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GENETIC ARCHITECTURE OF 1000-GRAIN WEIGHT IN *TRITICUM AESTIVUM*

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ABSTRACT

Mixed inheritance analysis for 1000-Grain Weight (1000-GW) was carried out by using statistical approach i.e. Joint segregation analysis of six basic generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) in two wheat crosses developed during crop growing seasons of 2012-13 and 2013-14. The results showed that the trait was mostly under control of mixed epistasis of two major genes plus polygenes (model E-1) for the two crosses during the first year. However, it was controlled by one major gene in combination with polygenes (model D-2) in cross 4 during the second year. Transgressive segregate on both upper and lower extremity of the trait in BC_1, BC_2 and F_2 indicated the presence of both favorable and reversed genes in the parents. Higher major gene heritability (33.61 to 45.56) for the trait was recorded than the polygenes heritability (4.17 to 15.80) in the segregating generations (BC_1, BC_2) while F_2 was ranged from (2.24 to 67.26). Moderate to high environmental variations (30.91 to 44.68) in the trait for segregating generations revealed that 1000-GW is under influence of the environmental fluctuations. Predominant additive effect over all other types of genetic effects suggests the delay in selection for 1000-GW until maximum favorable genes are accumulated in the individuals.

Keywords: 1000-Grain Weight, major genes, heritability, polygenes inheritance, *Triticum aestivum*

INTRODUCTION

Improved grain yield is the ultimate aim for cereal breeders and is based on the performance of yield components together with a conducive environmental condition [1]. The statistical approach used in the present investigation has the power to determine individual effects up to two major genes as well as, the collective epistatic effects of polygenes [2]. Because of the high cost of the molecular techniques, population and sample size restriction, and the interference of errors, QTL technique has limited applications in breeding [3]. Based on the efforts of Wang [4], joint segregation analysis (JSA) is the segregation-analysis method used to identify the mixed inheritance model of QTLs and to estimate related genetic parameters; this takes large advantage of the sample size available for plant quantitative traits [3]. In light of the superiority of the JSA over the previous approaches, the present study was undertaken to find out (i) the genetic diversity for 1000-GW among the genotypes to be used in cross combinations, (ii) genetic mechanism of 1000-GW through hybridization between the parents of maximum and minimum 1000-GW and vice versa and (iii) the number and individual effects of major genes, and cumulative effect of the major as well as, polygenes involved in controlling the 1000-GW.

MATERIALS AND METHODS

Genetically diverse parents (Table 1) were selected from wheat germplasm as reported by Irfaq *et al.* [5] for hybridization. In cross 1(1942×Dera-98), Dera-98 with minimum1000-GW as pollen donor while 1942 with maximum 1000-GW as pollen recipient, while in cross 2 (SVP-74×Zam-04), Zam-04with maximum1000-GW (pollen donor: P_2) and SVP-74 with smaller 1000-GW (pollen recipient: P_1) were used to develop populations for JSA during November, 2011 to April, 2012. Six basic populations $\{P_1, F_1, P_2, BC_1 (F_1 \times P_1), BC_2 (F_1 \times P_2),$ and $F_2\}$ of each cross were developed during 2011-12. The experiment for the populations of the two crosses was repeated for two years that is, 2012-13 (Year 1) and 2013-14 (Year 2). During each year, the populations of the crosses were planted as randomized complete block design (RCBD) in three replications. Keeping 5 m row length, two rows were planted on parents (P_1, P_2) and F_1 population, four rows on each of BC_1 and BC_2 and 8 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 2 seed per hill which were later thinned to single healthy seedling per hill after germination. Grain Weight from the selected plants of each of the populations was thrashed at maturity (stage 83, Zadoks' scale, Zadoks *et al.,* [6]. 1000-GW (g) was then weighted through electrical balance. Observations were recorded on 60 plants from each of the two homozygous parents (P_1 and P_2), 90 from each of first filial generation (F_1), 150 from each of the two backcrosses (BC_1 and BC_2), and 200 from each F_2 generation.

Statistical approach

Number of major genes and their effects controlling 1000-GW were determined by subjecting the data to the five groups consisting of 24 different genetic models described in table of the JSA specially designed for the six basic populations [3, 7, 8]. Based on the assumptions of Wang [4], Gai and Wang [3], Gai and Zhang [9] and Zhang *et al.,* [10] that is, diploid nuclear inheritance with no cytoplasmic effects, no linkage between major genes and polygenes, no selection and equal variances within the P_1, P_2 and F_1 populations as well as, normal distribution in any segregating generation due to the polygenic and environmental effects, suitable genetic models for each cross were determined by using maximum

log of likelihood values [11-13] and Akaike's information criterion [14]. As suggested [9, 10], further selection of the best fit model was made on the basis of all non- significant or least number of significant values of the three $\chi 2$ statistics (Table) that is, 2 1U =12 [Σ Yi –n/2] 2/n, ~ $\chi 2$ (1), to test whether the mean of Yi is 1/2, 2 2U = 45/4 (Σ Yi2-n/3) 2/n, ~ $\chi 2$ (1), to test whether the 2nd momentum of Yi is 1/3 and 2 3U = 180 [Σ (Yi –1/2) 2/n -12/ n]2/n, ~ $\chi 2$ (1), to test whether the variance of Yi is 1/12. Where; AIC= (-2) log (Maximum likelihood) +2 (Number of independent parameters). Likelihood-ratio test (LRT) was used to choose the simplest type within the model group. Where; LRT = λ =2 log (La) -2 log (L 0). Where; La and L0 are the maximum likelihoods under Ha and H0, respectively. Two other important completely distribution free tests (Table 6) that is, Smirnov's statistics (nW2) and Kolmogorove's statistics (Dn) where; D = Sup |F n (x) – Fo (x)| were used as goodness of fit tests to determine whether the selected model sufficiently explains the data. If, for a particular genetic model, none of these five statistics were significant, then the data adequately fit the model [9]. The data were analyzed by using sin.exe software and the major gene-polygenes mixed inheritance

