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RESEARCH ARTICLE

Genetic estimation of grain yield and its attributes in three wheat (*Triticum aestivum* L.) crosses using six parameter model

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Abstract. Grain yield is a complex polygenic trait representing a multiplicative end product of contributing yield attributes governed by simple to complex gene interactions. Deciphering the genetics and inheritance of traits/genes influencing yield is a prerequisite to harness the yield potential in any crop species. The objective of the present investigation was to estimate genetic variance components and type of gene action controlling yield and its component traits using six populations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of the three bread wheat crosses. Cross I (25th HRWSN 2105 × WH 1080), cross II (22ndSAWYT323 × RSP 561) and cross III (22ndSAWYT333 × WH 1080) involving elite stripe rust resistant wheat genetic stocks in combination with commercial check varieties were used for analysis. A combination of morpho-physiological, biochemical and disease influencing traits were evaluated, thus exploring the possibility of multi-trait integration in future. Results revealed that the estimated mean effects (m) were highly significant for all the traits in all crosses, indicating that selected traits were quantitatively inherited. The estimate of dominant gene effect was highly significant for plant height, number of tillers per plant in all the three crosses. Grain yield per plant was highly significant in the cross II while total protein content was highly significant in both crosses II and III. Glycine betaine content showed significant additive genes effect. Duplicate epistasis was the most significant for traits like plant height, total protein content and grain yield per plant. Dominance gene effect was more important than additive gene effects in the inheritance of grain yield and most other traits studied. The magnitude of additive × additive gene effects was high and positively significant whereas dominance × dominance was negatively significant for most of the traits studied in the three crosses. Additive × dominance gene effects was of minor significance, thus indicating that selection for grain yield and its components should be delayed to later generations of breeding.

Keywords. gene effects; epistasis; additive; dominance; six generation model.

Introduction

Generation mean analysis belongs to the quantitative biometrical methods based on measurements of phenotypic performances of quantitative traits on as many as possible plant individuals in basic experimental breeding generations (parental, filial, backcross and segregating generations). As outlined by Kearsey and Pooni (1996), generation mean analysis is a useful technique in plant breeding for estimating main gene effects (additive and dominance) and their digenic (additive × additive, additive × dominance, and dominance × dominance) interactions responsible for inheritance of quantitative traits. It helps us in understanding the performance of the parents used in crosses and potential of crosses to be used either for heterosis exploitation or pedigree selection (Sharma *et al*. 2003). Grain yield is a complex polygenic trait resulting from interaction among a number of inherent traits and environment. Wheat grain yield can be improved through indirect selection on the basis of yield components. Sufficient understanding of the inheritance of quantitative traits and information about heritability of grain yield and their components is essential to develop an efficient breeding strategy. Considering the fact that grain yield and quality of bread wheat are the most important complex traits and that their improvement is the most frequent goal of wheat breeding programmes in the world, selection of parental components in this study was done in attempt to fulfill these requirements. Acquiring of genetic information from many generations are more consistent than those taken from one generation. With A, B, C and D scaling tests, additive, dominance and epistatic effects were important for yield and its components characters. Some studies on generation mean

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analysis found additive and dominance genetic factors were important for most of plant traits in wheat (Sharma *et al*. 2003).

Cavalli (1952) reported that accuracy of gene effects increases with increasing number of segregating generations and number of observational plants. Besides gene effects, breeders would also like to know how much variation in a crop is genetic and to what extent this variation is heritable, because efficiency of selection mainly depends on additive genetic variance, influence of the environment. The study of the gene effect not only tells about the relative importance of various kinds of gene effect in the control of a character but also provides information about the cause of heterosis. Knowledge of the degree of heterosis and inbreeding depression plays a decisive role towards the choice of breeding methodology. Exploitation of heterosis is considered to be one of the outstanding achievements of plant breeding. In a self-pollinated crop like wheat, the scope for utilization of heterosis depends mainly upon its direction and magnitude. The present investigation was conducted to determine the extent of heterosis, inbreeding depression and nature of gene action involved in the inheritance of grain yield and some agronomic traits of three wheat crosses.

