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GENE ACTION APPRAISAL FOR SEED YIELD AND RELATED TRAITS IN BREAD WHEAT

N. Akhtar[1], A. Waseem[1], T. Mehmood[2], S. Bano[1], A. Raza[1] and Ahsan Aziz[3]

[1]Department of Plant Breeding and Genetics, College of Agriculture, University of Sargodha, Sargodha, Pakistan; [2]Department of Plant Breeding and Genetics, PMAS Arid Agriculture University, Rawalpindi, Pakistan; [3]Department of Agronomy, College of Agriculture, University of Sargodha, Sargodha, Pakistan.

Corresponding author: naeem.uca@gmail.com

ABSTRACT

The inheritance pattern understanding of wheat plant traits (qualitative and quantitative) is the prerequisite to improve seed yield of bread wheat. Gene action for seed yield and yield related parameters were studied by generation mean analysis. Two wheat crosses (PARI-73 × V-7682 and V-6055 × Chakwal-50) indicated that seed yield and other studied plant traits of crosses PARI-73 × V-7682 and V-6055 × Chakwal-50 showed significant differences among themselves. The model [md] gave the greatest fit for plant height and spikelets spike^{-1} in both crosses. In aforementioned crosses parameters like plant height, spikelets spike^{-1} and of grains spike^{-1} displayed additive or additive × additive of type gene actions which indicated that selection in early generations would improve these yield related traits. However, traits i.e., spike length, seed yield plant^{-1} and harvest index in cross PARI-73 × V-7682 showed epistatic effects i.e., [i], [j] and [l] types of gene interaction which demonstrated that genetic behaviour of these traits were complex as and needed more attention. Therefore, it concluded that additive genetic effects played a vital role in expression of most of the yield related traits in wheat and careful selection of these traits in segregating populations would be helpful to increase seed yield.

Key words: Bread wheat, gene action, epistasis, generation mean analysis.

INTRODUCTION

Bread wheat (*Triticum aestivum* L) is an important cereal crop in Pakistan. It is main staple food and a big source of caloric and other valuable nutrients of about 197.735 million population of Pakistan (PBS, 2017). It performs significant role in critical areas of food security and economic stability of our country. At present, though Pakistan has made a remarkable improvement in wheat sector and has attained 8th position in top 10 wheat-producing countries of the world (FAO 2016) but per acre wheat yield it still trailing the averages obtained similar ecologies elsewhere. In Pakistan, population is increasing day by day and to fulfill the demands of ever increasing population therefore, we need to increase wheat yield per unit area under limited resources. Currently, different breeding techniques are used to improve the productivity of wheat per unit area (Saeed and Iftihkar 2017). The achievement of any breeding program depends upon the presence of genetic variability for different wheat plant parameters and its proper utilization (Amawate and Behl, 1995 and Abbasi *et al*., 2014).

In literature, it is reported that green revolution i.e. significant increase in wheat production has been realized through the introduction of dwarfing genes. Vogel *et al* (1956) pointed out that Norin-10 was the first short statured wheat variety which approached the desirable combination of plant height, lodging resistance under climatic and soil conditions, especially favourable for vegetative growth and high yield. Many major and minor genes control plant height trait in wheat. Afzal (1986) described that dwarfness (short stature) in wheat plant is controlled by three independently inherited and dwarfness in accentuated as number of genes influencing that trait is increased.

The knowledge about the nature and extent of gene(s) is essential to improve the crop plants especially, in wheat. Such information indicates about the relative importance of different kinds of gene actions i.e. additive, dominance and epistatic in the control of different traits. Seed yield is the most complex plant parameter that is the product of combined effects (interactions) of different yield related traits and environmental factors (Alaa 2014).

In the view of previous studies in wheat, the research reported in this manuscript was conducted to observe the effects of different quantitative plant traits on seed yield in bread wheat through generation means analysis and generation variance analyses by using tall and dwarf locally adapted wheat genotypes, the purpose being to help in further decision making and advisability of using the genetic material in developing new wheat genotypes with better potential.

