**±0.152	-7.45**±0.2652	-5.65**±0.204	9.26**±0.2017	-4.02**±0.189	-1.73**±0.1719
h	-1.38**±0.391	2.34**±0.356	2.39**±0.347	11.17**±0.46	3.92**±0.254	-0.05**±0.4362	3.62**±0.323	10.94351**±0.33	-4.89**±0.368	0.73**±0.34786
χ ² (df=3)	80.052**	206.49**	16.40**	37.52**	151.89**	271.13**	22.10**	76.87**	65.50**	157.47**
Six Parameter										
m	72.48**±1.252	71.99**±1.20	78.52**±0.868	73.16**±0.9175	70.95**±1.034	60.92**±0.877	78.26**±0.869	65.28**±0.999	71.88**±1.015	72.99**±0.91
d	4.19±2.493	2.01±2.193	8.42**±2.693	7.86**±3.0727	8.64**±2.074	8.72**±2.282	1.54±2.261	-0.83±2.191	-4.62**±1.856	-0.19±2.4099
h	-8.01±7.077	7.29±6.511	-6.34±6.418	6.34±7.173	42.26**±5.862	54.33**±5.772	-11.83**±5.712	4.81±5.9419	22.38**±5.512	15.74**±6.050
i	-6.82±7.066	4.49±6.501	-8.83±6.408	-5.39±7.1577	38.21**±5.857	53.95**±5.756	-15.51**±5.70	-6.26**±5.9326	27.23**±5.500	14.48**±6.04
j	19.96**±5.007	15.31**±4.403	9.78±5.402	5.46±6.1565	8.41**±4.159	3.253±4.5949	-8.22±4.540	17.08±4.4007	-17.55**±3.73	-3.38±4.832
l	32.49**±11.185	34.72**±10.024	26.31**±11.340	29.21**±12.86	-26.51**±9.283	-48.431**±9.817	35.99**±9.710	33.95**±9.656	-33.52**±8.493	12.90±10.32
Type of gene interaction	--	--	---	---	Duplicate	Duplicate	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

Cross HJP81 x Rm-Ts17 also revealed the presence of duplicate epistasis for spike biomass under both seasons whereas cross HJP81xPBW502 indicated the characters viz. number of tillers per plant (WS₁), grain spike biomass ratio (both seasons) and kernel weight per spike (WS₂) to be governed by duplicate type of epistasis. The different types of epistatic effects were also previously reported by many researchers [7, 8, 13, 14, 20, 22]. The failure of six parameter model reflected when it was unsatisfactory to explain the genetic variation which implies the occurrence of either higher order gene interactions or linkage between the interacting loci or the presence of genotype x environment interaction which may also influence the expression of character(s).

It would be interesting to compare estimates obtained from the three parameter model to that of six-parameter model. The estimates of (d) and (h) from three parameter model were unquestionably biased due to the presence of epistasis. This might have led to the changes in magnitude of (d) and (h) and in some cases both magnitude and direction of (h) in six parameter model. The estimates of 'm' were practically same for all the characters in both the models whereas, the estimates of (d) and (h) were generally high on six-parameter model. This

discrepancy might be ascribed to relative change of error component term in inverse matrix.

Considerable amount of variation was envisaged among parents and their different generations for various morphological traits. Genetic analysis on wheat improvement has shown that grain yield in this crop is determined by highly complex and variable component traits and that genes for yield *per se* do not exist. The major yield components in wheat are tillers per plant, grains per spike and 1000-grain weight. Diallel and line x tester analysis, although effective and widely used, do not provide estimates of non-allelic interactions. Significant epistatic variation clearly indicates the roll of epistatic gene actions besides additive and dominance types, which play a major role in the expression of heterotic potential [7, 9, 10, 14]. Hence, it is essential to know the genetic architecture of this character for further improvement of yield. Obviously, the information obtained should have a direct bearing on the breeding programme for further advancement of this crop.