Materials and methods

A field experiment was conducted at the Research Farm of the Division of Plant Breeding and Genetics, SKUAST-Jammu, Chatha. Six populations, i.e. P_1, P_2, F_1, F_2, BC_1 and BC_2 of the three wheat crosses were grown during 2017–2018 in a randomized block design with three replicates in rows. The six population of each cross were planted in 36 rows, i.e. two rows for each P_1, P_2 and F_1, 10 rows for each of BC_1, BC_2 as well as F_2.

In each replicates, 10 plants for nonsegregating populations and 30 plants for segregating populations were selected randomly for recording observations on nine traits, namely: days to 50% flowering, number of tillers per plant, plant height (cm), days to maturity, total protein content (%), relative water content (%), canopy temperature depression (^{0}C), glycine betaine (μmolg^{-1}) and grain yield per plant (g).

Statistical and genetic procedures

Heterosis and inbreeding depression (%) were estimated according to Miller *et al*. (1958). The analysis was proceeded to estimate the various gene effects using six parameters genetic model of Jinks and Jones (1958) and Hayman (1958) as follows: *m*, mean effect; *d*, additive gene effect; *h*, dominance gene effect; *i*, additive × additive epistatic gene effects; *j*, additive × dominance epistatic gene effects; *l*, dominance × dominance epistatic gene effects. Additive–dominance model (three parameters) was found inadequate to calculate various nonallelic gene effects therefore six parameter model was used. Various gene effects were estimated using six parameter model as suggested by Hayman (1958).

Scaling test

The scaling tests as described by Hayman and Mather (1955) were used to check the adequacy of the additive–dominance model for different traits in each cross. The adequacy of scale must satisfy two conditions, namely additivity of gene effects and independence of heritable component from nonheritable ones. The test of first condition provides information regarding the absence or presence of gene interaction. If one of the four scaling tests found significant, it indicates the presence of epistasis and inadequacy of additive–dominance model. The A, B, C and D tests were made using the following equations for their values and variances.

$$A = 2\overline{B1} - \overline{P1} - \overline{F1}$$
$$B = 2\overline{B}_2 - \overline{P2} - \overline{F1}$$
$$C = 4\overline{F2} - 2\overline{F1} - \overline{P1} - \overline{P2}$$
$$D = 2\overline{F2} - \overline{B1} - \overline{B2}$$

The variances of the estimates were computed using following formulae:

$$V_A = 4V(\overline{B}_1) + V(\overline{P}_1) + V(\overline{F}_1)$$
$$V_B = 4V(\overline{B}_2) + V(\overline{P}_2) + V(\overline{F}_1)$$
$$V_C = 16V(\overline{F}_2) + 4V(\overline{F}_1) + V(\overline{P}_1) + V(\overline{P}_2)$$
$$V_D = 4V(\overline{F}_2) + V(\overline{B}_1) + V(\overline{B}_2)$$
$$V_D = 4V(\overline{F_2}) + V(\overline{B_1}) + V(\overline{B_2})$$

Results and discussion

Mean performance

Generation of the six populations (P_1, P_2, F_1, F_2, BC_1 and BC_2) for yield and yield components are presented in tables 1 and 2. The results of the generation means for all study traits in the three crosses revealed significant difference among all six generations indicating the presence of genetic variability for these traits. The F_1 population was higher than the respective parents in the three crosses for the most studied traits. The mean value of the F_2 population compared with their parents was higher than the highest parent for number of tillers per plant in the cross III (22nd SAWYT333 × WH 1080), grain yield per plant in cross II (22nd SAWYT323 × RSP 561), relative water content cross III (22nd SAWYT333 × WH 1080), total protein content cross II (22nd SAWYT323 × RSP 561) and glycine betaine cross II (22nd SAWYT323 × RSP 561), except days to 50% flowering, plant height (cm), days to maturity and canopy

Table 1. Analysis of variance for three families and their six generations in bread wheat.