model to a joint analysis of multi-generations. In case of the best fit model, the values of second order genetic parameters as well as σmg^2 and σpg^2 for BC_1, BC_2 and F_2 were worked out with the help of proposed formulae [8, 10] by using excel program of windows. Under the second order genetic parameters, the phenotypic variation (σp^2) is partitioned into genetic and environmental variation (σe^2) for the two crosses. The genetic component of variation in turn is subdivided into variation due to major genes (σmg^2) and polygenes (σpg^2). Based on Mather and Jinks [15], the values from μ_1 to μ_{69} of table 5 indicate different means of component distributions [10, 11] regarding six generations which are to be put in the formulae as suggested by Gai *et al.*, [8] for calculating 1st and 2nd order genetic parameters.
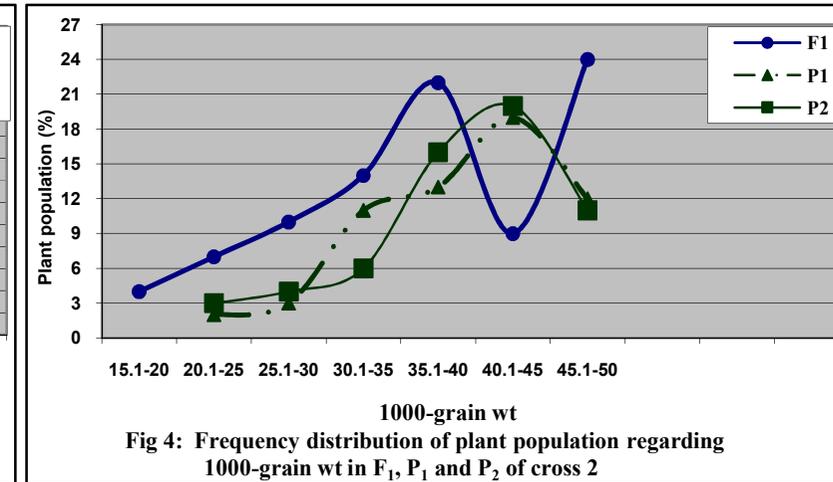
RESULTS

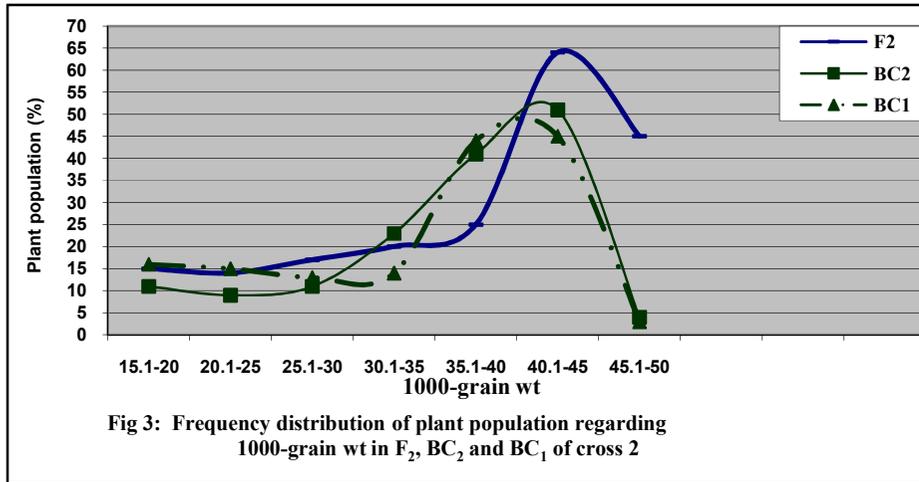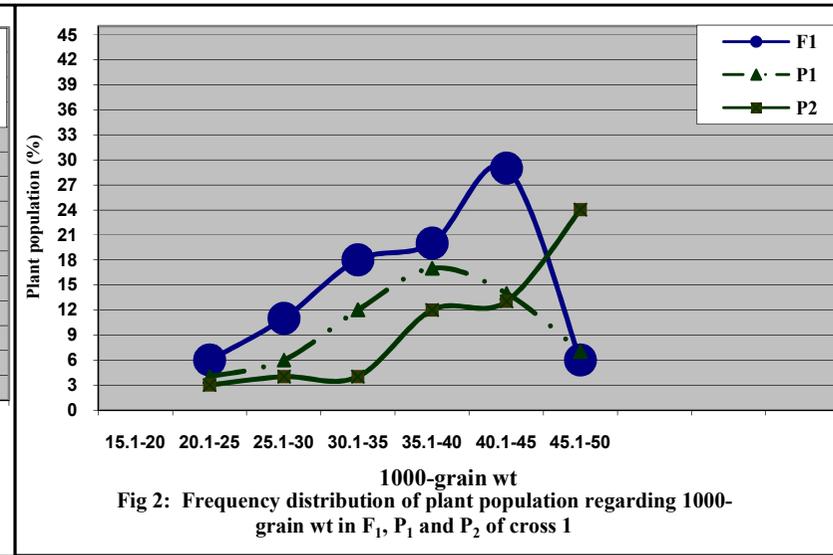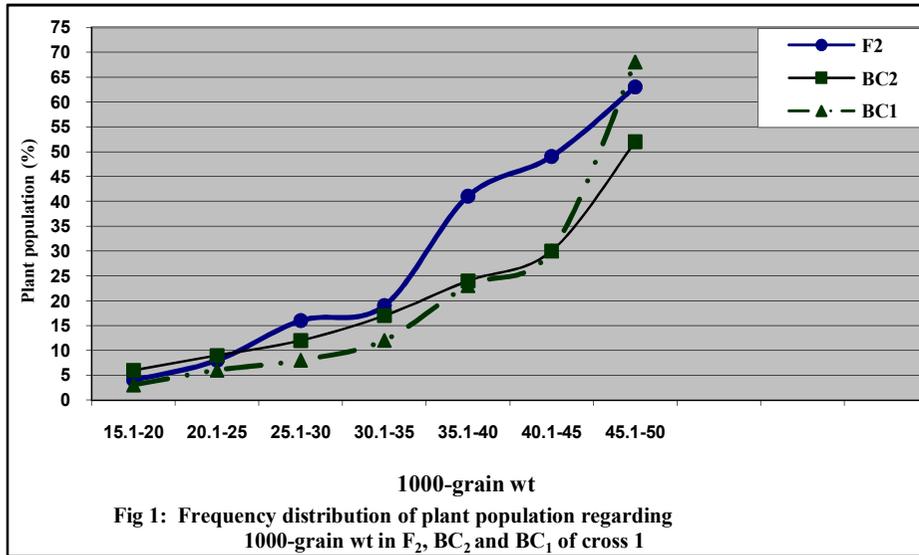### Frequency distribution and mean values