MATERIALS AND METHODS

Four parental wheat varieties/ lines viz, V-7682 and Chakwal-50 as tall and PARI-73 and V-6055 were used as dwarf parents in this experiment. Wheat variety PARI- 73 crossed with wheat line V-7682 and V-6055 with Chakwal-50 to develop six basic generations i.e. P_1, P_2, F_1, F_2, BC_1 and BC_2 for each cross. The cross combinations PARI-73 × V-7682 and V-6055 × Chakwal-50 named as Cross A and Cross B, respectively. The experiments were conducted in the research area of College of Agriculture, University of Sargodha, Pakistan during three consecutive growing seasons i.e. 2014 to 2016. All the basic generations were grown in the field followed by Randomized Complete Block Design (RCBD) in triplicate with 5-meter row length. A single row, each for parents and their F_1 generations, two rows for each backcross and three rows for F_2 generations were sown.

Ten plants from each parent and their F_1s, twenty plants from each back cross generation and thirty from each F_2 population were selected in each replication for recording data. The plant traits such as plant height, number of tillers per plant, spike length, spikelets spike^{-1}, number of seeds spike^{-1}, 1000-seed weight, seed yield per mother spike, biomass plant^{-1}, seed yield plant^{-1} and harvest index were recorded.

Analysis of variance technique was used to estimate the difference between generation means (Steel *et al.* 1997) and generation means analysis was used as described by Mather & Jinks (1982). Nested analysis of variance was performed and standard errors (S.E.) of generation means with partitioning of total variation into (i) between replications, (ii) between rows within replications and (iii) between plants within rows within replications were calculated as proposed by Snedecor & Cochran, 1989. Pooling of non-significant mean squares was done where needed. Best fitting models were chosen based on significant parameters and non-significant chi-squares at 5 % probability level. In addition, genetic variance components of variation like D (additive), H (dominance), E (environmental) were also estimated described by Mather and Jinks (1982). Heritability in narrow sense (h^2ns) was calculated using the components of variance from the best fit model of weighted least squares analysis

RESULTS

Generation means: Significant differences were observed among six generations i.e. parents, their F_1s, F_2 and back crosses for studied plant traits of Cross A and Cross B, respectively (Tables 1&2). The F_1 hybrids of Cross A manifested more 1000-seed weight and harvest index than both the parents while in Cross B plant parameters flag leaf area, spike length, 1000-seed weight, seed yield main spike^{-1} and harvest index showed greater F_1 mean values than parents (Tables 3&4). In both crosses A & B, the means of F_1 hybrids for plant traits like 1000 seed weight and harvest index were increased than the better parent showing over-dominance.

Genetic effects for seed yield and related traits: Three-parameters model [mdi] for flag leaf area was the best fitted from observed to expected generation means of Cross A (Table 5). The additive gene action [d] was observed lesser than additive × additive [i] gene action in this cross. In Cross B, model [mhi] was the best from observed and expected generation means for flag leaf area (Table 6). Additive × additive effects were found lesser than dominance effect [h] in this cross. Two parameters model [md] for plant height was best fitted for generation means in both the crosses and revealed that additive genetic effects were imperative for plant height trait in wheat crop. In case of number of tillers plant^{-1}, three parameters model [mhi] was found best fitted from observed and expected generation means in Cross A. It was observed that dominant as well as additive × additive type of gene action was important for the expression of tillers per plant.

In Cross B five traits model [mdhil] was found the best fitted for generation means of number of tillers per plant. In both crosses, it was observed that additive genetic effects [d] were greater than dominance gene action [h]. Regarding spike length five factors model [mhilj] exhibited best fit in Cross A and epistatic effects [i], [l] and [j] exhibited smaller effects than dominant gene action [h]. The positive [i] value indicates that spike length in wheat may be increased by fixing additive × additive effects. The non-allelic effects revealed that this trait has polygenic inheritance but complex. In Cross B two factors model [mh] was recorded best fitted for spike length and in the genetic makeup of this trait only dominance effects [h] were important. In case of spikelets spike^{-1}, two factors model [md] was found best fitted for generation means of both Crosses A and B and additive [d] effects were prominent for this plant parameter. Two factors model [md] was found the best fitted for number of seeds spike^{-1} in Cross A. The data was transformed for this trait to observe the gene action. The transformed data indicated that additive effects were important for this trait.