Source	d.f.	Mean sum of square								
		Days to 50 % flowering	Number of tillers/plant	Plant height (cm)	Days to maturity	Canopy temperature depression (°C)	Relative water content (%)	Total protein content (%)	Glycine betaine (μmol g^{-1})	Grain yield/plant (g)
Cross I (25thHRWSN2105×WH 1080)										
Replications	2	8.22	0.80	55.48	2.05	0.28	1.42	0.07	0.003	0.35
Generations	5	2.35	1.06	14.41	1.82	1.45*	13.52*	0.86**	12.19**	65.96**
Error	10	1.62	1.53	60.19	5.25	0.68	8.05	0.30	2.89	20.61
Cross II (22ndSAWYT323×RSP 561)										
Replications	2	0.22	0.61	79.01	1.55	0.49	2.40	0.06	5.95	4.46
Generations	5	3.38*	1.14	20.31	7.28**	0.55	11.69*	1.96**	16.23*	17.10
Error	10	1.15	1.62	34.20	4.75	1.09	3.43	0.31	2.08	20.81
Cross III (22ndSAWYT333×WH 1080)										
Replications	2	3.38	1.74	7.05	5.16*	0.47	4.55	0.14	1.49	0.38
Generations	5	1.25	0.19	24.88*	22.26**	1.30*	22.81**	2.70**	18.76**	16.55**
Error	10	0.98	1.47	7.16	1.03	0.67	1.44	0.15	2.21	11.92

*, ** Significant at 5% and 1%, respectively.

temperature depression indicating appreciable amount of genetic variability for these traits in the crosses.

Scaling test

Analysis of generation means having scaling test is very important to find out either nonallelic gene action is present or not and which model is suitable for this analysis. Four kinds of scaling tests were suggested by Mather and Jinks (1982).

Results indicated that in cross I, all the four scaling tests A, B, C and D were highly significant for days to 50% flowering, plant height, days to maturity and relative water content. But scaling tests A, C and D were significant for number of tillers per plant, A, B and D were significant for canopy temperature while A, B and C were highly significant for glycine betaine and total protein content. Scaling tests A and D were highly significant for grain yield per plant. Similar results were reported by Mahpara *et al.* (2017).

Scaling tests A, B, C and D were significant in cross II for days to 50% flowering, plant height, canopy temperature depression, total protein content and grain yield per plant, whereas B, C and D were significant for number of tillers per plant, B and D were significant for days to maturity while scaling tests B and C were significant for relative water content and A, B and C were significant for glycine betaine. Similar results were reported by Mahpara *et al.* (2008) when worked on wheat.

Scaling tests in cross III A, B, C and D were significant for days to 50% flowering, plant height, number of tillers per plant, days to maturity and grain yield per plant while scaling tests A, B and D were significant for canopy temperature depression. But scaling tests A, B and C were significant for relative water content, total protein content and glycine betaine. Magda and El-Rahman (2013) reported similar findings on genetic parameters in three bread wheat crosses.

Gene effects

The estimates of the six parameters, i.e. additive (*d*), dominance (*h*), additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*), and means (*m*) are presented in the table 3. The mean effects were significant for all the study traits in the three crosses, indicating that these traits are quantitatively inherited. The additive gene effects were negative and highly significant for plant height in all the three crosses, grain yield per plant in crosses I and II, relative water content in cross II (22nd SAWYT323 × RSP 561) and cross III (22nd SAWYT333 × WH 1080), canopy temperature depression in cross II (22nd SAWYT323 × RSP 561) and cross III (22nd SAWYT333 × WH 1080), glycine betaine in cross II (22nd SAWYT323 × RSP 561) and cross III (22nd SAWYT333 × WH 1080) whereas positive and significant additive gene effects exhibited in total protein content in all the three crosses. The estimate of dominance gene effect were found highly significant for days to 50% flowering, plant height, number of tillers per plant, relative water content, canopy temperature depression, glycine betaine in all the three crosses. Grain yield per plant was highly significant in the cross II (22ndSAWYT323 × RSP 561), total protein content found highly significant in two crosses (22ndSAWYT323 × RSP 561) cross II and (22ndSAWYT333 × WH 1080) cross III. The magnitude of additive gene effects were small relative to

Table 2. *Per se* performance of six generations in three crosses of bread wheat.