To determine the number of major genes, their individual effects, and combined effect due to polygenes, cross 1 and 2 were performed in the manner as given in the materials and methods under development of six populations. Mean 1000-GW of each parent is presented in table 1 and figures 1-8. The frequency distribution of six populations (P_1, F_1, P_2, BC_1, BC_2 and F_2)

along the range of 1000-GW and mean values (Table 1) indicate that F_1s of the two crosses during the two years were tended towards the parents with grater 1000-GW, except cross 1 during the first year which showed almost intermediate 1000-GW (50.87 gm) to those of P_1 (44.52 gm) and P_2 (40.23 gm). The mean values and frequency distribution further indicated that BC_1 and BC_2 were tended towards their respective pollen donor parents during the both years. However, they showed maximum 1000-GW than the parents of minimum 1000-GW. The situation is presented in table 1, that is, in cross 1, it was 62.22 and 89.93 for BC_1 and BC_2, respectively, during first year. The frequency distribution of six plant populations for 1000-GW have been given in table 1. The F_1 of cross Pari-73 × Hashim-08 was slightly higher than corresponding parents showing dominance and heterotic phenomenon in the cross. In the remaining crosses F_1 was equally distributed in between the parents. The BC_1, BC_2 and F_2 was equally distributed in the parents both through lower and upper proximity indicating mixed genetic control by major genes and polygene. During first year; the cross 1 showed 43.5 and 34.0 cm 2 for the same generations, respectively, during the second year. In case of cross 2,

Trait 54.9 and 63.3 cm2, 1000-GW was recorded for BC_1 and BC_2 during the first year while 49.8 and 56.9 cm2 during the second year. Few transgressive segregates were apparent on both upper and lower extremity along the range of 1000-GW in F_2 generation of the crosses during both years. Moreover, F_2s were normally distributed among the respective pollen donor and pollen recipient parents with increased 1000-GW (Table 1) than the Cross1 Year P_2.

Table 1: Frequency distribution of plant population for 1000-GW in six basic generations of four wheat crosses

Cross	Generation	Range of grains spike[-1]							Size	Mean	Variance
		15.1-20	20.1-25	25.1-30	30.1-35	35.1-40	40.1-45	45.1-50			
1942×Dera-98	P$_1$	-	4	6	12	17	14	7	60	38.53	44.52
	F$_1$	-	6	11	18	20	29	6	90	38.07	50.87
	P$_2$	-	3	4	4	12	13	24	60	41.90	40.23
	BC$_1$	3	6	8	12	23	30	68	150	42.52	62.22
	BC$_2$	6	9	12	17	24	30	52	150	39.49	89.93
	F$_2$	4	8	16	19	41	49	63	200	41.22	49.73
SVP-74×Zam-04	P$_1$	-	2	3	11	13	19	12	60	41.15	35.32
	F$_1$	4	7	10	14	22	9	24	90	38.63	70.55
	P$_2$	-	3	4	6	16	20	11	60	40.92	53.91
	BC$_1$	16	15	13	14	44	45	3	150	35.79	75.43
	BC$_2$	11	9	11	23	41	51	4	150	36.86	71.42
	F$_2$	15	14	17	20	25	64	45	200	38.85	80.03
Pari-73×Hashim-08	P$_1$	-	8	12	13	13	14	-	60	35.85	42.64
	F$_1$	-	15	19	22	16	7	11	90	34.77	54.68
	P$_2$	-	4	4	7	19	26	-	60	38.65	39.82
	BC$_1$	5	13	16	17	18	39	42	150	39.62	68.14
	BC$_2$	16	22	19	17	25	25	26	150	37.75	98.50
	F$_2$	13	39	17	20	34	46	31	200	35.33	112.62
SVP-83×Gomal-04	P$_1$	3	6	8	11	16	16	-	60	36.58	56.35
	F$_1$	10	15	13	19	26	7	-	90	32.61	74.85
	P$_2$	-	11	12	13	14	10	-	60	34.33	53.45
	BC$_1$	11	18	18	21	48	13	21	150	36.37	88.34
	BC$_2$	-	22	26	25	14	19	44	150	38.60	92.66
	F$_2$	25	29	29	16	26	25	50	200	34.87	121.08

Fig 1: Frequency distribution of plant population regarding 1000-grain wt in F_2, BC_2 and BC_1 of cross 1

Fig 2: Frequency distribution of plant population regarding 1000-grain wt in F_1, P_1 and P_2 of cross 1

Fig 3: Frequency distribution of plant population regarding 1000-grain wt in F_2, BC_2 and BC_1 of cross 2

Fig 4: Frequency distribution of plant population regarding 1000-grain wt in F_1, P_1 and P_2 of cross 2

Fig 5: Frequency distribution of plant population regarding 1000-grain wt in F_2, BC_2 and BC_1 of cross 3