Table-9 Estimates of different scaling tests and genetic effects for number of tillers/spike in the five wheat crosses for two sowing years: 2008-09(WS₁) and 2009-10(WS₂)

Crosses	Cross-I (HJP81 x Rm-Ts 17)		Cross-II HS 27 x PBW 502		Cross-III HJP81 x PBW 502		Cross-IV HS67 x PBW 502		Cross-V HG2 x HD 2009 _u	
	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂
Parameter	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
Scaling test										
A	2.20±0.901	2.76**±0.846	2.02±1.024	-3.97**±0.517	-4.83**±0.534	3.26**±0.8503	11.96**±1.008	2.86**±1.051	5.42**±0.923	1.94**±0.5240
B	4.95**±1.210	5.67**±1.048	3.50**±0.895	2.67**±0.6454	1.41**±0.670	1.35**±0.6873	16.02**±1.238	5.97**±0.8053	5.88**±1.172	1.57±0.9995
C	11.05**±1.242	7.75**±1.253	4.32**±1.516	9.88**±1.218	7.75**±1.253	13.72**±1.0793	7.08**±1.360	2.80**±1.3596	8.51**±1.100	9.55**±1.0607
D	-1.95**±0.846	0.34±0.873	0.60**±0.994	-5.58**±0.70	-5.58**±0.701	-4.55**±0.7034	10.45**±1.021	3.017**±0.924	1.40±0.893	-3.01**±0.725
Joint scaling test(Three Parameter)										
m	10.46**±0.139	10.62**±0.116	11.88**±0.095	11.05**±0.09	10.86**±0.114	10.67**±0.11948	14.32**±0.103	10.85**±0.10164	10.36**±0.076	10.22**±0.09920
d	2.71**±0.141	2.63**±0.117	3.37**±0.095	2.66**±0.09	2.38**±0.114	3.13**±0.121	4.01**±0.103	2.98**±0.10267	2.08**±0.077	-2.19**±0.1002
h	1.18**±0.334	2.64**±0.222	3.77**±0.171	3.64**±0.17	3.18**±0.219	2.99**±0.233	1.40**±0.184	3.76**±0.16674	2.53**±0.188	2.86**±0.20377
χ ² (df=3)	84.28**	68.89**	25.60**	154.35**	144.47**	167.04**	319.87**	64.27**	107.53**	86.73**
Six Parameter										
m	9.48**±0.241	10.44**±0.292	12.83**±0.369	10.44**±0.29	10.44**±0.292	9.48**±0.2413	13.72**±0.327	12.22**±0.3294	9.93**±0.257	9.74**±0.243
d	-1.48**±0.694	-1.24±0.649	-2.71±0.666	0.42±0.3880	0.42±0.388	-4.08**±0.5117	-2.15**±0.784	-1.51**±0.6471	-1.80**±0.731	2.06**±0.5389
h	6.79**±1.736	2.32±1.760	2.66**±1.996	14.86**±1.413	14.19**±1.420	12.79**±1.4274	-19.14**±2.05	-2.19±1.8546	0.32±1.797	9.40**±1.4665
i	3.90**±1.691	-0.69±1.745	-4.20**±1.988	11.17**±1.402	11.17**±1.402	9.10**±1.407	-20.91**±2.04	-4.03**±1.8470	-2.80±1.787	6.03**±1.451
j	2.75±1.418	2.91**±1.319	1.47**±1.345	6.64**±0.803	6.24**±0.812	-1.91±1.0537	4.05**±1.581	3.11**±1.3109	0.46±1.470	-0.36±1.097
l	3.25±3.042	9.13**±2.881	6.72**±3.064	-2.46**±1.973	-14.60**±1.99	-4.48±2.3139	48.89**±3.417	14.88**±2.924	14.11**±3.123	-2.51±2.40
Type of gene interaction	--		Complementary	Duplicate	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