Crosses	P_1	P_2	F_1	F_2	B_1	B_2	Critical difference (0.05 %)
Days to 50% flowering							
25thHRWSN2105 ×WH 1080	100.66	102.00	100.66	102.33	101.00	102.66	0.239
22ndSAWYT323 × RSP 561	103.00	101.00	103.66	104.00	102.66	103.33	0.137
22ndSAWYT333 × WH 1080	102.00	102.66	103.00	103.33	103.66	103.66	0.179
Plant height (cm)							
25thHRWSN2105×WH 1080	91.28	92.24	86.82	87.25	88.56	88.43	0.925
22ndSAWYT323× RSP 561	91.96	96.10	91.62	89.87	95.68	95.32	0.370
22ndSAWYT333× WH 1080	93.95	92.04	85.76	91.43	90.15	88.50	0.310
Number of tillers per plant							
25thHRWSN2105×WH 1080	8.86	9.46	8.33	8.46	9.80	8.53	0.095
22ndSAWYT323× RSP 561	8.80	9.13	10.00	10.13	9.20	10.26	0.131
22ndSAWYT333× WH 1080	9.66	10.06	10.40	10.26	10.00	9.93	0.151
Days to maturity							
25thHRWSN2105×WH 1080	140.33	141.00	140.33	142.33	141.00	140.33	0.303
22ndSAWYT323× RSP 561	138.33	141.66	140.33	141.33	139.00	138.00	0.222
22ndSAWYT333× WH 1080	143.00	141.66	138.33	136.33	138.00	136.66	0.151
Canopy temperature depression (°C)							
25thHRWSN2105×WH 1080	9.62	8.69	10.63	9.50	9.89	10.41	0.095
22ndSAWYT323× RSP 561	9.38	10.43	9.36	10.05	9.67	10.09	0.130
22ndSAWYT333× WH 1080	9.41	10.94	10.34	9.20	10.17	10.47	0.98
Relative water content (%)							
25thHRWSN2105×WH 1080	52.27	50.24	53.25	53.37	54.75	56.47	0.234
22ndSAWYT323× RSP 561	50.23	50.96	53.67	52.76	51.11	55.45	0.202
22ndSAWYT333× WH 1080	51.44	50.20	53.88	56.18	55.37	57.23	0.181
Total protein content (%)							
25thHRWSN2105×WH 1080	19.33	18.90	19.90	19.70	19.26	20.56	0.071
22ndSAWYT323× RSP 561	18.86	18.65	20.26	20.93	20.38	19.23	0.064
22ndSAWYT333× WH 1080	18.53	18.21	19.45	19.79	20.44	20.47	0.045
Glycine betaine ($\mu molg^{-1}$)							
25thHRWSN2105×WH 1080	22.23	21.63	24.43	23.63	27.10	25.30	0.204
22ndSAWYT323× RSP 561	20.83	22.50	25.10	24.53	25.43	27.43	0.140
22ndSAWYT333× WH 1080	19.63	22.26	23.56	22.60	26.20	26.10	0.124
Grain yield per plant (g)							
25thHRWSN2105×WH 1080	22.94	13.45	14.38	14.20	24.12	17.53	0.513
22ndSAWYT323× RSP 561	13.28	11.54	18.03	14.33	14.26	11.61	0.414
22ndSAWYT333× WH 1080	16.81	12.23	13.82	12.81	15.95	18.09	0.430

