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Genetic analysis through different generation means for grain yield and attributing traits in bread wheat (*Triticum aestivum* L.)

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Abstract
Wheat is the second most important crop after rice in India. Information on nature and magnitude of gene action controlling grain yield and its attributing traits is prerequisites for selection of parents. An experiment was conducted in randomized block design with two replications under timely and late sowing environments at Gwalior during *Rabi* season of 2013 -14 and 2014-15. The six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of bread wheat in three crosses viz., 'HPW -296 X LOK -1'; 'HPW - 296 X SONALIKA' and 'HPW - 296 X HW - 5205' were evaluated for gene effects. The scaling test revealed the presence of non-allelic gene interaction for most of the characters, thereby, signifying inadequacy of additive-dominance model to interpret the gene effects.

Gene action analysis revealed significant magnitudes of both additive and dominance gene effects for most of the traits. Both additive and additive X additive effects were significantly contributed in the expression of grain yield, grain filling period, days to physiological maturity, flag leaf area, and harvest index. The magnitudes of additive gene effects were relatively lower to corresponding dominance effects in most cases. Further both dominance and dominance x dominance effects were highly significant for plant height, days to physiological maturity, leaf canopy temperature, harvest index, biological yield and grain yield in all crosses. Whereas, only dominance x dominance effects were highly significant for spikes per plant, grains per spike, days to flowering, flag leaf area, seed index and in all crosses, thereby, showing importance of non- fixable components. Most of the traits were under the control of duplicate type of epistasis gene action. Heterosis over better and mid-parent in F_1 generation and inbreeding depression in F_2 generation showed significant for most of the characters also confirmed that these traits are highly under the control of non- fixable genetic components. Both additive as well as non additive effects were controlled expression of grain yield and some important attributing characters. Thus improvement of the characters needs intensive selection through later generation for fixing both additive as well as non additive gene action.

Keywords: bread wheat, *Triticum aestivum* L. generation mean analysis, gene effects, heterosis

Introduction
In India, wheat is the second most important crop after rice occupying India recorded remarkable wheat productivity of 3093 kg per ha and achieved a record production of 93.50 m tones (Anonymous, 2016) [2]. The main purpose of wheat breeding is to increase grain yield, however, yield is a very complex character which is governed by polygene and affects by many genetic and non-genetic factors, therefore, the knowledge about nature of gene action is essential to increase the efficiency of selection. In the present investigation, generation mean analysis was used for estimating gene effects and non-allelic gene interaction. Such analysis is very useful for the rapidly obtaining the overall information on various genetic system involved in segregating generations which may lead fixing favorable gene action for speedy gains.

Materials and Methods
Four varieties of wheat viz., HPW -296 (resistant to rust races Sr/31+, Lr/26+10 and Yr/9+), Lok-1 (well adopted, good for chapatti making quality), Sonalika (Suited for late sown condition under irrigated conditions) and HW-5205 (resistant to rust races Sr/31+2+, Lr/26+ and Yr/9+) were used to develop 6 generations (P_1, P_2, F_1, F_2, BC_1, BC_2) of 3 crosses viz., 'HPW- 296 X LOK-1'; 'HPW -296 X SONALIKA' and 'HPW -296 X HW -5205'.

Experiment consisting six generation of three crosses were sown in a randomized complete blocks design with two replication in timely and late sown conditions during *Rabi* seasons of 2013-14 and 2014-15. Generation P_1, P_2 & F_1 were sown in 2 rows, BC_1& BC_2 in 4 rows and F_2 in 8 rows. Rows spacing was 20 cm apart with 2 m row length. Recommended agronomical practices were adopted to raise good crop. Observation were recorded on randomly selected plants for grain yield and its attributing characters, 5 plants in parents and F_1's, 20 plants in backcross (BC_1 and BC_2) and 40 plants in F_2s generation plots. Mean values of different generation were pooled over timely and late sown conditions in both years. Pooled data evaluated for scaling test (A, B and C) to detect the presence of epistasis (Mather, 1949 and Hayman and Mather, 1955) [13]. Crosses showing presence of non–allelic interaction were further subjected to analysis of six parameters model to estimate all gene effects viz., m, d, h, i, j, & l (Hayman, 1958) [8]. Heterosis and inbreeding depression were also estimated according to Miller *et al.* (1958).