The joint scaling test of Cavalli (1952) has indicated the adequacy of simple additive-dominance model for plant height in cross HJP81 x PBW502, for kernel weight per spike in cross HS27 x PBW502 under WS₂ (2009-10) whereas for number of spikelets per spike in cross HJP81 x PBW502, for kernel weight in cross HS67 x PBW502. However, the individual scaling test was in agreement to such finding of absence of epistatic interaction due to the adequacy of simple additive-dominance model only for plant height and number of spikelets per spike as observed in cross HJP81 x PBW502 under WS₂ and WS₁, respectively for those characters. The adequacy of joint scaling test not only indicated the absence of epistatic interaction but also revealed the type of linkage for the plant height where the predominance of additive gene effect 'd' estimate being higher in magnitude exhibit the association of genes between the parents in such situation of being coupling phase of linkage. Additive effects for plant height were also reported by Novoselovic *et al.*, 2004; Erkul *et al.*, 2010; Akhtar and Chowdhry, (2006); Shekhawat *et al.* (2006). Additive effects for peduncle length were also reported by Shekhawat *et al.*, (2006).

Similar results were reported by Shekhawat *et al.*, (2006). Significant negative additive (d) gene effects were reported earlier by Shekhawat *et al.*, (2006). Significant positive additive gene effects were reported earlier by Akhtar and Chowdhry (2006). For number of tillers negative additive gene effects were reported by Shekhawat *et al.*, (2006); Fethi and Mohamed, (2010). Negative

additive gene effects were reported by Yadava *et al.*, 1995; Sharma *et al.*, (2015). 100 kernel weight (g) significant positive additive gene effects were reported earlier by Singh *et al.*, 1998.

This suggested that the additive gene effects played important role in the inheritance of all these attributes and simple selection would be adequate to improve such characters. The importance of additive gene effects in common bread wheat was also reported by many workers for various characters [Table-2.1].

In the present study, dominance effects were significant for plant height and similar results were reported by Singh *et al.*, 1986. Dominant gene effects were present in more number of characters as compared to additive effects. Also, in most of the above mentioned cases the relative magnitude of (h) was higher than (d). Gamble (1962) suggested that when inheritance of quantitative traits became complex the contribution of (h) to their inheritance becomes more. Their importance was indicated not only by their significance and relative magnitude but also by their signs in that particular direction. The significant and positive dominance effects suggested that they had an enhancing effect on their performance. The preponderance of dominance gene effects in wheat has been already reported by a number of investigators [Table-2.1]. Thus, results of present investigation confirm the earlier findings. By the application of six-parameter model, the epistatic gene effects were found for most of the characters, but the

type and magnitude of epistatic effects varied for character to character and cross to cross.

The perusal of [Tables-4.2 to 4.16] based on three parameter model indicated the failure of simple additive-dominance model in majority of the traits irrespective of cross and seasons which may be taken as that the observed genetic variation might not be ascribed wholly to the additive-dominance gene effects for majority of the characters in most of the populations vis-à-vis crosses. The failure of three parameter model may be either due to digenic or higher order interaction or on

account of presence of linkage between interacting genes. It is evident from this investigation that for majority of the characters, exhibiting continuous variation in wheat populations, the assumption of no epistasis is unrealistic as has been assumed in various biometrical mating designs such as diallel, line x tester and various North Carolina designs. Several workers have also reported the importance of non-allelic interactions in self-pollinated crops like wheat earlier reported by Novoselovic *et al.*, (2004); Sheikh *et al.*, (2009); Kumar and Gupta, (2010).

Table-10 Estimates of different scaling tests and genetic effects for grain yield/plant in the five wheat crosses for two sowing years: 2008-09(WS₁) and 2009-10(WS₂)