the corresponding dominance effect in most of the studied traits, suggesting that pedigree method of selection is an appropriate breeding strategy for improving these populations. Dominance gene effects were significant in yield and yield components while insignificant for additive gene effects (Sharma *et al*. 2002). Hasabnis and Kulkarni (2004) mentioned that the estimate of additive gene effects and dominance gene effects were highly significant. Additive × additive epistatic type of gene effects were highly significant for plant height in cross III (22ndSAWYT333 × WH 1080), number of tillers per plant in cross II (22ndSAWYT323 × RSP 561), grain yield per plant in cross I (25th HRWSN2015 × WH 1080) and cross II (22ndSAWYT323 × RSP 561), relative water content in all the three crosses, canopy temperature depression in cross I (25thHRWSN2105 × WH 1080) and cross II (22ndSAWYT323 × RSP 561) cross, total protein content in all the three crosses and glycine betaine in cross I (25th HRWSN2105 × WH 1080). The epistatic effect of dominance × additive were highly significant for days to flowering in cross III (22ndSAWYT333 × WH 1080), plant height in cross I (25th HRWSN2105 × WH 1080) and cross II (22ndSAWYT323 × RSP 561), number of tillers per plant in cross I (25th HRWSN2105 × WH 1080) and cross II (22ndSAWYT323 × RSP 561), days to maturity in cross I (25th HRWSN2105 × WH 1080) and cross III (22ndSAWYT333 × WH 1080), grain yield per plant in cross I (25thHRWSN2105 × WH 1080) and cross III (22ndSAWYT333 × WH 1080), relative water content, canopy temperature depression, total protein content and glycine betaine in all the three crosses. The digenic effects of dominance × dominance were highly significant in days to flowering in cross I (25thHRWSN2105 × WH 1080), plant height in cross II (22ndSAWYT323× RSP 561) and cross III (22ndSAWYT333 × WH 1080), number of tillers per plant in crosses I (25thHRWSN2105 × WH 1080) and III (22ndSAWYT333 × WH 1080), grain yield per plant in cross I (25thHRWSN2105 × WH 1080) and cross II (22ndSAWYT323 × RSP 561), relative water

Table 3. The result of scaling tests and estimates of gene effects in three crosses of bread wheat.

	Scaling test				Three parameter model		
Crosses	A	B	C	D	*m*	*d*	*h*
Days to 50 % flowering							
I	0.66**	2.66**	5.33**	1.00**	101.45**	−0.83**	1.45**
II	−1.33**	2.00**	4.66**	2.00**	102.62**	−0.26	1.04**
III	2.33**	1.66**	2.66**	−0.66**	103.34**	−0.01	0.28**
Plant height (cm)							
I	−0.98**	−2.20**	−8.16**	−2.48**	91.19**	−0.23*	−4.91*
II	7.77**	2.90**	−11.82*	−11.25*	94.21**	−2.25*	−2.23*
III	0.58**	−0.80*	8.20**	4.20**	93.26**	1.28*	−7.49*
Number of tillers per plant							
I	2.40**	−0.73	−1.13**	−1.40**	8.92**	−0.05	−0.72*
II	−0.40	1.40**	2.60**	0.80**	9.29**	−0.38	1.35**
III	−0.06**	−0.60**	0.53**	0.60**	9.81**	−0.09	0.51**
Days to maturity							
I	1.33**	−0.66**	7.33**	3.33**	140.62**	0.45*	0.044*
II	−0.66	−6.00**	4.66	5.66**	139.77**	−1.04*	−0.64
III	−5.33**	−6.66**	−16.00**	−2.00**	138.95**	−1.733*	−2.08
Canopy temperature depression (°C)							
I	−0.47**	1.48**	−1.59	−1.30**	9.07**	0.23*	1.56
II	0.60**	0.39**	1.66**	0.33**	10.09**	−0.44**	−0.46
III	0.58**	−0.33**	−4.20	−2.23**	10.17**	−0.66	−1.39
Relative water content (%)							
I	3.98*	9.45*	4.46*	−4.48*	51.39**	0.39**	6.24**
II	−1.67	6.26**	2.51**	−1.03	51.02**	−1.27	2.98*
III	5.40**	10.38**	15.30**	−0.24	51.67**	−0.03	7.60**
Total protein content (%)							
I	1.29**	1.71**	0.75**	−1.12	19.33**	0.23**	1.08
II	1.63**	2.13**	1.69**	−1.03**	19.19**	0.32**	1.81**
III	2.89**	3.27**	3.50**	−1.33	18.839**	0.29	2.19**
Glycine betaine (μmol g^{-1})							
I	7.53**	4.53**	1.80**	−5.13	22.28**	0.10**	3.96**
II	4.93**	7.26**	4.60**	−3.80	22.48**	−0.10	5.19**
III	9.20**	6.36**	1.36**	−7.10	21.36**	−0.85**	4.65**
Grain yield per plant (g)							
I	10.91**	7.23	−8.34	−13.24**	16.82**	3.51*	−3.30
II	−2.78*	−6.35*	−3.55*	2.78*	11.87**	0.557*	5.74**
III	1.28**	10.13**	−5.43**	−8.42**	14.60**	−2.26	−0.14