The four factors model [mdhl] showed the best fit of generation means for number of seeds spike^{-1} in Cross B. In this cross dominance type of gene action [h] was more prominent than additive [d] and non- allelic additive × additive [i] interaction for this plant parameter. The component of [h] and [l] showed complex inheritance for this trait. In case of 1000-seed weight, three parameters model [mdl] for both Crosses A and B was best fitted for generation means. In both crosses the effects of [l] were greater than [d]. Regarding seed yield per mother spike four parameters model [mdhi] for Cross A and three parameters model [mdh] for Cross B was found to be the best fitted. In both crosses [h] effects were found higher than [d] and [i] effects. Over-dominance or unidirectional or dispersion of genes in the parents may be the reasons for greater [h] effects. Positive [i] for this parameter in Cross A indicated that additive × additive interaction can be fixed in bread wheat to increase seed yield per mother spike. Regarding biomass plant^{-1}, three parameters model [mdh] was observed the best fit for generation means in both Crosses A and B. It was observed that additive interaction [d] was greater than dominant effects [h] in both the crosses. For seed yield plant^{-1} five-parameters model [mdijl] was found the best fit generation means of Cross A. In this cross additive × additive [i] interactions were found higher than additive [d], dominance × additive [j] and dominance × dominance [l] interactions. A single parameter model [m] was the best fitted for seed yield plant^{-1} in Cross B. According to this model none of gene effect or non-allelic interaction are significant for grain yield plant^{-1} in this stage and it is suggested that F$_3$ or further generations are required to study gene interaction of this trait. In case of harvest index five parameters model [mdijl] was observed the best fit in Cross A. Harvest index showed complex inheritance in this cross. Model [mdhi] was best fitted for generation means in Cross B (Table 6). In this cross [h] effects were found higher than [d] and [i] effects which were due to over-dominance or unidirectional or dispersion of genes in the parents.

Genetic variance components: Genetic variance analysis of Cross A is shown in Table 7. In this cross model DE (additive and environment) gave the best fit for flag leaf area, plant height, number of tillers plant^{-1}, spike length, spikelets spike^{-1}, number of seeds spike^{-1}, 1000-seed weight and seed yield per mother spike. In these trait only additive effects were important. The model DHE (additive-dominance-environment components) was best fitted for seed yield plant^{-1} and harvest index. While HE model for biomass plant^{-1}. The narrow sense heritability (h^2 ns) estimates of F$_2$ generation were ranged from 34.31 to 89.56 percent for all the studied plant traits. The narrow sense heritability (h^2 ns) estimates for infinity generation were consistently higher than F$_2$ generation and ranged between 52.66 to 95.72 percent for all traits.

Genetic variance analysis of Cross B is shown in Table 8. In case of Cross B, model DE (additive and environment) was the best fitted for plant height, number of tillers plant^{-1}, number of seeds spike^{-1}, 1000-seed weight, seed yield per mother spike, biomass plant^{-1} and seed yield plant^{-1}. In these trait only additive effects were important. Regarding flag leaf area and spike length model DHE (additive-dominance-environment components) gave the best fit while for spikelets spike^{-1} and harvest index only model E was the best fitted. The narrow sense heritability (h^2 ns) estimates of F$_2$ generation were ranged from 40.76 to 87.78 percent and for F infinity generation these estimates were ranged from 57.92 to 97.01 percent for studied plant traits.

Table 1. Mean squares values of basic six generations of wheat cross PARI-73 × V-7682 for various quantitative traits.

Plant Traits	Genotypes	Replications	Error
	(g-1) 5	(r-1) 2	(g-1) (r-1) 10
Flag leaf area	12.959**	13.876^{NS}	3.819
Plant height	837.624**	16.345^{NS}	12.014
Number of tillers plant^{-1}	2.371**	2.676^{NS}	0.685
Spike length	0.369**	0.268^{NS}	0.056
Spikelets spike^{-1}	1.015**	0.677^{NS}	0.091
Number of seeds spike^{-1}	51.065**	18.324^{NS}	6.998
1000-seed weight	12.093**	1.793^{NS}	1.896
Seed yield mother spike^{-1}	0.189**	0.056^{NS}	0.033
Biomass plant^{-1}	494.159**	70..630^{NS}	12.600
Seed yield plant^{-1}	83.255**	29.909^{NS}	2.547
Harvest index	47.068**	13.381^{NS}	5.379

** = P ≤ 0.01

Table 2. Mean squares values of basic six generations of wheat cross V-6055 × Chakwal-50 for various quantitative traits.