Fig 6: Frequency distribution of plant population regarding 1000-grain wt in F_1, P_1 and P_2 of cross 3
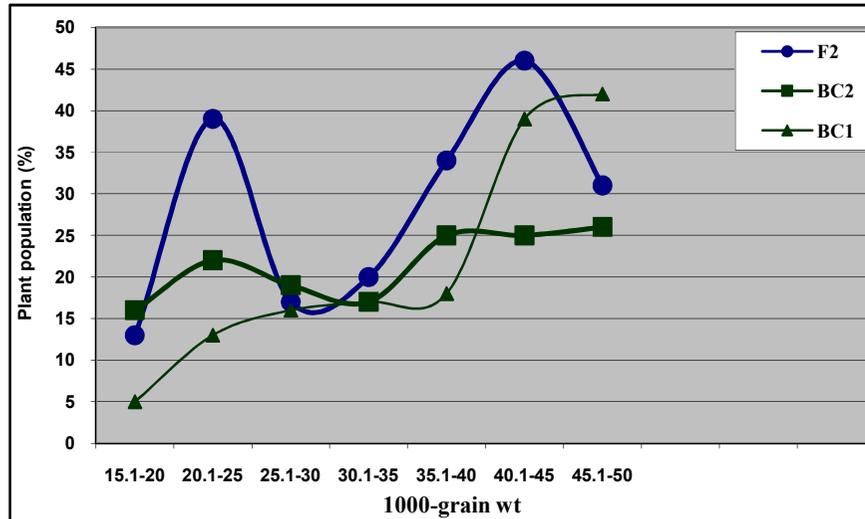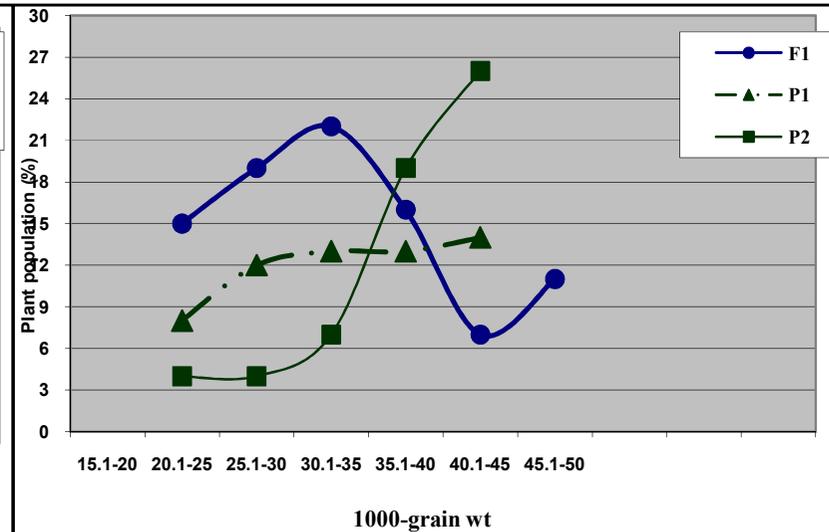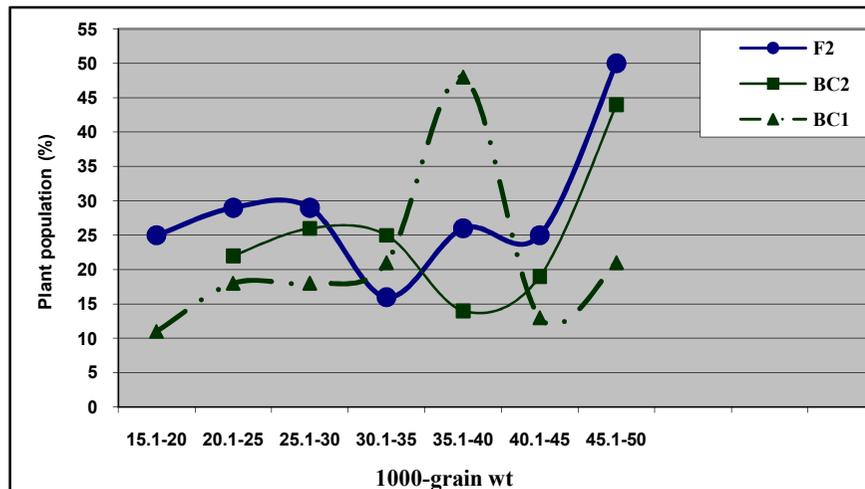

Fig 7: Frequency distribution of plant population regarding 1000-grain wt in F_2, BC_2 and BC_1 of cross 4
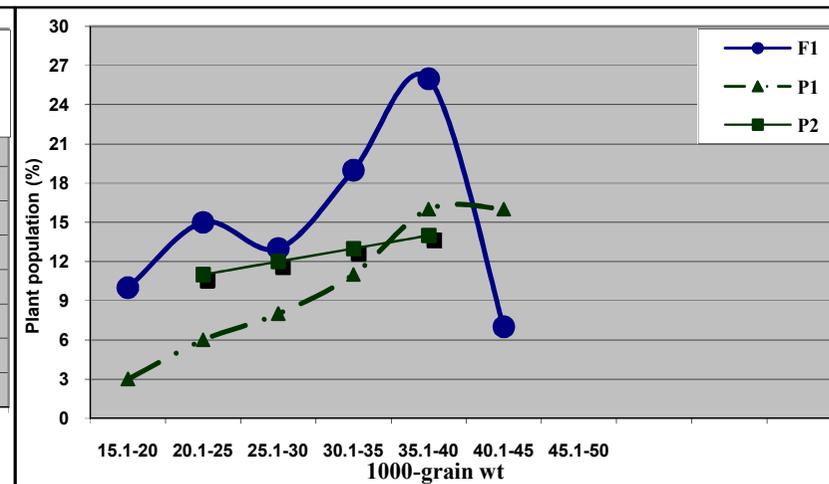

Fig 8: Frequency distribution of plant population regarding 1000-grain wt in F_1, P_1 and P_2 of cross 4

Gene action for 1000-GW in different crosses

The best fit model for cross 1942 × Dera-98 was found to be model E-1 indicating gene action of two major additive-dominance epistatic genes plus additive-dominant polygene (Table 6). In this cross the additive effect (d_a, d_b) was -4.21 each and dominant effects (h_a, h_b) was 3.49 and 3.50, respectively contributed by two major genes (A & B). The additive × additive effect (i) of major plus polygene was -4.02. The additive × dominant effect of gene A over gene B (J_{ab}) and that of gene B over gene A (J_{ba}) was 4.0 and 4.01, respectively. The dominant × dominant effect (l) was recorded as -3.00. The second order genetic parameters present the phenotypic variation for 1000-GW in segregating generations BC_1, BC_2 and F_2. The phenotypic variation is partitioned into genetic and environmental variation whereas genetic variation is further subdivided in to variation due to major genes and polygene. As the trait is controlled by major genes plus polygene, therefore the phenotypic variation was recorded maximum. The major gene heritability was 43.49, 46.64 and 31.38% for BC_1, BC_2 and F_2. The polygene heritability was 5.09, 17.79 and 4.28% for BC_1, BC_2 and F_2. The major gene variation and heritability was found maximum in comparison to minor gene variation and heritability showing that the major gene contribution was maximum in controlling 1000-GW in this cross.