Table 3 (*contd*)

Crosses	χ^2	Six parameter model						Gene interaction
		m	*d*	*h*	*l*	*i*	*j*	
Days to 50 % flowering								
I	0.36	103.33**	−0.66	−1.33	−2.54	−2.00	−1.00	Complementary
II	13.12**	106.00	−1.00	−5.66	3.33*	−4.00	−1.66	Duplicate
III	1.47	101.00**	−0.33	7.33*	−5.33	1.33**	0.33*	Duplicate
Plant height (cm)								
I	1.67	86.79**	−0.48	1.81*	−1.78**	4.97**	0.60	Duplicate
II	1.99	71.52**	−2.07	53.28*	−33.18	22.50**	2.43**	Duplicate
III	0.95	101.41**	0.95**	−24.27	8.62**	−8.41	0.69*	Duplicate
Number of tillers per plant								
I	0.02	6.36**	−0.30	6.43*	−4.46**	2.80**	1.56**	Duplicate
II	1.68	10.56**	−0.16**	−1.16	0.60*	−1.60*	−0.90	Duplicate
III	6.98	11.06**	−0.20	−2.53	1.86*	−1.20	0.26*	Duplicate
Days to maturity								
I	0.82	147.33**	−0.33	−13.00	6.00**	−6.66*	1.00**	Duplicate
II	29.69**	151.33**	−1.66	−29.00*	18.00**	−11.33	2.66**	Duplicate
III	2.55	138.33**	0.66**	−8.00	8.00	4.00**	0.66**	Duplicate
Canopy temperature depression (°C)								
I	16.36**	6.54**	0.46**	7.71	−3.63	2.61**	−0.97**	Duplicate
II	7.52**	10.57**	−0.52**	−0.88**	−0.330**	−0.667**	0.10**	Complementary
III	5.17	5.71**	−0.76	9.33**	−4.71	4.46**	0.46**	Duplicate
Relative water content (%)								
I	17.79**	42.28**	1.01**	33.37**	−22.41*	8.97*	−2.73*	Duplicate
II	3.90	48.52**	−0.36**	11.81*	6.66	2.07**	−3.97	Complementary
III	0.20	50.34**	0.62*	19.80**	−16.26	0.48**	−2.48**	Duplicate
Total protein content (%)								
I	2.18	16.86**	0.21**	8.29**	−5.25**	2.25**	−0.20	Duplicate
II	3.77	16.68**	0.10**	9.41**	−5.84	2.07**	−0.24**	Duplicate
III	4.54	15.71**	0.16**	12.57**	−8.82	2.66**	−0.19	Duplicate
Glycine betaine (μmol g^{-1})								
I	1.70	11.66**	0.30**	35.10**	22.33	10.26**	1.50**	Complementary
II	6.43	14.06**	−0.83	30.83**	−19.80	7.60**	−1.16	Duplicate
III	11.36**	6.75**	−1.31	46.58**	−29.76	14.20**	1.41**	Duplicate
Grain yield per plant (g)								
I	0.14	−8.29	4.74**	67.31**	44.63	26.48**	1.83*	Complementary
II	3.73	17.98**	0.86	−14.66	14.70**	−5.57	1.78**	Duplicate
III	1.58	−2.32	2.29*	44.40**	−28.26*	16.84**	−4.42	Duplicate

*, ** Significant at 5 % and 1%, respectively.

Table 4. Heterosis and inbreeding depression for yield and yield contributing traits for the three crosses of bread wheat.

