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Original Article

Genetic response of grain yield in wheat (*Triticum aestivum* L.) crosses

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Abstract

Genetic effects on grain yield (GY) were determined in four wheat crosses using mixed inheritance model. GY in cross 1 was controlled by Model E while it was under control of Model E-1 in other crosses. Additive effects of two major genes were observed in cross 1 while additive effects due to several polygene and negative additive effects related to the major genes were observed in controlling GY in the rest of the crosses. Transgressive segregates in the segregating populations of all the crosses indicated the presence of favorable and adverse genes in the parents for GY. Major genes heritability was higher than that of the polygene in the segregating populations of all the crosses with highest environmental influence. Additively controlled nature of the trait predicts that selection of desirable recombinants for higher GY may be delayed up to advance generations until favorable genes are accumulated in homozygous condition.

Keywords: Major genes + minor genes interaction, grain yield, *Triticum aestivum* L.

1. Introduction

Grain yield improvement in wheat (*Triticum aestivum L.*) is the ultimate goal of breeders to meet the food requirements of an increasing population. It is a complex trait because of its quantitatively controlled nature and association with different yield components. Effects of environmental fluctuations on yield and its components further add to the complexity of its inheritance. For the development of improved varieties, it is therefore, imperative to select desirable recombinants for grain yield at proper time from segregating populations resulted through cross combinations of genetically variable parents. To achieve the goal, a breeder has to make segregating populations of crosses in certain pattern and analyze the segregating data through an efficient genetic model. An efficient genetic model in fact is one, which can estimate all possible components of genetic variance with accuracy and precision (Sultan and Singh, 1976).

The present study was therefore, designed to understand the genetic control of GY in wheat by estimating number of major genes, presence of polygene, individual effects of major genes and cumulative effects of major genes and polygene. In addition to phenotypic variances, major genes as well as polygene variances and heritability values were estimated in order to know the appropriate time for selection of desirable recombinants among the segregating progenies. For this purpose, the most advance biometrical approach, i.e. joint segregation analysis (JSA) (Gai and Wang, 1998; Jiankang and Gai, 2001; Gai *et al*., 2003) was used with special superiority and merits (Wang *et al*., 2003) as summarized by Irfaq *et al*. (2012) over all other models proposed by Kearsey and Jinks (1968), Mather and Jinks (1982), and Kearsey and Pooni (1996), which have been used

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previously for estimating genetic effects in quantitatively controlled traits.

2. Materials and Methods

Using cluster analysis under field condition coupled with markers assisted genotyping of 45 bread wheat accessions, genetically diverse and suitable genotypes with contrasting traits, i.e. Bakhtawar-92 (B-92), Frontana, Saleem-2k, Tatara, Inqilab-91, Fakhr-e-Sarhad (FS), and Karwan were selected for hybridization. (Irfaq *et al.*, 2011). Cross combinations and six basic populations (P_1, F_1, P_2, B_1, B_2, and F_2) were developed for each of the four crosses i.e. B-92 × Frontana: (Cross 1), Saleem 2k × Tatara: (Cross-2), Inqilab-91 × FS: (Cross 3) and Karwan × FS: (Cross 4) according to the pattern of JSA (Wang, 1996; Gai and Wang, 1998; Gai *et al.*, 2003, Zhang *et al.*, 2003) as previously practiced (Irfaq *et al.*, 2009; 2012). The populations for each cross were planted in three replications with randomized complete block design (RCBD) at the experimental farm of Nuclear Institute for Food and Agriculture (NIFA), Peshawar, Pakistan, situated at latitude 34°01′ N and longitude 71°40′ E, at an altitude of 347 m above mean sea level during cropping season 2008-09. Keeping 5 m row length, two rows were planted on parents (P_1, P_2) and F_1 population, four rows on each of B_1 and B_2 and eight rows on F_2 populations of both the crosses in each replication. The plant to plant and row to row spacing was maintained 10 and 30 cm, respectively. Seeds were sown at 2.5 cm depth at the rate of two seeds per hill, which were later thinned to single healthy seedling per hill after germination (Irfaq *et al.*, 2009; 2012).

The observations for GY were recorded by manual threshing of selected plants, separately and weighing their seeds in grams using electronic balance from each of the six populations i.e. 60 from each of two homozygous parents (P_1 and P_2), 90 from first filial generation (F_1), 150 from each of the two backcrosses (B_1 and B_2), and 200 from each of the F_2 generation for all the crosses.