Results and Discussion

Estimates of scaling test (A, B and C) by using six generations of 3 crosses of bread wheat *viz*., 'HPW -296 X LOK-1', 'HPW 296 X SONALIKA' and 'HPW-296 X HW-5205' were significant for all or either one or two scale effects revealed presence of non- allelic gene interaction for all 20 traits, thereby, suggested inadequacy of the additive-dominance model to interpret the gene effects. Thus epistasis contributions could be explained by using six parameter model suggested by Hayman (1958) [8] in (Table 1, 2, 3).

Gene effects analysis revealed that both additive (d) as well as dominance (h) effects were significant in positive direction for grain yield in 2 crosses 'HPW- 296 X SONALIKA' and 'HPW -296 X HW -5205 and opposite direction in cross 'HPW- 296 X LOK-1'. Both additive and dominance effects were significant in positive direction for productive tillers and days to 50 % flowering in 'HPW -296 X LOK-1', and Biological yield in 'HPW -296 X SONALIKA' and 'HPW-296 X HW - 5205' and harvest index in 'HPW -296 X HW - 5205'. Whereas, both additive and dominance effects were significant in opposite direction in all 3 crosses for tillers per plant, for peduncle length, days to physiological maturity and flag leaf area in 'HPW -296 X LOK-1', plant height and days to 50 % flowering in 'HPW 296 X SONALIKA' and flag leaf area, 1000 grain weight in 'HPW- 296 X HW -5205'. Significant additive and dominance gene effects were in negative direction only for spike length in cross 'HPW- 296 X SONALIKA'. Only additive effects were significant in positive direction for grain yield, harvest index and days to physiological maturity in all the 3 crosses and for spike per plant in 'HPW -296 X LOK-1'. Negative additive gene effects (d) were noticed for tillers per plant in all 3 crosses. Similar results for different traits were reported by Hosary *et al.* (2000), Esmail and Khattab (2002) [5], Salem (2006), Zaazaa *et al.* (2012) [21] and Hassan *et al.* (2014) [7]. Only dominance gene effects (h) were significant in positive direction for tillers per plant, spike length, grain weight per spike and leaf canopy temperature in 'HPW-296 X LOK-1', and spike per plant in 'HPW-296 X HW-5205' and negative estimates for second internode length and grain filing period in 'HPW 296 X HW-5205', second internode length in 'HPW-296 X LOK-1' and leaf canopy temperature in 'HPW -296 X HW-5205'. The dominance gene effects were reported by Mostafavi *et al.* (2005), Khattab *et al*. (2010) [10], Abbasi *et al*. (2014) [1] and Hassan *et al*. (2014) [7].

Among the epistasis effects, additive X additive gene effects (i) were significant in positive direction for peduncle length in all the 3 crosses, grain yield in crosses 'HPW -296 X SONALIKA' and 'HPW- 296 X HW-5205', tiller per plant, productive tillers per plant, spikes length, days to 50 % heading, days to 50% flowering and leaf canopy temperature in 'HPW- 296 X LOK-1' and spike per plant, days to 50 % heading, flag leaf area and harvest index in 'HPW -296 X HW - 5205' and plant height in 'HPW -296 X SONALIKA'. However, it was significant but in negative direction for grains per spike and days to physiological maturity in all crosses and grain yield in HPW-296 X LOK-1, flag leaf area and 1000 grain weight in 'HPW 296 X LOK-1' and 'HPW 296 X SONALIKA', plant height and second internode length in 'HPW-296 X LOK-1' and 'HPW-296 X HW-5205',spike per plant and harvest index in 'HPW-296 X LOK-1', leaf canopy temperature and biological yield in 'HPW-296 X HW-5205'. Both additive and additive X additive gene effects showed significant values but in opposite direction for most of characters in all crosses, thereby, cancelling or lowering fixable type of gene action, thus fixable epistasis effect should be considered while planning the improvement for yield and its attributes. The significant role of additive gene effects was also reported earlier by Singh *et al.* (1998) [15], Dhyal *et al*. (2003) [3], Kavr *et al.* (2007) and Sonia *et al.* (2005) [20].