Heterosis				
Traits	Crosses	Mid-parent (%)	Better parent (%)	Inbreeding depression
Days to 50% flowering	I	−0.658	−1.307	−1.656
	II	1.634*	2.640*	−0.322
Plant height (cm)	III	0.651*	0.980	−0.324
	I	−5.883	−5.390	−0.499
	II	−2.559	−0.362	1.914*
	III	−7.778**	−8.714**	−6.607
Number tillers per plant	I	−9.091	−6.015	−1.600
	II	11.524**	13.636**	−1.333
	III	5.405*	7.586*	1.282*
Days to maturity	I	−0.237	−0.473	−1.425
	II	0.238	1.446	−0.713
	III	−2.810**	−2.353**	1.446*
Canopy temperature depression (°C)	I	16.100*	22.307*	10.686**
	II	−5.532	−0.249	−7.369
	III	1.605	9.844	10.961*
Relative water content (%)	I	3.886	5.984	−0.225
	II	6.084*	6.855*	1.695*
	III	6.020**	7.330**	−4.262
Total protein content (%)	I	4.123*	5.308*	1.038*
	II	8.004**	8.612**	1.612*
	III	5.915**	6.846**	1.713*
Glycine betaine (μmolg^{-1})	I	11.398**	12.943	3.274**
	II	15.846**	20.480**	2.258*
	III	12.490*	20.034**	4.102**
Grain yield per plant (g)	I	−20.938	−37.295	1.251*
	II	45.228**	56.149**	20.503**
	III	−4.843	12.970*	7.284*

*, ** Significant at 5% and 1%, respectively.

content and canopy temperature depression in all the three crosses and glycine betaine in cross I (25thHRWSN2105 × WH 1080) and cross III (22ndSAWYT333 × WH 1080).

The dominance gene effect was higher than additive gene effect for all the studied traits in the three crosses indicating predominant role of dominant component of gene action in inheritance of these traits, so the selection for these traits should be delayed to later generation when dominant effect is diminished. Similar conclusion was given by Novoselovic *et al*. (2004). Menon and Sharma (1995) earlier reported that both additive and nonadditive gene effects are important for the inheritance of these traits. Estimates of additive effects can be small due to a high degree of dispersion of increasing alleles between parents and dominance can be small due to its bidirectional nature (Snape 1987). The magnitude of additive × additive gene effects was high and positive whereas dominance × dominance was negative (Hasabnis and Kulkarni 2004).

In cross I (25th HRWSN2105 × WH 1080) dominance (*h*) and dominance × dominance (*l*) gene effects displayed opposite signs in all the traits except days to 50% flowering, glycine betaine and grain yield per plant reported duplicate type of gene interaction. It indicates that glycine betaine and grain yield per plant displayed complementary type of epistatic gene interaction. The complementary type suggested the possibility of considerable amount of heterosis for these two traits in this particular cross (Punia *et al.* 2011). Duplicate type of nonallelic gene interaction for most of studied traits with few exceptions further confirms the prevalence of dominance effects (Singh and Sharma 2001). Presence of duplicate epistasis indicates that variability in segregating generations may be reduced which hinder the selection process (Kumar and Patra 2010), hence it is difficult to utilize them in breeding programmes (Sameer *et al.* 2009).

Cross II (22ndSAWYT323 × RSP 561) showed opposite sign for dominance (*h*) and dominance × dominance (*l*) for all the traits except canopy temperature depression and relative water content, depicting duplicate type of gene interaction. The opposite signs of *h* and *l* counter balance each other, thus leading to reduced heterosis (Kumar *et al.* 2010).

The generation mean analysis of the data revealed that these traits exhibited all type of epistatic gene interactions (additive, dominance and epistatic) and suggested that complex additive effects are important in controlling these traits (Hussain *et al*. 2011). Fethi and Mohamed (2010) reported that dominance effects and dominance × dominance epistasis were more important than additive effects and other epistatic components for grain per spike. Kaur and Singh (2004) stated that the nature and magnitude of gene effect vary within the different crosses for different characters; necessitating specific breeding strategies need to be adopted for particular crosses to obtain improvement.