2.1 Statistical approach

Individual genetic effects due to major genes and commutative effects due to polygene for GY were determined by using joint segregation analysis (JSA) or mixed inheritance model with five different groups of 24 genetic models (Table 2, 3); with certain assumptions of Wang (1996), Gai and Wang (1998), Gai and Zhang (2003), and Zhang *et al.*, (2003) as described by Irfaq *et al.* (2012). Akaike's information criterion "*AIC*" (Akaike, 1977) and maximum log of likelihood values (MLLE), estimated through iterated expectation and conditional maximization (IECM) algorithm (Dempster *et al.*, 1977, McLachlan, 1988; Wang and Gai, 1997) were used for the choice of the most suitable genetic models in each cross. Further selection of the best fit genetic model was made on the basis of non-significant or smallest number of least significant values of χ^2 statistics with one degree of freedom (Gai and Wang, 1998). Likelihood-ratio test (LRT) was used to choose the simplest type within the model group, with LRT: λ: 2 log (L_a) -2 log (L_0) where L_a and L_0 are the maximum likelihoods under H_a and H_0, respectively. Two other important completely distribution free tests (Table 3) i.e. Smirnov's statistics (nW^2) and Kolmogorove's statistics (D_n) with D: Sup $|F_n(\times) - F_o(\times)|$ (Gai and Wang, 1998) were used as goodness of fit tests to determine whether the selected model sufficiently explains the data (Zhang *et al.*, 2003). If, for a particular genetic model, none of these five statistics were significant, then it was the indication that the data adequately fit the model. The data were analyzed by using Sin. Exe software, the major gene-polygene mixed inheritance model to a joint analysis of multi-generations (Gai *et al.*, 2003). In case of the best fit model, the values of second order genetic parameters as well as σ_{mg}^2 and σ_{pg}^2 for B_1, B_2 and F_2 were worked out with the help of proposed formulae (Gai *et al.*, 2003) by using MS Excel® program of Windows®. Under the second order genetic parameters (Table 5), the phenotypic variation (σ_p^2) is partitioned into genetic and environmental variation (σ_e^2) for the two crosses. The genetic component of variation in turn is subdivided into variation due to major genes (σ_{mg}^2) and polygene (σ_{pg}^2). The values from μ_1 to μ_{69} of Table 4 indicate different means regarding six generations, which were to be put in the suggested formulae for calculating 1st and 2nd order genetic parameters (Gai *et al.*, 2003). Percent environmental variation (V_e) for each generation was calculated by dividing environmental variance (σ_e^2) over collective phenotypic variance (σ_p^2) of the respective generation, i.e. (σ_e^2/σ_p^2) × 100.

3. Results

3.1 Frequency distribution for GY in different populations

Mean values of the parents (13.8, 13.5 g plant^{-1}) in cross 1 (Bakhtawar-92 × Frontana) were at par to each other whereas F_1 showed higher grain yield (14.8 g plant^{-1}) than both of the parents. In cross 2 (Saleem-2k × Tatara), mean GY of F_1 (14.8) was lower than both of the parents (17.1, 15.0) indicating the accumulation of adverse genes from parents in F_1. In cross 3 (Inqilab-91 × FS) and 4 (Karwan × FS) mean GY of F_1 (15.1, 13.4 g plant^{-1}, respectively) was higher than those of their respective parents i.e. 10.7, 12.6 and 10.1, 12.6 g plant^{-1}, respectively. Mean GY for B_1 and B_2 (15.2, 13.4; 18.2, 15.7; 15.7, 17.3; and 15.9, 17.1 g plant^{-1}) showed tendency towards their respective pollen donor parents in all the crosses (Table 1). F_2 was normally distributed among the parents in the crosses. Transgressive segregates though very few on the upper and few on the lower limit of the range for GY were observed in B_1, B_2 and F_2 populations of all the crosses (Table 1).

Table 1. Frequency distribution of plant population for grain yield in P_1, P_2, F_1, B_1, B_2 and F_2 of four bread wheat crosses.

Cross[1]	Generation[2]	Range of grain yield per plant (g)										Size[3]	M-GY[4]	Variance[5]	SD(±)[6]
		1.0-5	5.1-10	10.1-15	15.1-20	20.1-25	25.1-30	30.1-35	35.1-40	40.1-45	45.1-50				
1	P_1		12	19	20	7	2					60	13.8	24.4	4.9
	F_1		18	30	26	12	4					90	14.8	28.9	5.4
	P_2		16	24	12	7	1					60	13.5	24.1	4.9
	B_1		38	45	38	14	9	4	2			150	15.2	47.7	6.9
	B_2		52	49	26	15	7	1				150	13.4	40.2	6.3
	F_2	6	32	71	40	20	9	11	6	4	1	200	16.9	79.3	8.9
2	P_1		4	20	17	18	1					60	17.1	26.5	5.1
	F_1		15	34	30	8	3					90	14.8	21.6	4.6
	P_2		11	24	15	6	4					60	15.0	27.9	5.3
	B_1		25	40	42	15	9	8	7	1	3	150	18.2	82.1	9.1
	B_2		40	51	28	10	9	9	3			150	15.7	69.6	8.3
	F_2	8	21	57	51	15	19	11	8	6	4	200	18.9	100.1	10
3	P_1	2	35	13	7	3						60	10.7	20.4	4.5
	F_1		16	39	23	5	4	3				90	15.1	31.5	5.6
	P_2	1	23	22	9	3	2					60	12.6	25.3	5.0
	B_1		26	60	35	13	8	3	5			150	15.7	50.3	7.1
	B_2	8	32	42	25	22	11	4	3	3		150	17.3	103.7	10.2
	F_2	3	32	62	30	27	15	15	8	5	3	200	18.6	98.8	9.9
4	P_1	8	29	9	13	1						60	10.1	23.0	4.8
	F_1	5	25	27	18	14	1					90	13.4	31.0	5.6
	P_2	1	23	22	9	3	2					60	12.6	25.3	5
	B_1		39	14	32	31	20	10	4			150	15.9	55.3	7.4
	B_2	6	18	51	25	26	10	7	4	3		150	17.1	70.4	8.4
	F_2	10	42	49	37	19	21	7	7	5	3	200	17.6	103.4	10.2