In cross SVP-74 × Zam-04 the best fit model for 1000-GW was model E-1 which explains that the trait was under the influence of mixed gene action of two major additive-dominance epistatic genes plus additive-dominant polygene (Table 6). The first and second order genetic parameters are presented in (Table 6). The additive effect of major gene A was positive (1.50) whereas that of gene B was negative (-7.40). The dominant effect of both the major genes A and B was 16.14 and 11.40, respectively. The additive × additive genetic effect (i) was positive (8.28) and dominant × dominant non allelic interaction (l) was negative (-18.85). The additive × dominant effect of gene A over gene B was positive (7.73) whereas that of gene B over gene A was negative (-8.05). The second order genetic parameters are also presented in (Table 6). The second order genetic parameters showed that major gene variation and heritability for BC_1, BC_2 and F_2 was 25.35, 31.50 and 36.61 while heritability was 33.61, 44.11 and 45.74%, respectively which was higher than that of the minor

genes variation and heritability 11.92, 1.76 and 5.26 and heritability as 15.80, 2.46 and 6.57%. This shows the contribution of major gene was higher in controlling 1000-GW in the cross as compared to the proportion shared by polygene.

The best fit model for cross Pari-73 × Hashim-08 was found to be model E-1 indicating genetic effects of two major additive dominance epistatic genes plus additive dominant polygene (Table 4.54). In this cross the additive effect (d_a, d_b) was -0.80 each and dominant effects (h_a, h_b) was 7.79 and 17.81, respectively contributed by two major genes (A and B). The additive × additive effect (i) of major genes plus polygene was 3.61. The additive × dominant effect of gene A over gene B (J_{ab}) and that of gene B over gene A (J_{ba}) was 0.82 and 10.85, respectively. The dominant × dominant effect (l) was recorded as -7.84. The second order genetic parameters present the phenotypic variation for 1000-GW in segregating generations BC_1, BC_2 and F_2. The phenotypic variation is partitioned into genetic and environmental variation whereas genetic variation is further subdivided in to variation due to major genes and polygene.

As the trait is controlled by major genes plus polygene, therefore the phenotypic variation was recorded maximum. The major gene heritability was 45.56, 64.88 and 67.26% for BC_1, BC_2 and F_2. The polygene heritability was 9.06, 3.73 and 5.29% for BC_1, BC_2 and F_2. The major gene variation and heritability was found maximum in comparison to those of the minor gene accordingly, showing that the major gene contribution was maximum in controlling 1000-GW in this cross.

In cross SVP-83 × Gomal-08 the best fit model as selected through maximum log of likelihood (Table 6), and Akaiki's information criteria (Tables 3, 4) was Model D-2 indicating mixed one additive major gene and additive dominant effect of polygene. The population mean was estimated to be 36.70. The dominant effect of single major gene was 11.29 whereas dominant effect was 0. The major gene variation was higher than that of the polygene. Higher major gene heritability (45.29, 49.83, and 60.85%) was recorded for BC_1, BC_2 and F_2 then their respective polygene heritability (4.17, 1.27, and 2.24%).

Table 2: Maximum log of likelihood values and *AIC* values for 1000-GW under various genetic models estimated through the IECM algorithm

Cross 1: 1942 × Dera-98			Cross 2: SVP-74 × Zam-04		
Model	**Maximum log of likelihood**	***AIC***	**Model**	**Maximum log of likelihood**	***AIC***
A-1	-2469.22	4946.44	A-1	-2524.35	5056.70
A-2	-2471.11	4948.21	A-2	-2528.46	5062.92
A-3	-2470.95	4947.90	A-3	-2527.17	5060.34
A-4	-2469.63	4945.25	A-4	-2528.87	5063.73
B-1	-2424.51	4869.03	B-1	-2452.24	4924.48
B-2	-2461.34	4934.68	B-2	-2520.76	5053.53
B-3	-2543.91	5095.81	B-3	-2575.63	5159.26
B-4	-2471.11	4948.21	B-4	-2528.47	5062.94
B-5	-2467.98	4943.97	B-5	-2526.82	5056.64
B-6	-2470.97	4947.94	B-6	-2527.23	5060.46
C	-2444.39	4908.78	C	-2509.27	5038.54
C-1	-2458.55	4931.10	C-1	-2522.09	5058.17
D	-2419.70	4863.41	D	-2474.13	4972.26
D-1	-	-	D-1	-2495.84	5009.68
D-2	-	-	D-2	-2495.83	5007.65
D-3	-2456.58	4929.17	D-3	-2495.89	5007.79
D-4	-2414.55	4845.09	D-4	-2495.84	5007.68
E	-2409.74	4855.47	E	-2471.22	4978.43
E-1	-2410.79	4851.57	E-1	-2450.22	4930.43
E-2	-2415.56	4853.12	E-2	-2511.48	5044.97
E-3	-2447.89	4913.78	E-3	-2454.26	4926.51
E-4	-2458.31	4932.62	E-4	-2521.96	5059.91
E-5	-2458.54	4935.09	E-5	-2512.45	5042.91
E-6	-2486.37	4988.74	E-6	-2609.77	5235.54
Cross 3: Pari-73× Hashim-08			Cross 4: SVP-83 × Gomal-08		
Model	**Maximum log of likelihood**	***AIC***	**Model**	**Maximum log of likelihood**	***AIC***
A-1	-2574.41	5156.82	A-1	-2617.20	5242.39
A-2	-2578.12	5162.25	A-2	-2619.97	5245.95
A-3	-2578.74	5163.47	A-3	-2619.29	5244.58
A-4	-2578.10	5162.20	A-4	-2615.95	5237.90
B-1	-2514.12	5048.23	B-1	-2584.10	5188.20
B-2	-2536.80	5085.60	B-2	-2597.50	5207.01
B-3	-2638.03	5284.07	B-3	-2648.00	5304.00
B-4	-2578.21	5162.42	B-4	-2619.98	5245.96
B-5	-2561.40	5130.80	B-5	-2609.03	5226.06
B-6	-2578.74	5163.47	B-6	-2619.40	5244.81
C	-2542.00	5104.00	C	-2595.65	5211.31
C-1	-2556.74	5127.48	C-1	-2608.66	5231.32
D	-2509.30	5042.60	D	-2571.12	5166.24
D-1	-2490.18	4998.35	D-1	-2665.18	5148.37
D-2	-2490.18	4996.36	D-2	-2565.18	5146.36
D-3	-2553.94	5123.88	D-3	-2597.23	5210.45
D-4	-2506.07	5028.17	D-4	-2595.23	5206.47
E	-2488.84	5013.68	E	-2566.58	5169.17
E-1	-2487.93	5005.86	E-1	-2566.21	5162.41
E-2	-2509.05	5040.09	E-2	-2588.17	5198.33
E-3	-2514.85	5047.71	E-3	-2573.67	5165.34
E-4	-2538.36	5092.72	E-4	-2599.35	5214.71
E-5	-2556.70	5131.39	E-5	-2589.05	5196.09
E-6	-2559.04	5134.08	E-6	-2656.48	5328.96