Heterosis and inbreeding depression

Data presented in table 4 showed heterotic effect calculated as percentage over mid and better parents and inbreeding depression for study traits in the three crosses. The results denoted significant or highly significant positive as well as negative heterosis relative to mid parents for all studied traits in the three crosses. Sharma *et al*. (2002) stated that significant and positive heterosis over the mid parents and better parent were observed for yield and yield components. Sharma *et al*. (2003) mentioned that significant positive heterosis over the better parent was observed in wheat. Significant heterobeltiosis in wheat is attributed to the major combined effects of additive × dominance and dominance × dominance gene effects. Absence of significant heterosis in some cases could be due to the internal cancellation of heterosis components. The results of heterosis revealed that hybrid vigour is available for the commercial production of wheat and selection of desirable hybrids among the crosses having heterotic and heterobeltiotic effects in other character is the best way to improve the grain yield of bread wheat (Memon 2010).

With respect to the inbreeding depression related to F_1 result revealed that significant positive inbreeding

Table 5. Gene interactions for yield and its contributing traits in three crosses of bread wheat.

Gene action	Days to 50% flowering	Plant height (cm)	Number of tillers per plant	Days to maturity	Canopy temperature depression (°C)	Relative water content (%)	Soluble protein content (%)	Glycine betaine (μmolg^{-1})	Grain yield per plant (g)
Mean (*m*)	**	**	**	**	**	**	**	**	**
Additive (*d*)	–	**	**	**	–	**	**	–	*
Dominance (*h*)	*	**	*	–	**	**	**	**	**
Dominance × dominance (*l*)	*	*	*	**	–	*	–	–	**
Additive × additive (*i*)	**	**	**	**	**	**	**	**	**
Additive × dominance (*j*)	*	**	**	*	**	*	–	**	**

*, ** Significant at 5% and 1%, respectively.

depression for most studied traits in the three crosses (table 5). However, inbreeding depression exhibited insignificant for days to 50% flowering in all the three crosses, plant height in cross I (25th HRWSN2015 × WH 1080) and cross III (22ndSAWYT333 × WH 1080), number of tillers per plant in cross I (25thHRWSN2015 × WH 1080) and cross III (22ndSAWYT333 × WH 1080), days to maturity in crosses I (25thHRWSN2015 × WH 1080) and II (22ndSAWYT323 × RSP 561), relative water content in cross I (25thHRWSN2015 × WH 1080) and cross III (22ndSAWYT333 × WH 1080) cross and canopy temperature depression in cross II (22ndSAWYT323 × RSP 561) cross. Sharma *et al*. (2002) reported that significant negative inbreeding depression was recorded frequently for yield and yield contributing traits indicating that the F_2 was superior to the F_1. Significant inbreeding depression was observed for yield and yield contributing traits in the wheat crosses (Sharma *et al*. 2003). The coincidence of sign and magnitude of heterosis and inbreeding depression was detected for most of the traits in the three wheat crosses.

In summary, the additive (*d*) as well nonadditive gene actions (*h*, *l*, *i*) were important for plant height, number of tillers per plant and relative water content, whereas for grain yield per plant and total soluble protein content, additive gene action was important. Further, grain yield per plant, glycine betaine, canopy temperature depression and number of tillers per plant were also controlled by both additive and nonadditive gene actions and grain yield per plant is mainly governed by dominance gene action table 5.

In conclusion, in any breeding programme, improving yield becomes the main breeding objective, and yield is a collective manifestation of several other component traits. Based on the present investigation, it could be inferred that yield and its contributing traits exhibited all three types of gene actions, i.e. additive, dominant and epistasis. The traits examined in the present study revealed complex genetic behaviour. Thus, a simple selection procedure in the early segregating generations may not play significant role in improvement of these traits. The complex genetic behaviour particularly additive and dominance components could be successfully exploited in later generation. It is suggested that selection for the improvement of the examined traits should be delayed to later generation of segregation population in wheat.

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