The additive X dominance gene effects (j) was significant in positive direction for days to 50% heading in all 3 crosses and grain yield, productive tillers, 1000 grain weight and harvest Index in 'HPW -296 XLOK-1' and plant height, peduncle and biological yield in 'HPW-296 X SONALIKA', days to 50% heading and days to physiological maturity in 'HPW -296 X HW-5205'. Negative estimates of additive X dominance gene effects were significant for 1000 grain weight in'HPW-296 X SONALIKA' and 'HPW-296 X HW-5205', tillers per plant and days to 50 % flowering in 'HPW-296 XLOK-1' and plant height in 'HPW-296 X HW 5205'. The dominance X dominance gene effects (l) were significant in positive direction for grain yield, plant height, spike per plant, grains per spike and biological yield in all 3 crosses and for flag leaf area, harvest index in 'HPW-296 XLOK-1' and 'HPW-296 X SONALIKA', second internode length, days to physiological maturity and 1000 grain weight in 'HPW-296 XLOK-1' and 'HPW-296 X HW-5205', days to 50 % flowering in 'HPW-296 X SONALIKA' and 'HPW-296 X HW-5205',tillers per plant and leaf canopy temperature in 'HPW-296 X HW-5205', productive tillers per plant and spike length in 'HPW-296 X SONALIKA'. Whereas, significant negative estimates of dominance X dominance gene effects (l) were recorded for peduncle length and grain filling period in and 'HPW-296 X SONALIKA', and for tillers per plant, productive tillers per plant, spike length, grain weight per spike in 'HPW -296 X LOK -1'.The signs of (h) and (l) were opposite in most cases suggesting duplicate type of non-allelic interaction for these traits. Whereas, complementary epitasis type of gene effects noticed for grain yield along with few attributing traits in 'HPW- 296 X SONALIKA' and 'HPW- 296 X HW -5205'. Both additive and dominance gene effects showed significant in opposite direction for most of the characters, thereby, reducing control of non additive gene action and also supported by earlier workers *Shekhawat et al.* (2000), Frozanfar *et al.* (2009) [6], Dobariya *et al.* (2010) [4] and Hassan *et al.* (2014) [7]. Therefore present results suggested that selection in early segregating generations would be effective and wherever the non-additive portions were larger than additive the improvement of these characters needs intensive selection in later generation for fixing additive X additive gene action.

Table 1: Estimates of gene effects, heterosis and inbreeding depression for yield and its attributes in pooled mean over four environments in "HPW-296 X LOK-1"

HPW-296 X LOK-1	m	D	H	I	J	l	Heterosis %		ID %
							MP	BP	
Plant height	107.04**	1.86	-9.07**	-10.64**	-0.48	17.30**	1.49	3.79**	-0.20
Second internode length	9.85**	-0.42	-6.39**	-5.71**	-0.87	7.48**	-7.39**	-2.68**	-107.02**
Peduncle length	39.12**	-3.24**	18.13**	13.38**	-0.99	-5.29**	11.26**	5.61**	-36.62**
First internode length	4.02**	0.32	-0.61	-0.84	0.25	0.02	7.71**	16.06**	-97.39**
Tillers per plant	11.23**	-5.18**	16.73**	12.30**	-2.70**	-6.15**	32.48**	12.11**	-44.14**
Productive tillers	12.23**	2.31**	5.41**	4.23**	2.85**	-4.13**	9.34**	4.91**	-74.05**
Spike length	11.71**	-1.52	5.74**	4.48**	-0.88	-0.94	9.62**	4.44**	-67.29**
Spike per plant	17.39**	6.44**	-1.55	-3.05**	4.44**	8.72**	8.67**	-2.59**	-73.72**
Grains per spike	17.19**	-0.96	-6.39**	-9.93**	0.63	21.63**	22.30**	11.17**	-69.20**
Grain weight per spike	3.58**	0.45	2.23**	1.65	0.39	-2.63**	16.87**	14.96**	-84.61**
Days to 50% heading	82.77**	0.63	1.00	3.78**	3.74**	1.53	-3.22**	0.39	-15.30**
Days to 50% flowering	101.71**	3.35**	7.55**	5.10**	-2.85**	-21.75**	2.51**	9.46**	-1.61
Grain filing Period	13.54**	0.85	0.55	1.22	-0.08	-7.27**	-5.33**	2.13**	-100.86**
Days to physiological maturity	113.37**	2.22**	-11.18**	-12.13**	-0.78	15.48**	0.86	3.67**	10.11**
Flag leaf area	54.90**	-4.44**	1.40	-2.38**	0.16	12.10**	6.88**	-1.40	-35.03**
Leaf canopy temperature	27.14**	0.12	2.41**	2.34**	0.95	-0.56	0.23	3.30**	-68.03**
1000 grain weight	50.33**	-6.72**	0.49	-9.90**	-2.09**	32.97**	21.47**	10.88**	-26.75**
Harvest index	41.02**	3.32**	-13.54**	-10.31**	1.36	17.24**	-7.72**	-3.18**	-67.82**
Biological yield	106.64**	7.81**	10.76**	-0.90	5.62**	35.70**	10.67**	8.50**	32.78**
Grain yield per plant	44.60**	6.03**	-8.64**	-11.73**	3.23**	34.55**	6.73**	0.59	-42.26**