Table 3: Tests for goodness-of-fit regarding 1000-GW of models B-1, E-3, E, E-1 and E-2 for crosses 1942 × Dera-98 and SVP-74 × Zam-04

				Cross 1: 1942 × Dera-98		
Model	Generation	U_1^2	U_2^2	U_2^3	nW^2	D
E	P_1	0.84(0.36)	1.90(0.17)	3.85*	0.54(>0.05)	0.24(>0.05)
	F_1	0.93(0.33)	4.81*	25.29***	1.28(>0.05)	0.25(>0.05)
	P_2	1.95(0.16)	2.14 (0.14)	0.20(0.65)	1.05(>0.05)	0.33(>0.05)
	B_1	3.57(0.59)	1.48(0.22)	6.01**	1.38(>0.05)	0.24(>0.05)
	B_2	1.61(0.20)	1.95(0.16)	0.44(0.51)	1.19(>0.05)	0.23(>0.05)
	F_2	0.18(0.67)	0.12(0.73)	0.06(0.80)	1.61(>0.05)	0.24(>0.05)
E-1	P_1	1.47(0.23)	2.91(0.09)	4.52*	0.62(>0.05)	0.25(>0.05)
	F_1	1.49(0.22)	6.11**	26.61***	1.35(>0.05)	0.26(>0.05)
	P_2	2.12(0.15)	2.35 (0.13)	0.25(0.62)	1.07(>0.05)	0.33(>0.05)
	B_1	1.89(0.17)	0.44(0.51)	7.23**	1.22(>0.05)	0.23(>0.05)
	B_2	1.26(0.26)	1.52(0.22)	0.34(0.56)	1.14(>0.05)	0.23(>0.05)
	F_2	0.23(0.63)	0.17(0.68)	0.04(0.84)	1.63(>0.05)	0.24(>0.05)
E-2	P_1	0.00(0.99)	0.19(0.66)	3.15**	0.41 (>0.05)	0.18(>0.05)
	F_1	0.08(0.78)	2.35(0.13)	25.65***	1.20 (>0.05)	0.24(>0.05)
	P_2	1.96(0.16)	2.33(0.13)	0.46(0.61)	1.05 (>0.05)	0.33(>0.05)
	B_1	29.33***	26.23***	0.24(0.14)	4.54(>0.05)	0.35 (>0.05)
	B_2	0.07(0.79)	0.08(0.78)	0.01(0.09)	0.95 (>0.05)	0.20(>0.05)
	F_2	11.24***	7.40**	4.43***	2.71 (>0.05)	0.28(>0.05)
				Cross 2: SVP-74 × Zam-04		
Model	Generation	U_1^2	U_2^2	U_2^3	nW^2	D
E-1	P_1	0.23(0.63)	0.39(0.53)	0.41(0.39)	0.50(>0.05)	0.25(>0.05)
	F_1	0.31(0.58)	3.75*	31.34***	0.96(>0.05)	0.21(>0.05)
	P_2	0.73(0.39)	1.41(0.29)	0.94(0.22)	0.54(>0.05)	0.25(>0.05)
	B_1	0.06(0.81)	1.01(0.32)	9.61***	1.02(>0.05)	0.21(>0.05)
	B_2	0.46(0.50)	0.02(0.88)	4.04*	0.64(>0.05)	0.15(>0.05)
	F_2	16.47***	16.69***	0.39(0.53)	3.82(>0.05)	0.32(>0.05)
E-3	P_1	0.01(0.94)	0.02(0.23)	0.09(0.76)	0.45(>0.05)	0.23(>0.05)
	F_1	0.01(0.91)	1.41(0.24)	27.00***	0.85(>0.05)	0.19(>0.05)
	P_2	0.04(0.83)	0.11(0.74)	0.25(0.62)	0.42(>0.05)	0.22(>0.05)
	B_1	0.16(0.69)	1.39(0.24)	10.08***	1.04(>0.05)	0.20(>0.05)
	B_2	0.65(0.42)	0.07(0.80)	4.32*	0.66(>0.05)	0.15(>0.05)
	F_2	26.23***	30.99***	5.92**	4.84(>0.05)	0.35(>0.05)
B-1	P_1	0.94(0.33)	1.34(0.25)	0.73(0.39)	0.59(>0.05)	0.28(>0.05)
	F_1	0.01(0.93)	1.57(0.21)	28.67***	0.88(>0.05)	0.19(>0.05)
	P_2	1.73(0.19)	2.50(0.11)	1.53(0.22)	0.67(>0.05)	0.27(>0.05)
	B_1	0.12(0.73)	1.30(0.25)	10.53***	1.03(>0.05)	0.21(>0.05)
	B_2	0.38(0.54)	0.01(0.95)	4.43*	0.64(>0.05)	0.15(>0.05)
	F_2	18.14***	18.82***	0.74(0.39)	4.00(>0.05)	0.33(>0.05)

*, **, *** represents the 0.05, 0.01, 0.001 significance levels respectively

Table 4: Tests for goodness-of-fit regarding 1000-GW of model E-1, E, D-2, and D-1 for crosses Pari-73 × Hashim-08 and SVP-83 × Gomal-08