Plant Traits	Genotypes	Replications	Error
	(g-1) 5	(r-1) 2	(g-1) (r-1) 10
Flag leaf area	63.180**	1.078^{NS}	2.643
Plant height	506.583**	20.480^{NS}	11.229
Number of tillers plant^{-1}	14.108**	0.607^{NS}	1.532
Spike length	0.190**	0.055^{NS}	0.017
Spikelets spike^{-1}	5.825**	0.298^{NS}	0.972
Number of seeds spike^{-1}	261.582**	2.163^{NS}	35.593
1000-seed weight	9.599**	5.075^{NS}	2.525
Seed yield mother spike^{-1}	0.648**	0.100^{NS}	0.060
Biomass plant^{-1}	124.980**	2.587^{NS}	3.946
Seed yield plant^{-1}	10.011**	1.603^{NS}	0.816
Harvest index	37.768**	0.042^{NS}	6.674

** = P ≤ 0.01

Table 3. Generation means and ± standard error of various quantitative traits for cross PARI-73 × V-7682 wheat genotypes.

Plant Traits	**P$_1$**		**P$_2$**		**F$_1$**		**F$_2$**		**BC$_1$**		**BC$_2$**	
	Mean	**±S.E**	**Mean**	**±S.E**	**Mean**	**±S.E**	**Mean**	**±S.E**	**Mean**	**±S.E**	**Mean**	**±S.E**
Flag leaf area	38.57 ^{a}	1.50	35.10 ^{ab}	1.08	35.58 ^{ab}	1.24	32.63 ^{b}	0.96	37.48 ^{a}	0.93	35.05 ^{ab}	1.20
Plant height	78.10 ^{e}	0.84	127.77 ^{a}	1.40	103.37 ^{c}	0.97	108.63 ^{c}	2.03	116.92 ^{b}	1.48	92.18 ^{d}	1.72
Number of tillers plant^{-1}	10.67 ^{ab}	0.48	10.53 ^{ab}	0.58	8.07 ^{c}	0.18	10.20 ^{a}	0.28	9.23 ^{abc}	0.33	8.70 ^{bc}	0.28
Spike length	12.74 ^{b}	0.20	12.86 ^{b}	0.19	12.48 ^{bc}	0.22	12.26 ^{c}	0.15	13.31 ^{a}	0.17	12.81 ^{b}	0.17
Spikelets spike^{-1}	22.90 ^{a}	0.30	21.30 ^{a}	0.28	21.70 ^{cd}	0.28	21.73 ^{cd}	0.20	22.43 ^{ab}	0.25	22.23 ^{bc}	0.26
Number of seeds spike^{-1}	61.20 ^{bc}	1.26	69.90 ^{a}	1.71	64.17 ^{bc}	1.65	60.47 ^{c}	1.16	70.03 ^{a}	1.23	65.73 ^{ab}	1.25
1000-seed weight	44.90 ^{bc}	0.44	46.54 ^{b}	0.52	49.82 ^{a}	0.35	45.60 ^{bc}	0.59	45.67 ^{bc}	0.58	44.03 ^{c}	0.75
Seed yield mother spike^{-1}	2.75 ^{b}	0.09	3.26 ^{a}	0.08	3.25 ^{a}	0.08	2.81 ^{b}	0.07	3.35 ^{a}	0.08	3.04 ^{ab}	0.07
Biomass plant^{-1}	37.57 ^{d}	0.77	62.79 ^{a}	1.32	42.25 ^{cd}	0.61	48.69 ^{bc}	1.97	51.47 ^{b}	2.73	40.33 ^{d}	2.45
Seed yield plant^{-1}	17.63 ^{cd}	0.59	25.47 ^{a}	0.64	21.66 ^{b}	0.63	20.14 ^{bcd}	0.77	21.14 ^{bc}	1.10	1.18 ^{d}	1.07
Harvest index	46.81 ^{a}	0.81	41.19 ^{b}	0.49	51.01 ^{a}	0.88	42.64 ^{b}	0.75	42.21 ^{b}	1.21	44.09 ^{b}	1.10

Means sharing the same letters are non-significant.