*and ** revealed significant at 5 % and 1 % probability levels, respectively; MP= Mid Parent; BP= Better Parent and ID =Inbreeding depression

Table 2: Estimates of gene effects, heterosis and inbreeding depression for yield and its attributes in pooled mean over four environments in "HPW-296X SONALIKA

HPW - 296X SONALIKA	m	D	H	I	J	l	Heterosis%		ID%
							MP	BP	
Plant height	104.30**	7.97**	-6.04**	-7.43**	4.62**	17.93**	1.33	4.69**	7.15**
Second internode length	8.58**	-0.66	-1.35	-0.70	-0.20	0.61	-7.46**	-2.36**	-98.43**
Peduncle length	41.60**	-1.64	9.69**	7.91**	0.76	-6.42**	4.14**	-1.36	-47.94**
First internode length	4.02**	0.32	-0.61	-0.84	0.25	0.02	6.67**	8.93**	-104.35**
Tillers per plant	14.14**	-3.15**	2.20**	1.38	-1.48	0.43	5.68**	-5.25**	-76.79**
productive tillers	12.33**	-0.09	0.02	-0.85	0.24	3.83**	7.04**	4.31**	-79.42**
Spike length	14.62**	-2.42**	-5.20**	-7.35**	-2.18**	8.25**	18.05**	15.74**	-89.74**
Spike per plant	16.21**	0.50	0.60	-1.62	-0.68	7.57**	13.76**	6.05**	-69.68**
Grains per spike	17.43**	-0.57	-1.40	-3.90**	0.03	5.10**	16.13**	11.80**	-78.81**
Grain weight per spike	3.54**	0.06	0.36	-0.19	-0.01	0.79	16.52**	13.97**	-86.41**
Days to 50% heading	81.99**	-0.01	1.20	2.36**	3.06**	12.05**	0.09	4.30**	-12.94**
Days to 50% flowering	105.51**	1.90	-0.02	-1.80	2.28**	4.20**	3.02**	7.85**	-1.56
Grain filing Period	14.07**	0.75	1.33	-0.88	-0.95	1.88	-8.73**	0.44	-107.25**
Days to Physiological maturity	113.98**	2.94**	-11.53**	-6.02**	4.94**	12.95**	1.99	4.21**	12.48**
Flag leaf area	51.40**	-1.99*	3.92**	3.84**	0.17	-7.33**	16.53**	4.58**	-30.34**
Leaf canopy temperature	28.84**	-0.61	-3.50**	-3.62**	0.11	4.28**	-0.05	2.74**	-71.35**
1000 grain weight	47.62**	-4.71**	4.93**	0.33	-2.05*	20.32**	9.50**	8.22**	-31.32**
Harvest index	39.95**	3.25**	3.41**	5.26**	1.48	-6.07**	6.69**	3.78**	-47.91**
Biological yield	106.42**	4.25**	3.93**	-2.47**	-1.40	32.68**	1.75	-1.22	21.43**
Grain Yield per Plant	43.11**	3.64**	6.89**	6.48**	-0.81	3.99**	10.39**	4.37**	-32.41**