1: Cross 1= Bakhtawar-92 (P_1) × Frontana (P_2), cross 2 = Saleem-2k (P_1) × Tatara (P_2), cross 3 = Inqilab-91 (P_1) × Fakhr-e-Sarhad (P_2) and cross 4= Karwan (P_1) × Fakhr-e-Sarhad (P_2); 3: Sample size; 4: Sample mean grain yield per plant (g); 5: Phenotypic variance; 6: Standard deviation.

3.2 Choice of the best fitting models for the crosses from suitable genetic models

Based on values of maximum log of likelihood, Akaike's information criterion values (Table 2) and the smallest number of least significant or non-significant values of five goodness of fit tests, i.e. U_1^2, U_2^2, U_2^3, W^2 and D_n (Table 3) suggested by Gai and Wang (1998). Zhang *et al.* (2003) suitable as well as alternative genetic models for the trait are presented in Table 2 for the crosses. Among the suitable models in each cross, the best fit model was chosen on the basis of non-significant or smallest number of least significant values of five statistics for goodness of fit test viz. U_1^2, U_2^2, U_2^3, and χ^2 statistics, $_nW^2$ (Smirnov's statistics) and $_n$ (Kolmogorov's statistic) as presented in Table 3. The best fitting genetic model in cross 1 was E, indicating that the trait is under control of mixed two major additive dominance epistatic genes plus additive dominant epistasis of polygene (Table 2). Whereas for the rest of the crosses (Cross 2, 3 and 4), model E-1 was the best fitting representing the control of the trait under mixed two major additive dominance epistatic genes plus additive dominant polygene (Table 2).

3.3 Calculation of genetic effects on GY

Under the 1st order genetic parameters for cross 1, the values from m_1 to m_6 represent the population means of P_1, F_1, P_2, B_1, B_2 and F_2, respectively. The additive effects due to major genes A and B ($d_a = d_b = 6.1$) were equal and positive (Table 5). The dominant components due to the major genes i.e. A & B were equal and negative ($h_a = h_b = -3.5$). Under the epistasis the additive × additive effect (i) due to the two major genes and the dominant × dominant genetic effects (l) due to the major genes in combination with polygene were 5.5 and 11, respectively. Under the mixed epistasis, the additive × dominant components due to the major genes were equal and negative ($J_{ab} = J_{ba} = -3.1$).

In case of cross 2, 3 and 4, the population mean was recorded as 23.1, 20.3, and 17.9, respectively. Positive additive effect (7.4) was estimated due to first major gene (A) for cross 2 whereas in cross 3 and cross 4 the additive effects due to first major gene (A) were negative (-6.0 and -8.2, respectively). The additive effect due to second major gene (B) in cross 2 was negative (-6.9) whereas positive additive effects were 5.5 and 8.2 as a result of the second major gene (B) in cross 3 and cross 4, respectively. Partial negative dominant effects recorded due to first major gene (A) were -0.3 and -2.6 in cross 2 and 3, respectively. However, partial dominant effect due to the first major gene (A) was positive (1.1) in case of cross 4. The dominant effect due to second major gene (B) was negative (-0.2) in cross 2. Positive dominant effects due to the second major gene (B) estimated in cross 3 and 4 were 1.1 and 2.1, respectively. Negative additive × additive epistatic effects (i) were -7.5, -8.7 and -6.4 in cross 2, 3 and 4, respectively. Similarly, negative dominant × dominant component (l) was estimated in cross 2, 3 and 4 was -6.9, -7.5 and -10, respectively. Under the mixed epistasis due to the major genes as well as polygene, the additive × dominant effect due to the first major gene (J_{ab}) was positive in cross 2 and 4 (3.2, 0.7, respectively) whereas negative effect (J_{ab}) was -3.7 for cross 3. Negative additive × dominant effects due to second major gene (J_{ba}) in cross 2, 4 were -1.6 and -1.7, respectively. The same was positive (2.2) for cross 3.

3.4 Genetic, phenotypic, environmental variations and heritability estimates

The phenotypic variances from the sample observations were almost at par and less for parents (P_1: 4.9, 5.1, 4.5, and 4.8; P_2: 4.9, 5.3, 5, and 5) and F_1 population (5.4, 4.6, 5.6, and 5.6) in all the crosses as compared to those of segregating populations i.e. back crosses (B_1: 6.9, 9.1, 7.1, and 7.4; B_2: 6.3, 8.3, 10.2, and 8.4) and F_2 (8.9, 10, 9.9, and 10.2) populations (Table 1). As evident from the 2nd order genetic parameters for cross 1 (Table 5), variance due to major genes (σ_{mg}^2 = 23.6, 16.8 and 55.2) and major gene heritability (h_{mg}^2 = 49.4, 41.7 and 69.7) were higher than those of the polygene (σ_{pg}^2 = 3.1, 2.3 and 3.01, and h_{pg}^2 = 6.5, 5.8 and 3.8) for segregating generations B_1, B_2 and F_2, respectively. Similarly, variance (σ_{mg}^2) and heritability (h_{mg}^2) due to major genes was higher in cross 2, 3 and 4 as compared to the variance (σ_{pg}^2) and heritability (h_{pg}^2) due to polygene for B_1, B_2 and F_2, respectively. Higher environmental variations (*Ve*) in the range of 22.4 to 52.5 were observed for segregating populations in all the crosses.