Table 4. Generation means and standard error of various quantitative traits for the cross V-6055 × Chakwal-50 wheat genotypes.

Plant Traits	**P$_1$**		**P$_2$**		**F$_1$**		**F$_2$**		**BC$_1$**		**BC$_2$**	
	Mean	**±S.E**	**Mean**	**±S.E**	**Mean**	**±S.E**	**Mean**	**±S.E**	**Mean**	**±S.E**	**Mean**	**±S.E**
Flag leaf area	34.77 ^{d}	0.85	34.01 ^{d}	0.78	46.45 ^{a}	0.87	38.22 ^{bc}	0.88	40.28 ^{b}	1.12	36.26 ^{cd}	0.75
Plant height	72.80 ^{a}	0.95	110.90 ^{a}	1.14	89.60 ^{cd}	1.03	92.74 ^{c}	1.69	99.80 ^{b}	1.48	84.82 ^{d}	1.60
Number of tillers plant^{-1}	14.93 ^{a}	0.31	9.60 ^{bc}	0.34	9.23 ^{c}	0.25	11.60 ^{b}	0.32	9.43 ^{bc}	0.40	11.30 ^{bc}	0.42
Spike length	13.53 ^{bc}	0.12	13.18 ^{d}	0.12	13.77 ^{ab}	0.12	13.50 ^{c}	0.12	13.92 ^{a}	0.19	13.60 ^{bc}	0.11
Spikelets spike^{-1}	20.80 ^{d}	0.24	24.73 ^{a}	0.33	22.27 ^{bcd}	0.32	22.80 ^{bc}	0.20	23.97 ^{ab}	0.21	22.10 ^{cd}	0.24
Number of seeds spike^{-1}	53.00 ^{d}	1.62	77.67 ^{ab}	1.54	68.90 ^{abc}	1.57	67.03 ^{bc}	1.44	78.70 ^{a}	1.86	66.07 ^{c}	1.36
1000-seed weight	43.89 ^{bc}	1.08	46.44 ^{ab}	0.71	47.94 ^{a}	0.89	44.95 ^{bc}	0.70	44.69 ^{bc}	0.56	42.93 ^{c}	0.64
Seed yield mother spike^{-1}	2.46 ^{c}	0.08	3.51 ^{ab}	0.16	4.56 ^{ab}	0.10	3.29 ^{b}	0.09	3.79 ^{a}	0.10	3.14 ^{b}	0.08
Biomass plant^{-1}	49.79 ^{b}	2.68	60.20 ^{a}	2.79	42.71 ^{c}	3.51	57.47 ^{a}	2.50	57.15 ^{a}	3.29	51.22 ^{b}	2.51
Seed yield plant^{-1}	22.29 ^{c}	1.22	25.40 ^{a}	1.46	20.47 ^{d}	1.60	23.73 ^{bc}	1.13	25.06 ^{ab}	1.39	23.52 ^{bc}	1.27
Harvest index	44.84 ^{bc}	0.73	41.89 ^{c}	1.16	48.67 ^{ab}	1.35	41.39 ^{c}	0.75	44.41 ^{bc}	0.63	50.17 ^{a}	3.52

Means sharing the same letters are non-significant.

Table 5. Best model fit estimates for generation mean parameters by weighted least squares analysis of various quantitative traits for the cross PARI-73 × V-7682 wheat genotypes.

Plant traits	Parameters												
	m	±S.E	[d]	±S.E	[h]	±S.E.	[i]	S.E.	[j]	±S.E	[l]	±S.E	X^2 (df)
Flag leaf area	34.54	0.61	2.17**	0.78			2.81*	1.17					7.29 (3)
Plant height	103.80	0.52	25.22**	0.72									7.25 (4)
Number of tillers plant^{-1}	12.37	0.79			-4.95**	1.23	-2.57**	0.87					7.49 (3)
Spike length	11.28	0.44			2.80**	0.79	1.52**	0.45	1.30**	0.31	-1.60**	0.40	0.20 (1)
Spikelets spike^{-1}	22.00	0.10	0.66**	0.18									8.46 (4)
Number of seeds spike^{-1}	1.81	0.01	0.03**	0.01									4.98 (4)
1000-seed weight	1.65	0.00	0.01*	0.00							0.04**	0.00	6.55 (3)
Seed yield mother spike^{-1}	0.37	0.03	0.04**	0.12	0.14**	0.04	0.10**	0.03					2.66 (2)
Biomass plant^{-1}	54.26	0.74	17.53**	0.74	-12.09**	0.97							4.35 (3)
Seed yield plant^{-1}	18.43	0.74	6.74**	0.43			6.90**	0.89	-471**	1.70	3.37**	1.03	2.56 (1)
Harvest index	40.72	0.76	3.13**	0.47			6.91**	0.93	-10.19**	1.85	10.09**	1.26	1.44 (1)