*and ** revealed significant at 5 % and 1 % probability levels, respectively; MP= Mid Parent; BP= Better Parent and ID =Inbreeding depression

Table 3: Estimates of gene effects, heterosis and inbreeding depression for yield and its attributes in pooled mean over four environments in "HPW-296 X HW-5205

HPW-296 X HW-5205	m	D	H	I	J	l	Heterosis%		ID%
							MP	BP	
Plant height	106.36**	1.57	-13.65**	-14.07**	-2.46**	37.74**	0.39	4.26**	11.37**
Second internode length	10.07**	-0.41	-5.48**	-5.46**	-0.54	6.61**	-0.22**	1.30	-103.12**
Peduncle length	42.48**	-1.21	3.73**	4.01**	-0.87	1.95	-0.62	-1.36**	-49.91**
First internode length	3.30**	-0.28	1.35	1.07	-0.38	-0.95	8.17**	11.64**	-84.58**
Tillers per plant	13.69**	-3.69**	3.30**	1.35	-1.54	9.22**	12.42**	-1.12	-59.93**
Productive tillers	12.29**	0.28	-2.03**	-1.38	0.57	1.87	-5.24**	-7.48**	-92.88**
Spike length	12.56**	0.46	0.07	0.09	0.54	1.51	-0.17	-0.84	-83.86**
Spike per plant	16.08**	-1.41	5.53**	2.20**	-0.59	10.03**	18.45**	13.26**	-53.97**
Grains per spike	14.69**	-1.31	-0.95	-3.00**	-0.36	13.93**	13.10**	6.63**	-65.32**
Grain weight per spike	3.78**	0.15	-0.28	-0.55	0.12	1.12	7.31**	6.66**	-92.48**
Days to 50% heading	81.99**	-0.01	1.20	2.36**	3.06**	12.05**	-1.34	2.27**	-10.18**
Days to 50% flowering	105.51**	1.90	-0.02	-1.80	2.28**	4.20**	1.69	1.33	7.52**

Grain filing period	14.07**	0.75	1.33	-0.88	-0.95	1.88	16.92**	34.51**	-77.36**
Days to physiological maturity	113.98**	2.94**	-11.53**	-6.02**	4.94**	12.95**	-4.70**	-3.04**	9.18**
Flag leaf area	51.40**	-1.99*	3.92**	3.84**	0.17	-7.33**	0.16	-3.88**	-48.23**
Leaf canopy temperature	28.84**	-0.61	-3.50**	-3.62**	0.11	4.28**	0.45	3.11**	-74.25**
1000 grain weight	47.62**	-4.71**	4.93**	0.33	-2.05*	20.32**	9.10**	3.64**	-31.15**
Harvest index	39.95**	3.25**	3.41**	5.26**	1.48	-6.07**	-4.41**	-8.26**	-59.39**
Biological yield	106.42**	4.25**	3.93**	-2.47**	-1.40	32.68**	5.81**	0.65	25.24**
Grain yield per plant	43.11**	3.64**	6.89**	6.48**	-0.81	3.99**	0.85	-7.86**	-43.11**

*and ** revealed significant at 5 % and 1 % probability levels, respectively; MP= Mid Parent; BP= Better Parent and ID =Inbreeding depression

Heterosis and inbreeding depression

Estimates of heterosis revealed significant positive heterosis over MP and BP for 1st internodes length, grains per spike, grain weight per spike and 1000 grain weight in all 3 crosses and for grain yield in 'HPW-296 XSONALIKA', productive tillers, spike length and grain filling period in 'HPW-296 X LOK-1'and 'HPW-296 XSONALIKA' and spike per plant in 'HPW-296 XSONALIKA' and 'HPW-296 X HW-5205'. Further, peduncle length, tillers per plant and biological yield showed significant heterosis over MP and BP in cross 'HPW-296 X LOK-1', flag leaf area and harvest index, in 'HPW-296 XSONALIKA' and grain filling period in 'hpw-296 xhw-5205'. However inbreeding depression were significant for all most all traits in all three crosses. In present crosses per cent heterosis did not show appreciable for grain yield to exploit as hybrids.

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