4. Discussion

To determine the genetic basis of GY, as desired by Cox and Murphy (1990) regarding parental selection for crosses, suitable genotypes were selected through cluster analysis coupled with genotyping of 45 wheat genotypes (Irfaq *et al.*, 2011) and the crosses were attempted between the parents with contrast in the trait. Four cross combinations were made between the contrasting genotypes using parents with low grain yield as pollen recipient in cross 1, 2 and those with high GY as pollen donors in cross 3, 4. However, both the parents with respect to GY were at par in cross 1 (Table 1). Using JSA as biometrical approach, number of major genes, presence of polygene, genetic effects due to individual major genes, and collective effects due to major genes in combination with polygene for controlling GY were determined in the same way as outlined for determining genetic effects on area under disease progress cure (Irfaq *et al.*, 2009) and flag leaf area in wheat (Irfaq *et al.*, 2012).

As evident from Table 1, mean grain yield plant^{-1} of F_1 populations (14.8, 15.1, and 13.4) was higher than the average of their respective parents in cross 1, 3 and 4. These indicate the accumulation of favorable genes from the parents in their respective F_1 generations (Table 1). The reversed situation in cross 2 reveals that some adverse genes dispersed in the parents (Saleem-2k and Tatara) for GY have

Table 2. Maximum log of likelihood estimates (MLLE) and Akaike's information criterion (*AIC*) values for grain yield per plant in 24 genetic models estimated through the iterated expectation and conditional maximization (IECM) algorithm.

Model group, code, and implication of model type	Cross combination							
	Cross 1		Cross 2		Cross 3		Cross 4	
	MLLE	*AIC*	MLLE	*AIC*	MLLE	*AIC*	MLLE	*AIC*
Group 1: One major gene								
A-1: additive and dominant	-2394.4	4796.8	-2506.5	5021.0	-2521.2	5050.5	-2501.2	5010.1
A-2: additive	-2395.8	4797.6	-2509.1	5024.2	-2530.7	5067.3	-2505.7	5017.4
A-3: dominance	-2394.9	4795.8	-2511.5	5029.1	-2533.5	5072.9	-2508.5	5023.0
A-4: negative dominance	-2397.6	4801.2	-2506.0	5018.0	-2525.9	5057.9	-2497.1	5000.5
Group 2: Two major genes								
B-1: additive dominance and epistasis	-2312.0	4644.1	-2376.3	4772.5	-2389.5	4799.2	-2387.2	4794.4
B-2: additive and dominance	-2360.6	4733.3	-2465.2	4942.4	-2480.1	4972.1	-2470.1	4952.3
B-3: additive	-2367.3	4742.6	-2488.4	4984.8	-2598.4	5204.7	-2471.7	4951.5
B-4: equal additive	-2396.2	4798.5	-2510.1	5026.2	-2531.2	5068.4	-2506.3	5018.6
B-5: dominance	-2382.1	4772.2	-2500.4	5008.7	-2487.8	4983.7	-2484.3	4976.6
B-6: equal dominance	-2395.2	4796.5	-2511.9	5029.8	-2533.5	5072.9	-2508.6	5023.3
Group 3: Polygene								
C: additive dominance and epistasis	-2351.6	4723.2	-2451.0	4921.9	-2450.2	4920.3	-2434.2	4888.5
C-1: additive and dominance	-2360.9	4735.7	-2462.4	4938.8	-2477.3	4968.5	-2468.0	495.0
Group 4: One major gene plus polygene								
D: mixed one major-gene and additive dominance-epistasis polygene	-2329.7	4683.4	-2408.3	4840.5	-2407.1	4838.3	-2415.0	4854.1
D-1: mixed one major gene and additive dominance polygene	-2357.2	4698.3	-2429.9	4877.7	-2434.7	4887.5	-2429.6	4877.3
D2: mixed one additive major gene and additive-dominance polygene	-2388.2	4701.2	-2429.9	4875.7	-2434.7	4885.4	-2429.6	4875.3
D-3: mixed one dominance major gene and additive-dominance polygene	-2352.5	4720.9	-2454.7	4925.3	-2434.7	4885.6	-2429.7	4875.3
D-4: mixed one negative dominance major gene and additive dominant polygene	-2321.4	4658.7	-2429.9	4875.7	-2457.71	4931.4	-2448.8	4913.6
Group 5: Two major genes plus polygene								
E: mixed two major additive dominance epistatic genes plus additive dominant-epistasis of polygene.	-2299.2	4634.4	-2377.8	4791.6	-2383.6	4803.4	-2380.3	4796.7
E-1: mixed two major additive dominance epistatic genes plus additive dominant polygene	-2304.2	4638.3	-2375.7	4781.4	-2383.3	4796.7	-2382.0	4794.0
E-2: mixed two major additive dominant genes plus additive dominant polygene	-2356.3	4734.5	-2455.7	4933.5	-2465.2	4952.4	-2461.7	4945.4
E-3: mixed two major additive genes plus additive dominant polygene	-2307.2	4632.4	-2381.9	4781.7	-2386.1	4790.2	-2392.1	4802.3
E-4: mixed two major equal additive genes plus additive dominant polygene	-2360.8	4737.5	-2462.3	4940.6	-2477.1	4970.3	-2467.9	4951.7
E-5: mixed two major dominant genes plus additive dominant polygene	-2360.8	4739.7	-2462.4	4942.8	-2465.2	4948.4	-2463.9	4945.8
E-6: mixed two major equal dominant genes plus additive dominant polygene	-2505.4	5026.8	-2483.3	4982.6	-2573.3	5162.5	-2558.8	5133.6