m = Mean, [d] = Additive effects, [h] = Dominance effects, [i] = Additive × additive effects, [l] = Dominance × dominance effects,
* = $p \leq 0.05$, ** = $p \leq 0.01$.

Table 6. Best model fit estimates for generation mean parameters by weighted least squares analysis of various quantitative traits for the cross V-6055 × Chakwal-50 wheat genotypes.

Plant traits	Parameters												
	m	±S.E	[d]	±S.E	[h]	±S.E.	[i]	S.E.	[j]	±S.E	[l]	±S.E	X^2 (df)
Flag leaf area	29.59	1.87			16.73**	2.44	4.71*	1.98					6.23 (3)
Plant height	91.54	0.49	18.48**	0.69									8.83 (4)
Number of tillers plant^{-1}	1.17	0.04	-0.10**	0.01	-0.30**	0.06	-0.10**	0.04			0.08**	0.03	1.62 (1)
Spike length	13.37	0.08			0.43**	0.14							7.91 (4)
Spikelets spike^{-1}	22.82	0.10	1.96**	0.17									3.37 (4)
Number of seeds spike^{-1}	65.19	1.08	12.81**	1.05	13.27**	2.73					-9.80**	2.35	5.32 (2)
1000-seed weight	44.33	0.33	1.11*	0.51							3.00**	0.86	5.68 (3)
Seed yield mother spike^{-1}	3.06	0.07	0.57**	0.07	0.59**	0.12							5.23 (3)
Biomass plant^{-1}	56.89	1.78	5.22**	1.72	-7.78*	3.62							7.80 (3)
Seed yield plant^{-1}	23.47	0.53											7.56 (5)
Harvest index	34.15	2.02	1.28*	0.64	14.70**	3.06	9.34**	2.13					4.02 (2)

m = Mean, [d] = Additive effects, [h] = Dominance effects, [i] = Additive × additive effects, [l] = Dominance × dominance effects,
* = $p \leq 0.05$, ** = $p \leq 0.01$.

Table 7. Additive (D), dominance (H) and environmental (E) components of variation and narrow sense heritability estimates of various quantitative traits for cross PARI-73 × V-7682 wheat genotypes.

Plant traits	Variance Components						Heritability (NS)		
	(D)	±S.E	(H)	±S.E	(E)	±S.E.	X^2 (df)	h^2(F$_2$)	h^2(F$_2$)
Flag leaf area	67.03*	27.51			49.68**	6.99	4.26 (4)	40.28	57.43
Plant height	575.06**	67.87			33.51**	4.98	3.09 (4)	89.56	94.50
Number of tillers plant^{-1}	0.02*	0.01					0.02 (4)	42.86	60.00
Spike length	1.83**	0.65			1.12**	0.16	0.34 (4)	44.96	62.03
Spikelets spike^{-1}	2.97*	1.42			2.67**	0.37	2.04 (4)	35.74	52.66
Number of seeds spike^{-1}	87.37*	39.53			73.35**	10.28	0.14 (4)	37.33	54.36
1000-seed weight	64.84**	8.68			6.37**	0.94	9.24 (4)	83.58	91.09
Seed yield mother spike^{-1}	0.57**	0.14			0.21**	0.03	1.28 (4)	57.58	73.08
Biomass plant^{-1}			1430.18**	149.17	22.97**	3.34	1.32 (4)		
Seed yield plant^{-1}	-0.07**	0.03	0.22**	0.05	0.004**	0.00	0.25 (3)	36.84	94.59
Harvest index	-116.36**	51.45	364.28**	88.99	18.27	2.72	0.51 (3)	34.73	

* = $p \leq 0.05$,
** = $p \leq 0.01$.