Crosses	Cross-I (HJP81 x Rm-Ts 17)		Cross-II HS 27 x PBW 502		Cross-III HJP81 x PBW 502		Cross-IV HS67 x PBW 502		Cross-V HG2 x HD 2009 _M	
	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂	WS ₁	WS ₂
Parameter	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
Scaling test										
A	7.17**±1.091	5.34**±1.065	0.37**±1.192	-2.20**±0.8693	-0.41±0.998	6.62**±0.817	6.76**±0.912	8.81**±1.137	-2.85**±1.298	-1.03 ±1.44
B	3.88**±0.563	4.21**±0.852	6.95**±1.123	5.95**±1.0146	3.86**±1.043	-3.03**±0.618	1.23±0.911	1.194 ±0.622	2.51**±0.960	0.38±0.6146
C	11.15**±1.355	6.58**±1.251	-3.94**±1.456	4.63**±1.3358	11.71**±1.303	15.33**±1.538	3.26±1.919	3.40±1.6957	8.13**±1.178	11.90**±1.464
D	-0.05±0.893	1.48±0.905	5.64**±1.088	-0.44±0.938	-4.15**±0.958	-5.87**±0.898	2.36**±2.251	3.30**±1.05	-4.23**±0.967	-6.27**±1.066
Joint scaling test(Three Parameter)										
m	19.87**±0.074	19.61**±0.086	11.77**±0.016	9.97**±0.05	12.63**±0.060	14.41**±0.070	15.36**±0.047	12.59**±0.061	9.68**±0.082	9.6**±0.04824
d	-2.16**±0.074	-2.38**±0.087	3.64**±0.016	2.85**±0.05	3.25**±0.061	-0.22**±0.047	0.81**±0.070	-0.30**±0.061	4.31**±0.082	4.23**±0.04828
h	-1.93**±0.149	-2.41**±0.149	4.96**±0.105	4.15**±0.085	3.62**±0.129	1.04**±0.148	-0.01±0.159	2.83**±0.144	5.30**±0.193	5.12**±0.09947
χ ² (df=3)	147.06**	72.85**	46.30**	52.7**	94.08**	191.73**	59.085**	66.26**	58.36**	66.87**
Six Parameter										
m	16.44**±0.330	16.96**±0.304	15.25**±0.360	10.92**±0.3312	11.64**±0.319	11.79**±0.375	15.21**±0.418	13.28**±0.4175	10.56**±0.277	9.24**±0.3626
d	0.57±0.602	1.82**±0.671	-0.35±0.815	1.18 ±0.6644	-1.11±0.715	-2.40**±0.495	-2.51**±0.634	-3.50**±0.638	-1.74**±0.793	-3.54**±0.781
h	-1.47**±1.793	-5.25**±1.816	-6.29**±2.178	5.05**±1.8784	12.08**±1.921	13.93**±1.804	-3.48±2.106	-3.60±2.107	14.05**±1.944	17.73**±2.134
i	0.10±1.787	-2.96±1.810	-11.28**±2.175	0.89±1.8765	8.30**±1.916	11.74**±1.796	-4.72**±2.100	-6.607**±2.102	8.46**±1.934	12.55**±2.131
j	-3.22±1.213	-1.12±1.353	6.58**±1.631	8.15**±1.3325	4.27**±1.435	-9.66**±1.000	-5.53**±1.272	-3.89**±1.2819	5.37**±1.594	1.42±1.566
l	10.95**±2.763	12.52**±2.961	18.61**±3.571	2.85±2.974	-4.85±3.142	-8.15**±2.506	12.72**±3.055	10.88**±3.0639	-8.80**±3.382	-10.21**±3.4491
Type of gene interaction	---	--	Duplicate	----	----	Duplicate	---	----	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

However, dominance effect (h) is higher in magnitude than additive effect (d) as observed for plant height in cross HJP81 x PBW502, for kernel weight in cross HS27 x PBW502 under season 2009-10 (WS₂) and for number of spikelets per spike in cross HJP81 x PBW502 and for kernel weight in cross HS67 x PBW502 under season 2008-09 (WS₁) reveal the possibility of gene dispersion among the parents for these traits. In such situation, transgressive segregants are expected to be derived in later segregating generations and until then the populations need to be advanced followed single seed descend approach.

In the present investigation, the presence of epistasis was indicated on the basis of individual scales for most of the characters of studied i.e. 100-kernel weight, number of kernels per spike, number of tillers per plant, spike biomass, grain yield per plant and also for grain : spike biomass ratio.