Source of different model groups and model types (Gai and Wang, 1998, Gai et al., 2003)

Table 3. Tests for goodness-of-fit regarding grain yield plant^{-1} for suitable models in four wheat crosses.

Crosses 1: Bakhtawar-92 × Frontana							Cross 2: Saleem-2k × Tatara						
Model	P	U$_1^2$	U$_2^2$	U$_2^3$	nW^2	D$_n$	Model	P	U$_1^2$	U$_2^2$	U$_2^3$	nW^2	D$_n$
E-3	P$_1$	0.05(0.83)	0.03(0.85)	0.01(0.1)	0.22(>0.05)	0.12*	B-1	P$_1$	0.29(0.59)	1.07(0.30)	4.28**	0.25(>0.05)	0.15**
	F$_1$	0.73(0.39)	1.16(0.28)	1.00(0.32)	0.28 (>0.05)	0.11*		F$_1$	0.12(0.73)	0.03(0.86)	0.40(0.53)	0.06 (>0.05)	0.08*
	P$_2$	0.96(0.33)	0.87(0.35)	0.00(0.95)	0.12 (>0.05)	0.09*		P$_2$	0.13(0.72)	0.21(0.64)	0.20(0.65)	0.07 (>0.05)	0.07*
	B$_1$	13.07***	12.65***	0.05(0.82)	1.42(0.16)	0.16(>0.05)		B$_1$	3.60*	3.98*	0.40(0.53)	0.42(>0.05)	0.09*
	B$_2$	26.16***	27.18***	1.09(0.30)	2.77**	021(0.05)		B$_2$	10.65***	10.52***	0.11(0.74)	1.37**	0.16(>0.05)
	F$_2$	0.87(0.35)	1.34(0.25)	1.06(0.30)	0.33(>0.05)	0.09*		F$_2$	2.10(0.15)	3.79*	4.73*	0.46(>0.05)	0.10*
E	P$_1$	0.70(0.40)	0.37(0.54)	0.67(0.41)	0.37(>0.05)	0.17*	E-1	P$_1$	0.23(0.63)	1.05(0.31)	5.00**	0.26(>0.05)	0.16*
	F$_1$	1.32(0.25)	0.23(0.64)	6.57**	0.58 (>0.05)	0.16(>0.05)		F$_1$	0.28(0.60)	0.15(0.70)	0.23(0.62)	0.06 (>0.05)	0.08*
	P$_2$	0.31(0.58)	0.13(0.71)	0.52(0.47)	0.14 (>0.05)	0.11*		P$_2$	0.08(0.77)	0.18(0.67)	0.37(0.55)	0.07 (>0.05)	0.08*
	B$_1$	4.59**	7.62**	7.53**	0.68(>0.05)	0.12*		B$_1$	3.6(0.06)	4.17**	0.67(0.42)	0.46(>0.05)	0.10*
	B$_2$	2.11(0.15)	2.62(0.11)	0.71(0.40)	0.41(>0.05)	0.09*		B$_2$	9.88***	9.95***	0.20(0.65)	1.28*	0.16(>0.05)
	F$_2$	0.28(0.59)	0.18(0.67)	0.15(0.70)	0.33(>0.05)	0.09*		F$_2$	2.36(0.12)	3.85*	3.62(0.06)	0.45(>0.05)	0.10(>0.05)
E-1	P$_1$	0.06(0.81)	0.04(0.84)	0.03(0.87)	0.25(>0.05)	0.14(0.05)	E-3	P$_1$	0.45(0.50)	1.24(0.27)	3.47(0.06))	0.25 (>0.05)	0.16**
	F$_1$	0.61(0.44)	0.09(0.78)	3.57*	0.44(>0.05)	0.11*		F$_1$	1.70(0.19)	1.08(0.92)	0.81(0.37)	0.18(>0.05)	0.10*
	P$_2$	7.00**	7.64**	0.65(0.41)	0.82(>0.05)	0.13*		P$_2$	0.95(0.33)	0.99(0.32)	0.04(0.85)	0.12(>0.05)	0.09**
	B$_1$	0.40(0.53)	0.32(0.57)	0.03(0.87)	0.15(>0.05)	0.09*		B$_1$	6.32**	6.63**	0.32(0.57)	071(>0.05)	0.11*
	B$_2$	0.01(0.98)	0.04 (0.8)	1.21(0.27)	0.10(>0.05)	0.09*		B$_2$	18.02***	16.83***	0.00(0.97)	2.01**	0.19(>0.05)