Cross 3: Pari-73 × Hashim-08						
Model	**Generation**	U_1^2	U_2^2	U_2^3	$_nW^2$	D
E-1	P_1	0.06(0.81)	1.10(0.29)	10.58***	0.51(>0.05)	0.22(>0.05)
	F_1	0.02(0.88)	1.48(0.22)	18.26***	0.70(>0.05)	0.20(>0.05)
	P_2	2.32(0.13)	2.66(0.10)	0.39(0.53)	1.16(>0.05)	0.35(>0.05)
	B_1	1.17(0.28)	0.75(0.39)	0.52(0.47)	1.32(>0.05)	0.26(>0.05)
	B_2	1.85(0.17)	1.95(0.16)	0.10(0.75)	0.55(>0.05)	0.16(>0.05)
	F_2	0.67(0.41)	0.48(0.49)	0.16(0.69)	0.71(>0.05)	0.15(>0.05)
E	P_1	0.10(0.75)	1.25(0.10)	10.47***	0.52(>0.05)	0.22(>0.05)
	F_1	0.03(0.86)	1.53(0.18)	18.01***	0.70(>0.05)	0.20(>0.05)
	P_2	2.16(0.14)	2.44(0.67)	0.31(0.58)	1.14(>0.05)	0.35(>0.05)
	B_1	0.22(0.64)	0.00***	3.66(0.06)	1.18(>0.05)	0.23(>0.05)
	B_2	1.49(0.22)	1.43***	0.00(0.95)	0.52(>0.05)	0.15(>0.05)
	F_2	0.01(0.92)	0.23***	2.30(0.13)	0.73(>0.05)	0.19(>0.05)
D-1	P_1	0.39(0.53)	0.01(0.93)	7.76**	0.48(>0.05)	0.21(>0.05)
	F_1	0.52(0.47)	0.08(0.78)	15.13***	0.67(>0.05)	0.21(>0.05)
	P_2	1.39(0.24)	1.36(0.24)	0.01(0.92)	1.03(>0.05)	0.33(>0.05)
	B_1	25.37***	23.02***	0.10(0.75)	3.92(>0.05)	0.33(>0.05)
	B_2	4.27*	4.17*	0.03(0.87)	0.83(>0.05)	0.17(>0.05)
	F_2	2.40(0.12)	0.63(0.43)	8.05***	1.29(>0.05)	0.17(>0.05)
Cross 4: SVP-83 × Gomal-08						
Model	**Generation**	U_1^2	U_2^2	U_2^3	$_nW^2$	D
D-2	P_1	0.07(0.79)	0.49(0.48)	3.11(0.08)	0.40(>0.05)	0.21(>0.05)
	F_1	0.47(0.49)	2.51(0.11)	13.46***	0.76(>0.05)	0.22(>0.05)
	P_2	0.08(0.78)	0.63(0.43)	4.40(0.04)	0.35(>0.05)	0.20(>0.05)
	B_1	5.01**	4.69**	0.00(0.99)	1.16(>0.05)	0.23(>0.05)
	B_2	0.32(0.57)	0.30(0.58)	0.00(0.98)	0.59(>0.05)	0.15(>0.05)
	F_2	8.21***	3.53(0.06)	12.86***	2.16(>0.05)	0.23(>0.05)
E	P_1	0.47(0.50)	1.38(0.24)	4.23*	0.46(>0.05)	0.23(>0.05)
	F_1	1.16(0.28)	4.16*	15.88***	0.88(>0.05)	0.23(>0.05)
	P_2	0.14(0.71)	0.85(0.36)	5.02**	0.37(>0.05)	0.20(>0.05)
	B_1	0.01(0.94)	0.00(0.97)	0.18(0.67)	0.55(>0.05)	0.17(>0.05)
	B_2	4.32*	6.18**	3.61(0.06)	1.17(>0.05)	0.21(>0.05)
	F_2	0.09(0.77)	0.38(0.54)	1.72(0.19)	0.87(>0.05)	0.16(>0.05)
E-1	P_1	1.90(0.17)	3.90(0.05)	6.63(0.01)	0.65(>0.05)	0.27(>0.05)
	F_1	5.70**	12.44***	23.63***	1.42(>0.05)	0.28(>0.05)
	P_2	1.99(0.16)	4.19*	7.42**	0.59(>0.05)	0.25(>0.05)
	B_1	0.32(0.57)	0.64(0.42)	1.04(0.31)	0.60(>0.05)	0.19(>0.05)
	B_2	0.98(0.32)	0.56(0.45)	0.68(0.41)	0.70(>0.05)	0.16(>0.05)
	F_2	1.87(0.17)	0.54(0.46)	5.53**	1.15(>0.05)	0.16(>0.05)

U_1^2, U_2^2 , U_2^3 : χ² **statistics with 1 degree of freedom;** $_nW^2$ **: Smirnov's statistics ;** D_n: **Kolmogorov's statistics**

Table 5: Maximum likelihood estimates of component parameters regarding 1000-GW for four wheat crosses in their respective best fit models

Cross 1: 1942 × Dera-98 (Model E-1) Alternative model= E

Parameter	Estimate	Parameter	Estimate	Parameter	Estimate	Parameter	Estimate
μ_1	38.29	μ_{44}	46.3	μ_{62}	42.27	μ_{68}	42.7
μ_2	37.87	μ_{51}	39.65	μ_{63}	43	μ_{69}	43.39
μ_3	41.85	μ_{52}	39.38	μ_{64}	42.27	σ^2	31.99
μ_{41}	29.86	μ_{53}	39.38	μ_{65}	42.98	σ_4^2	31.99
μ_{42}	45.59	μ_{54}	40.07	μ_{66}	42.66	σ_5^2	47.99
μ_{43}	45.59	μ_{61}	26.53	μ_{67}	43	σ_6^2	31.99

Cross 2: SVP-74 × Zam-04 (Model E-1) Alternative model= E-3

Parameter	Estimate	Parameter	Estimate	Parameter	Estimate	Parameter	Estimate
μ_1	99.1	μ_{44}	102.45	μ_{62}	111.03	μ_{68}	92.56
μ_2	99.49	μ_{51}	95.72	μ_{63}	91.01	μ_{69}	104.57
μ_3	97.44	μ_{52}	118.61	μ_{64}	91.08	σ^2	38.16
μ_{41}	96.14	μ_{53}	89.2	μ_{65}	99.09	σ_4^2	50.08
μ_{42}	114.39	μ_{54}	101.2	μ_{66}	121.98	σ_5^2	39.92
μ_{43}	94.45	μ_{61}	92.78	μ_{67}	73.21	σ_6^2	38.16