Table 8. Additive (D), dominance (H) and environmental (E) components of variation and narrow sense heritability estimates of various quantitative traits for cross V-6055 × Chakwal-50 wheat genotypes.

Plant traits	Variance Components						Heritability (NS)		
	(D)	±S.E	(H)	±S.E	(E)	±S.E.	X^2 (df)	h^2(F$_2$)	h^2(F$_2$)
Flag leaf area			157.70**	26.97	21.43**	3.19	8.53 (4)		
Plant height	445.54**	55.15			32.54**	4.83	0.35 (4)	87.25	93.19
Number of tillers plant^{-1}	20.63**	3.06			2.76**	0.41	3.83 (4)	78.89	88.20
Spike length	-0.01**	0.003	0.03**	0.005	0.0004**	0.00	0.02 (3)	45.14	97.01
Spikelets spike^{-1}					3.1**1	0.25	2.23 (5)		
Number of seeds spike^{-1}	262.37**	57.31			77.67**	11.26	8.09 (4)	62.81	77.16
1000-seed weight	29.85*	12.09			21.69**	3.07	6.97 (4)	40.76	57.92
Seed yield mother spike^{-1}	0.56**	0.21			0.36**	0.05	4.67 (4)	43.75	60.87
Biomass plant^{-1}	617.47**	190.61			311.54**	44.42	6.26 (4)	49.77	66.47
Seed yield plant^{-1}	112.16**	39.90			68.85**	9.75	1.64 (4)	44.89	61.96
Harvest index					0.004**	0.00	0.14 (5)		

* = $p \leq 0.05$,
** = $p \leq 0.01$.

DISCUSSION

Generation means: The results of generation means indicated that six generations had significant differences among themselves for studied plant characters of both the crosses A and B. In Cross A, 1000- seed weight revealed heterosis while in Cross B plant characters like 1000-seed weight, flag leaf area, harvest index and spike length showed heterosis (Mohamed 2014; Alla 2014). Over all, the F_1 means of harvest index and 1000-seed weight exceeded than the better performing parent which indicated the over-dominance effects in both the crosses. Based on results it is suggested that these traits are helpful for improving seed yield in bread wheat. (Munir *et al.,* 1999; Akhtar and Chowdhry 2006; Fellahi *et al*., 2015) also reported maximum heterosis for above studied plant traits. Thus it is suggested that harvest index, 1000-seed weight, flag leaf area and spike length are important yield related traits and during plant selection process emphasis should be laid on these parameters to develop high yielding wheat genotypes (Saad *et al*., 2010; Kumar *et al*., 2011; Irshad *et al*., 2012 and Fellahi *et al*., 2015).