	F$_2$	0.00(0.96)	0.03(0.86))	0.24(0.61)	0.10(>0.05)	0.05*		F$_2$	0.55(0.46	1.2(0.27)	2.42(0.12)	0.28 (>0.05)	0.09*
Cross 3: Inqilab-91 × Fakhr-e-Sarhad (FS)							Cross 4: Karwan × Fakhr-e-Sarhad (FS)						
E-3	P$_1$	0.86(0.35)	1.22(0.27)	0.68(0.41)	0.42 (>0.05)	0.19(>0.05)	E-1	P$_1$	0.66(0.42)	0.35(0.55)	0.61(0.43)	0.30(>0.05)	0.14*
	F$_1$	1.59(0.21)	1.23(0.27)	0.19(0.66)	0.31 (>0.05)	0.12*		F$_1$	0.86(0.36))	0.05(0.82)	7.06**	0.43(>0..05)	0.15*
	P$_2$	0.98(0.32)	1.09(0.30)	0.12(0.73)	0.43 (>0.05)	0.21(>0.05)		P$_2$	1.20(0.27)	1.37(0.24)	0.14(0.71)	0.46(>0.05)	0.22(>0.05)
	B$_1$	7.87**	10.86**	5.37**	1.07**	0.13(>0.05)		B$_1$	0.09(0.76)	0.45(0.50)	2.31(0.13)	0.17(>0.05)	0.08*
	B$_2$	3.02(0.08)	3.21(0.07)	0.19(0.66)	0.39 (>0.05)	0.10*		B$_2$	0.34(0.56)	0.87(0.35)	2.17(0.14)	0.15(>0.05)	0.06*
	F$_2$	0.36(0.55)	0.16(0.68)	0.52(0.47)	0.09(>0.05)	0.05(>0.05)		F$_2$	1.31(0.25)	1.15(0.28)	0.02(0.89)	0.16(>0.05)	0.06*
E-1	P$_1$	0.97(0.32)	1.30(0.25)	0.56(0.45)	0.43(>0.05)	0.20(>0.05)	B-1	P$_1$	1.84(0.18)	1.28(0.26)	0.51(0.47)	0.43 (>0.05)	0.18**
	F$_1$	1.02(0.31)	0.77(0.37)	0.14(0.71)	0.24(>0.05)	0.11*		F$_1$	0.11(0.74)	0.03(0.86)	4.05**	0.27 (>0.05)	0.12*
	P$_2$	0.38(0.54)	0.54(0.46)	0.29(0.59)	0.34 (>0.05)	0.19(>0.05)		P$_2$	0.77(0.38)	1.09(0.30)	0.60(0.44)	0.41(>0.05)	0.21(>0.05)
	B$_1$	2.79(0.10)	4.66**	4.71**	0.53(>0.05)	0.11*		B$_1$	0.13(0.73)	0.71(0.40))	4.04**	0.22(>0.05)	0.09*
	B$_2$	2.07(0.15)	2.06(0.15)	0.03(0.86)	0.30 (>0.05)	0.0.9*		B$_2$	6.87**	9.52***	4.06**	0.81(>0.05)	0.13*
	F$_2$	1.31(0.25)	1.66(0.21)	0.52(0.47)	0.18(>0.05)	0.06(>0.5)		F$_2$	0.28(0.60)	0.14(0.71)	0.30(0.58)	0.44 (>0.05)	0.12*
B-1	P$_1$	2.83(0.09)	3.24(0.07)	0.48(0.48)	0.68 (>0.05)	0.24(>0.05)	E	P$_1$	0.27(0.60)	0.08(0.77)	0.74(0.39)	0.25(>0.05)	0.13*
	F$_1$	0.33(0.57)	0.39(0.53)	0.09(0.76)	0.16 (>0.05)	0.10*		F$_1$	0.32(0.57)	0.02(0.88)	7.76**	0.38(>0.05)	0.13*
	P$_2$	0.54(0.46)	0.87(0.35)	0.76(0.38)	0.38(>0.05)	0.20(>0.05)		P$_2$	0.91(34)	1.00(0.32)	0.09(0.76)	0.41 (>0.05)	0.21(>0.05)
	B$_1$	3.66*	6.63**	8.43***	0.76(>0.05)	0.13 (>0.05)		B$_1$	1.61(0.20)	2.13(0.14)	0.85(0.36)	0.31(0.05)	0.09*
	B$_2$	2.70(0.10)	2.88(0.09)	0.18(0.67)	0.33(>0.05)	0.10*		B$_2$	6.16**	9.50***)	7.59**	0.90 (>0.05)	0.13(>0.05)

Table 4. Maximum likelihood estimates of component parameters regarding grain yield per plant for four wheat crosses in their respective best fit models