Further the genetic differences between the parents of specific crosses may be virtually lacking for few of the characters and in that case, neither of the component of gene effect i.e. additive or dominance may have the estimates as significant despite the adequacy of simple additive-dominance model as also observed earlier by some workers in wheat. Such a situation may also be attributed either to sampling error leading to high standard error of the estimates or the cancellation of the gene effects. The characters under study which could not be explained on simple additive-dominance model as tested through scaling tests were analysed on digenic epistatic model of Hayman (1958). The estimates of mean (m), additive (d), dominance (h), additive x additive (i), additive x dominance (j) and dominance x dominance (l) were estimated from six generations i.e. P₁ P₂ F₁, F₂, BC₁ and BC₂.

In the present investigation, the failure of six parameter to reveal the presence of epistatic interaction effect has been observed for cross HJP81 x Rm-Ts17 in respect of characters plant height, number of spikelets per spike under season WS₁ i.e. 2008-09 and for characters plant height, kernel weight/spike, 100-kernel weight under season WS₂ (2009-10). The absence of epistasis based on six-

parameter model has been observed in cross HS27 x PBW502 for kernel weight/spike whereas for cross HJP81 x PBW502 for plant height under both seasons, for number of spikelets per spike. The cross HS67 x PBW502 indicated the inadequacy of six parameter to detect the epistasis for characters plant height and kernel weight in both the seasons and for spike biomass in WS₂ whereas in cross HG2 x HD2009_M such an inadequacy of six parameter model for detection of any type of epistatic effect i.e. failure of model has been observed for number of fertile spikelets per spike and spike biomass under WS₂. The inconsistency of non-allelic interactions over the environments for majority of traits reveals that expression of non-allelic interaction is influenced by the genotype x environment interaction to large extent. Therefore, experiments should be conducted over environments to have valid estimates of non-allelic interactions. Contrary, the goodness of fit for three parameter model may not show the significance of any of the gene effects as observed and described for above crosses. This situation may be attributed either to sampling error leading to high standard error as visualized in most cases for the estimates of gene effects or to the cancellation of gene effects. The inconsistency of findings being apparent may also be attributed to the differences in the material and the genotype x environment interactions. However, it need to be borne in mind that inconsistency of results should be interpreted cautiously and more detailed investigations over the larger environments are required to have a definite and concrete conclusion. In general, there has been close agreement between the results of joint scaling test and that of six-parameter model. However, the epistasis predicted by the joint scaling test may not be detected in six parameter model in few cases as described above. However, the frequency of such disagreement is quite low when we take into consideration the fifteen characters studied in five crosses under two growing seasons i.e. leading to a total of 150 cases or combinations out of which merely 27 cases have been in discordant based on the information obtained for the estimates under joint scaling test and six parameter model. Further, the non-significance of the genetic

components of gene effects might be due to high standard error of estimates or cancelling effect of contribution of individual loci in towards the net effect in such cases of non-conformity.

For those characters, where digenic model has been found as adequate, largely the characters have been observed where there has been preponderance of both 'additive' and 'dominance' components and among epistatic components mostly 'i' type (additive x additive) and 'l' type (dominance x dominance) epistasis contributed significantly towards the gene effects. Moreover, in some other situations either 'i-type' epistasis alone or 'i-type' epistasis in combination with 'j-type' epistasis or all the three types of epistasis were found significantly contributing to the gene effects. It is interesting to note that 'j' type of epistasis alone has been reported only in few cases viz. spike biomass in cross HS67 x PBW502 in WS₂ and WS₁, for kernel weight/spike in cross HJP81 x Rm-TS17 under both seasons. The lesser frequency of 'j-type' of interaction has also been reported in six wheat crosses. Preponderance of additive x additive (i-type) epistasis or gene interaction suggested that such traits in the population maybe improved through random mating of the selected desirable plants followed by selection. This approach will lead to the exploitation of additive (d); additive x additive (i-type) of gene effects and interactions in the populations. The high frequency of occurrence of dominance (h) and dominance x dominance (l-type) gene effects and interactions may paradoxically suggest the exploitation of heterosis in wheat. However, a close examination for the sign of 'h' and 'l' type of epistasis reveal that magnitude of the two if found in opposite direction than contribution to the phenotypic mean imply thereby antagonistic effects in heterosis expression and it has been termed as 'duplicate' type of epistasis which may be explained on the basis of fact that majority of the parents involved in the cross were selections towards a single optimum phenotype and as such it is this selection for optimum type that has favoured the duplicate but not the complementary interaction [15]. Hence, it is difficult to improve the populations in the presence of duplicate type of epistasis.