In both Crosses A and B, three factors models i.e. [mdi] and [mhi] were important for flag leaf area and seed yield plant^{-1}, respectively. In these crosses positive [i] showed the possibility to enhance additive non-allelic interaction to increase flag leaf area which ultimately results to enhance photosynthetic activity of the plant. The significant [d] undoubtedly revealed that the additive effects are pronounced in Cross A and [h] showed that dominance effects are important in Cross B for seed yield improvement (Chowdhry *et al*., 1999; Satyavart *et al*., 2000; Hassan and Khaliq 2008; Zaazaa *et al*., 2012). Similarly, plant height showed simple inheritance in both crosses of wheat genotypes and additive effects were important for plant height. Thus, simple selection in early generations may be helpful to get semidwarf plants to enhance seed yield in wheat (Kathiria and Sharma, 1996; Ojaghi and Akhundova 2010). In Cross A, three parameters model [mhi] and in Cross B, five parameters model [mdhil] showed that dominant effects were important in Cross A and additive inheritance was significant in Cross B to control the number of tillers per plant. While negative value of [i] indicated that it was difficult to enhance additive genetic effects to increase tillers per plant in this cross. Similar type of findings was also documented by (Chowdhry *et al*., 1999; Inamullah *et al*., 2006; Saeed and Iftihkar, 2017). In both crosses dominant gene action was more prominent than other genetic effects for this trait. In case of spike length, Cross A showed complex and polygenic effects than Cross B. It indicated that further generations should be taken to improve spike length in new wheat genotypes due to its complex nature. (Chowdhry *et al*., 1999) and Inamullah *et al*., 2006) also reported complex and polygenic effects for spike length. Two parameters models [md] was found best fit for spikelets per spike in both crosses. This indicated that additive gene action was prominent and showed simple inheritance for the improvement of spikelets spike^{-1}. The results are in conformity with Dimittrijevic *et al*., 1995 who concluded that additive effects play significant role for the inheritance of spikelets per spike. In Cross A, two parameter models [md] were also important for number of seeds spike^{-1}. The data was transformed for this trait to study the genetic effects through generation mean analysis. The additive [d] genetic effects are important for this trait and improvement can be possible through selection in segregating generations (Akhtar and Chowdhry 2006; Inamullah *et al*., 2006; Fellahi *et al.,* 2015). But in case of Cross B, both dominance and additive [mdhl] gene actions were important and played significant role to express the trait. The components of [h] and [l] for this trait indicated the existence of duplicate gene action and difficult to improve line/variety (Dimitrijevic *et al*., 1995). For 1000-seed weight, three parameters model [mdl] was significant for both Crosses A and B and indicated that dominance × dominance [l] as well as additive [d] genetic effects were significant for the expression of 1000-seed weight. These gene interactions revealed that 1000-seed weight was an important plant trait which could be fixed in going on generations (Chowdhry *et al*., 1999; Inamullah *et al*., 2006). For seed yield per mother spike, four parameters [mdhi] and three parameters [mdh] models of Crosses A and B, respectively indicated that dominance genetic effects were more prominent and vital than others. This effect may be due to over dominance or dispersion of genes in the parents, which reduces additive effects. The positive 'i' for seed yield mother spike^{-1}means that it is possible to fix additive × additive interaction in the existing crosses and this trait is also very helpful to increase seed yield of wheat. In the both Crosses A and B, three factors model [mdh] was found the best fitted for biomass per plant. The dominance gene action was observed more important than additive effects for this trait in Cross B which indicated that dominance may be due to dispersion of genes in parents or over dominance (Singh *et al*., 1986; Farshadfar *et al*., 2008; Zaazaa *et al*., 2012). In case of seed yield plant^{-1} five-parameter model [mdilj] was important for Cross A. The positive value [i] indicated the possibility to enhance additive gene action which would be helpful to increase seed yield plant^{-1} in existing wheat genotype. In Cross B, model [m] was best fitted which expressed that genetic effects were not observed in this generation for seed yield plant-^{1}and to detect gene action for this trait we would have to study F_3 or F_4 generations. In case of harvest index, five parameters model [mdijl] was important in Cross A which indicated that additive [d] and epistasis effects were significant for this trait. The epistatic effects exhibited complex and polygenic inheritance which could not be improved easily

(Ciulca *et al.,* 2012). In Cross B, [mdhi] model was best fitted for harvest index which indicated greater dominance [h] effects than others and due to dispersion of genes in the parents. Positive i showed that additive × additive gene interaction was important to improve harvest index in this cross (Mehla *et al*., 2000; Fellahi *et al*., 2015).

Generation variance analysis revealed that two parameter model (D and E) was the best fitted for inheritance of plant height and most of the studied traits in Crosses A and B. This model indicated that additive variance accounted for the largest portion of the total genetic variance in both crosses. Significant and large [D] component exhibited that all increasing alleles were not associated with one parent but existed alongwith decreasing alleles in the same parent. Narrow sense heritability estimates for all the traits were higher in F infinity (F) generation than in F_2 generation which indicated that it had good response to selection from segregating populations with possibility of deriving superior recombinant lines.

Conclusion: Based on the results of present study it was accomplished that flag leaf area, 1000-grain weight and harvest index were the best traits for heterosis in both crosses and these plant parameters might be considered as selection criteria traits in wheat breeding to develop high yielding wheat genotypes. Moreover, additive genetic effects were more imperative to control quantitative plant tts like plant height, flag leaf area, 1000-seed weight, spikelets spike^{-1}, harvest index and seed yield plant^{-1} in both crosses which indicated that selection of these traits in early segregating populations might be helpful to increase seed yield in wheat. Non- allelic interaction for seed yield revealed its genetic complexity requiring greater attention for evolving high yielding wheat varieties.

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