Parameter	Cross 1 Model: E Estimate	Cross 2 Model: E-1 Estimate	Cross 3 Model: E-1 Estimate	Cross 4 Model: E-1 Estimate
μ_1:	13.8	16.9	10.8	10.4
μ_2:	14.8	14.3	15.0	13.7
μ_3:	13.5	14.4	12.4	12.7
μ_{41}:	29.5	15.8	12.8	12.2
μ_{42}:	11.3	33.1	13.5	13.2
μ_{43}:	11.3	13.9	27.1	26.3
μ_{44}:	15.8	15.4	13.1	11.9
μ_{51}:	21.7	14.6	13.3	12.9
μ_{52}:	11.3	30.2	12.0	14.3
μ_{53}:	11.3	11.2	33.1	29.4
μ_{54}:	11.0	14.0	14.1	13.5
μ_{61}:	34.9	15.4	12.9	12.7
μ_{62}:	16.7	32.7	13.6	13.7
μ_{63}:	11.8	44.1	19.4	9.0
μ_{64}:	16.7	13.6	27.2	26.9
μ_{65}:	21.2	15.0	13.2	12.4
μ_{66}:	10.8	30.5	11.9	13.8
μ_{67}:	11.8	15.5	42.4	42.2
μ_{68}:	10.8	11.6	33.0	28.9
μ_{69}:	10.5	14.4	14.0	13.0
σ^2:	21.0	23.4	23.2	24.1
σ_4^2:	24.2	27.5	23.2	24.1
σ_5^2:	23.4	23.4	30.9	28.6
σ_6^2:	24.1	23.4	23.2	24.1

σ^2: Phenotypic variance of P_1, F_1 and P_2; σ_4^2: polygenic + environmental variance of B_1; σ_5^2: polygenic + environmental variance of B_2; σ_6^2: polygenic + environmental variance of F_2.

been accumulated in F_1. The tendency of B_1 and B_2 populations to their respective pollen donor parents reveals that the trait is almost under control of nuclear genes (Table 1). Normal distribution of F_2 population between their respective parents for GY in the crosses indicates the quantitatively controlled nature of the trait in wheat. Highest phenotypic variances (Table 1) for segregating populations (B_1, B_2 and F_2) reveal that the trait is under the influence of environmental fluctuations. Occurrence of transgressive segregates in B_1, B_2 and specially F_2 populations of the crosses on both upper and lower limits of the parental populations is the indication that both favorable and adverse genes for GY are dispersed in the parents of all the crosses.

As evident from the first order genetic parameters of Table 5, all types of additive effects (d_a, d_b, and i) were significantly positive in cross 1. Mixed dominant × dominant (l) effect due to major genes in combination with polygene was also significantly positive. However, the additive types of interactions were pre dominant over the dominant type of interactions. The results of cross 1 are almost in accordance with those of Novoselovic *et al.*, (2004) who used generation mean analysis and found complementary type of digenic epistasis in wheat cross at one location as well as significant additive, additive × additive, additive × dominant and dominant × dominant type of gene interaction in other crosses at different locations. Gurdev *et al.*, (1986) reported epistatic effects of additive × additive, additive × dominant gene effect on grain yield and additive × dominant interaction on seed weight. Contrary to the present studies, Kashif and Ihsan (2003) have suggested an over dominant gene effect on GY. Imran and Salam (2003) reported partial dominance for controlling the trait. However, the little deviations in the present findings and those of the previous investigators may be due to differences in the genetic background of the material used, different agro-environments, and the use of different statistical approach.

Table 5. Estimates of first and second order genetic parameters for grain yield per plant in four bread wheat crosses.

Cross 1: Bakhtawar-92 × Frontana						Cross 2: Saleem-2k × Tatara					
Model type: E						Model type: E-1					
1st order parameters	Estimates	2nd order parameters	Estimates			1st order parameters	Estimates	2nd order parameters	Estimates		
			B_1	B_2	F_2				B_1	B_2	F_2
m_1=	12.9	σ_p^2	47.7	40.2	79.3	m=	23.1	σ_p^2	82.1	69.6	100
m_2=	10.8	σ_{mg}^2	23.6	16.8	55.2	d_a=	7.4	σ_{mg}^2	54.6	46.3	76.8
m_3=	20.2	σ_e^2	21.1	21.1	21.1	d_b=	-6.9	σ_e^2	23.4	23.4	23.4
m_4=	11.9	σ_{pg}^2	3.1	2.3	3.01	h_a=	-0.3	σ_{pg}^2	4.1	0	0
m_5=	17.8	h_{mg}^2(%)	49.4	41.7	69.7	h_b=	-0.2	h_{mg}^2 (%)	66.5	66.5	76.7
m_6=	16.5	h_{pg}^2(%)	6.5	5.8	3.8	h_a/d_a =	-0.2	h_{pg}^2 (%)	5	0	0
d_a=	6.1	$V_{e=}$	44.2	52.5	26.6	h_b/d_b =	0.1	$V_{e=}$	28.5	33.6	23.4
d_b=	6.1					i =	-7.5				
h_a=	-3.5					j_{ab}=	3.2				
h_b=	-3.5					j_{ba}=	-1.6				
h_a/d_a	-0.6					l =	-6.9				
h_b/d_b	-0.6					[d] =	15.1				
i =	5.5					[h] =	-1.5				
j_{ab}=	-3.1										
j_{ba}=	-3.1										
l =	11.0										
Cross 3: Inqilab-91 × Fakhr-e-Sarhad						Cross 4: Karwan × Fakhr-e-Sarhad					
Model type: E -1						Model type: E -1					
m=	20.3	σ_p^2	50.3	103.7	98.8	m=	17.9	σ_p^2	55.3	70.4	103.4
d_a=	-6	σ_{mg}^2	27.0	72.8	75.6	d_a =	-8.4	σ_{mg}^2	31.3	41.8	79.3
d_b=	5.5	σ_e^2	23.2	23.2	23.2	d_b =	8.2	σ_e^2	24.1	24.1	24.1
h_a=	-2.6	σ_{pg}^2	0	7.7	0	h_a =	1.1	σ_{pg}^2	0	4.5	0
h_b=	1.1	h_{mg}^2 (%)	53.8	70.2	76.5	h_b=	2.1	h_{mg}^2 (%)	56.5	59.4	76.7
h_a/d_a =	0.4	h_{pg}^2 (%)	0	7.4	0	h_a/d_a =	-0.1	h_{pg}^2 (%)	0	6.4	0
h_b/d_b =	0.2	$V_{e=}$	46.2	22.4	23.5	h_b/d_b =	0.3	$V_{e=}$	43.5	34.2	23.3
i =	-8.7					i =	-6.4				
j_{ab}=	-3.7					j_{ab}=	0.7				
j_{ba}=	2.2					j_{ba}=	-1.7				
l =	-7.5					l =	-10				
[d] =	6.4					[d] =	5.5				
[h] =	3.7					[h] =	2.7				