Further in this situation of presence of duplicate epistasis, the positive sign of "h" indicate that dominance was contributed by higher scoring parent i.e. the parent which express to higher manifestation for the trait under consideration and vice-versa. Opposite sign of 'h' and 'l' components of gene effect and interaction indicate the presence of duplicate type of epistasis. The complementary type of epistasis interaction has been observed for cross HG2 x HD2009_M for plant height, and number of kernels per spike under season 2009-10 (WS₂) and for spike biomass under season 2008-09 (WS₁). The cross HS27 x PBW502 indicated the complementary type of interaction for number of tillers per plant under WS₁ and for 100-kernel weight under WS₂ whereas the cross HJP81 x PBW502 exhibited this kind of epistasis under both the seasons i.e. WS₁ and WS₂ for 100-kernel weight and for number of kernels per spike under WS₂ only. The cross HS67 x PBW502 hold good for complementary type of interaction in respect of number of kernels per spike under WS₁ only. The cross HS67 x PBW502 under both seasons has exhibited negative value of 'h' for number of tillers per plant and grain spike biomass ratio whereas positive for 100-kernel weight under WS₁. The cross HG2 x HD2009_M has revealed the presence of duplicate type of epistasis with sign of 'h' as positive for characters namely grain: spike biomass ratio, number of kernels per spike under WS₁ and for grain yield under both seasons. The cross HS27 x PBW502 exhibited duplicate type of epistasis with positive sign of 'h' component for plant height (both seasons), number of tillers per plant under WS₂ and with having negative sign of 'h' for grain yield per plant, kernel weight per spike, spike biomass under WS₁. Cross HJP81 x Rm-Ts17 also revealed the presence of duplicate epistasis for spike biomass under both seasons whereas cross HJP81 x PBW502 indicated the characters viz. number of tillers per plant (WS₁), grain spike biomass ratio (both seasons) and kernel weight per spike (WS₂) to be governed by duplicate type of epistasis. The different types of epistatic effects were also previously reported by many researchers [Table-2.1].

The failure of six parameter model reflected when it was unsatisfactory to explain the genetic variation which implies the occurrence of either higher order gene interactions or linkage between the interacting loci or the presence of genotype x environment interaction which may also influence the expression of character(s). It would be interesting to compare estimates obtained from the three parameter

model to that of six-parameter model. The estimates of (d) and (h) from three parameter model were unquestionably biased due to the presence of epistasis. This might have led to the changes in magnitude of (d) and (h) and in some cases both magnitude and direction of (h) in six parameter model. The estimates of 'm' were practically same for all the characters in both the models whereas, the estimates of (d) and (h) were generally high on six-parameter model. This discrepancy might be ascribed to relative change of error component term in inverse matrix [20].

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Conclusion: Genetic analysis on wheat improvement has shown that grain yield in this crop is determined by highly complex and variable component traits and that genes for yield *per se* do not exist. In this study, considerable amount of variation was envisaged among parents and their different generations for various morphological traits. Significant epistatic variation clearly indicates the roll of epistatic gene actions besides additive and dominance types, which play a major role in the expression of heterotic potential. Hence, it is essential to know the genetic architecture of this character for further improvement of yield. Obviously, the information obtained should have a direct bearing on the breeding programme for further advancement of this crop. On the basis of present analysis it is suggested that the additive gene effects played important role in the inheritance of all these attributes and simple selection would be adequate to improve such characters.

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Author Contributions:

PAWAN KUMAR¹: He is main contributor to this paper as it is a part of his Ph.D. research work

RAMESH KUMAR YADAVA^{2*}: Major advisor to first author who guided him for the present study

SANDEEP KUMAR³: He helps in collection and analysis of research data also contribute in preparation and editing the present paper.

PRITAM KUMAR⁴: He helps in collection and analysis of research data also contribute in preparation and editing the present paper.

Abbreviations: cm: centimeter,

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