d_a, d_b: additive effect due to major gene A and B, respectively; h_a, h_b: dominant effect due to major gene A and B, respectively; h_a/d_a, h_b/d_b: ratio of dominance to additiveness due to major gene A and B, respectively; i: additive x additive component due to major genes; $J_{ab} = d_a \times h_b$: first major gene with additive x second major gene with dominant effect; $J_{ba} = d_b \times h_a$: second major gene with additive x first major gene with dominant effect; l: mixed dominant x dominant component due to major as well as polygene; [d]: additive component due to polygene; [h]: dominant component due to polygene; σ_p^2: collective phenotypic variation of P_1, F_1, and P_2; σ_{mg}^2: variance due to major genes; ó$_{pg}^2$: variance due to polygene; σ_e^2: environmental variance; h_{mg}^2, h_{pg}^2: heritability due to major genes and polygene, respectively; V_e: variation due to environment.

Table 5 further reveals that under the epistasis of the major genes, partial dominance i.e. 0.4 and 0.2 was observed in cross 3 due to both the major genes A and B. However, partial dominance i.e. 0.1, 0.3 was only due to the second major gene (B) in cross 2, 4, respectively. These results coincide with those of Imran and Salam (2003) who reported partial dominance to be responsible for controlling GY in wheat. Additive effect due to the polygene [d] was pronounced in the last three crosses for grain yield plant^{-1} which agrees with the results of Esmail (2007) who used triple test cross method and suggested additive × additive type of gene interaction for grain yield plant^{-1} in wheat. Using five parent diallel analyses, Salam *et al.* (2000) also reported additive gene action on GY wheat. The dominant effect due to the polygene [h] in the last two crosses was also positive and significant (3.7, 2.7) except cross 2 where it was negative (-1.5). Using diallel analysis, partial dominance for grain yield plant^{-1} in wheat has also been reported previously (Asif *et al.*, 1999).

The fitness of two different models, i.e. E in cross 1 and E-1 in cross 2, 3 and 4 for genetic analysis of GY may be due to either of the two reasons. First, segregating population composed of component distributions is under control of major genes and this is modified by polygene system as well as variable genetic background of the material (Sharma and Sain, 2004). Second, being a theoretical approach, JSA analyze the segregating data of quantitatively controlled trait like the Mendelian procedure and the best-fitting genetic model can be chosen according to Akaike's information criterion, a likelihood ratio test and tests for goodness of fit (Gai *et al.*, 2007). Highest phenotypic variations (Table 1, 5) and higher values of major gene variance (σ_{mg}^2) as well as major gene heritability (h_{mg}^2) in comparison to polygene variance (σ_{pg}^2) and polygene heritability (h_{pg}^2) for the segregating progenies (B_1, B_2 and F_2) for all the crosses (Table 5) indicate that GY is highly influenced by environmental fluctuations.

Though the model test is polygenic (E-1) yet some of the values of polygene variance (σ_{pg}^2) and polygene heritability (h_{pg}^2) in the last three crosses (Table 5) are equal to zero for the segregating populations. The smaller values (~ 0) for σ_{pg}^2 and h_{pg}^2 might be due to interactions between the major genes and polygene. Another suggestion is that environmental variance (σ_e^2) may not be estimated as the environmental variation in segregating generations (Jiankang and Gai, 2001). In view of additively controlled nature of the trait due to major genes (cross 1) as well as polygene (cross 2, 3 and 4), it is therefore, suggested that progeny selection for grain yield improvement might be delayed to advanced generations such that maximum favorable genes are accumulated in more or less homozygous conditions in the individual plants.

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