Cross 3: Pari-73 × Hashim-08 (Model E-1)

Parameter	Estimate	Parameter	Estimate	Parameter	Estimate	Parameter	Estimate
μ_1	35.98	μ_{44}	43.23	μ_{62}	43.18	μ_{68}	43.13
μ_2	34.79	μ_{51}	42.97	μ_{63}	21.73	μ_{69}	30.56
μ_3	38.62	μ_{52}	22.96	μ_{64}	43.18	σ^2	30.91
μ_{41}	27.47	μ_{53}	43	μ_{65}	43.1	σ_4^2	30.91
μ_{42}	43.31	μ_{54}	30.43	μ_{66}	23.09	σ_5^2	30.91
μ_{43}	43.31	μ_{61}	27.34	μ_{67}	21.73	σ_6^2	30.91

Cross 4: SVP-83 × Gomal-08 (Model D-2) Alternative model= E-1 and E

Parameter	Estimate	Parameter	Estimate	Parameter	Estimate	Parameter	Estimate
μ_1	36.98	μ_{44}		μ_{62}	42.02	μ_{68}	
μ_2	32.93	μ_{51}	46.06	μ_{63}	23.4	μ_{69}	
μ_3	34.42	μ_{52}	30.56	μ_{64}		σ^2	44.68
μ_{41}	41.68	μ_{53}		μ_{65}		σ_4^2	44.68
μ_{42}	28.23	μ_{54}		μ_{66}		σ_5^2	44.68
μ_{43}		μ_{61}	42.79	μ_{67}		σ_6^2	44.68

Table 6: Estimates of first and second order genetic parameters for 1000-GW in four bread wheat crosses

Cross 1: 1942 × Dera-98 (Model E-1)

1st order parameter	Estimate	1st order parameter	Estimate	2nd order parameter	Estimates		
					BC_1	BC_2	F_2
$m =$	41.33	$i =$	-4.02	σ_p^2	62.22	89.93	49.73
$d_a =$	-4.21	$j_{ab} =$	4.00	σ_{mg}^2	27.06	41.94	15.61
$d_b =$	-4.21	$j_{ba} =$	4.01	σ_e^2	31.99	31.99	31.99
$h_a =$	3.49	$l =$	-3.00	σ_{pg}^2	3.17	16.00	2.13
$h_b =$	3.50	$[d] =$	27.06	$h_{mg}^2(\%)$	43.49	46.64	31.38
$h_a/d_a =$	-0.83	$[h] =$	-10.21	$h_{pg}^2(\%)$	5.09	17.79	4.28
$h_b/d_b =$	-0.83						

Cross 2: SVP-74 × Zam-04 (Model E-1)

1st order parameter	Estimate	1st order parameter	Estimate	2nd order parameter	Estimates		
					BC_1	BC_2	F_2
$m =$	89.99	$i =$	8.28	σ_p^2	75.43	71.42	80.03
$d_a =$	1.50	$j_{ab} =$	7.73	σ_{mg}^2	25.35	31.50	36.61
$d_b =$	-7.40	$j_{ba} =$	-8.05	σ_e^2	38.16	38.16	38.16
$h_a =$	16.14	$l =$	-18.85	σ_{pg}^2	11.92	1.76	5.26
$h_b =$	11.40	$[d] =$	61.22	$h_{mg}^2(\%)$	33.61	44.11	45.74
$h_a/d_a =$	10.74	$[h] =$	0.81	$h_{pg}^2(\%)$	15.80	2.46	6.57
$h_b/d_b =$	-1.54						

Cross 3: Pari-73 × Hashim-08 (Model E-1)

1st order parameter	Estimate	1st order parameter	Estimate	2nd order Parameters	Estimates		
					BC_1	BC_2	F_2
$m =$	33.68	$i =$	3.61	σ_p^2	68.14	98.50	112.62
$d_a =$	-0.80	$j_{ab} =$	0.82	σ_{mg}^2	31.05	63.91	75.75
$d_b =$	-0.80	$j_{ba} =$	10.85	σ_e^2	30.91	30.91	30.91
$h_a =$	7.79	$l =$	-7.84	σ_{pg}^2	6.18	3.68	5.96
$h_b =$	17.81	$[d] =$	19.93	$h_{mg}^2(\%)$	45.56	64.88	67.26
$h_a/d_a =$	-9.70	$[h] =$	-16.67	$h_{pg}^2(\%)$	9.06	3.73	5.29
$h_b/d_b =$	-22.16						

Cross 4: SVP-83 × Gomal-08 (Model D-2)

1st order parameter	Estimate	1st order parameter	Estimate	2nd order parameter	Estimates		
					BC_1	BC_2	F_2
m	36.70	$h =$	0.00	σ_p^2	88.34	92.66	121.08
d	11.29			σ_{mg}^2	40.01	46.18	73.68
$[d]$	-11.55			σ_e^2	44.68	44.68	44.68
$[h]$	-1.77			σ_{pg}^2	3.69	1.18	2.72
				$h_{mg}^2(\%)$	45.29	49.83	60.85
				$h_{pg}^2(\%)$	4.17	1.27	2.24

DISCUSSION

In cross 1942 x Dera-98, SVP-74 x Zam-04 and Pari-73 x Hashim-08 1000-GW was under the control of mixed additive-dominant polygenes plus two major additive-dominance epistatic genes (model E-1). Whereas In cross SVP-83 x Gomal-08 it was under the influence of mixed additive dominance of polygenes and one additive major gene (model D-2). The additive effects were negative while dominant effects were positive for both the major genes A and B in cross 1942 × Dera-98, SVP-74 × Zam-04 and Pari-73 × Hashim-08 showing

that both the major genes contribute dominantly in enhancing the trait. Additive gene action has also been reported by Inamullah *et al.*, [16]. In segregating populations BC_1, BC_2 and F_2, the major gene heritability and variations was more than that of polygene heritability and variations in all the crosses. These findings suggest that in all the crosses the 1000-GW was mainly controlled by major genes with very less donation of polygenes. These results are in close conformity with the previous findings of Ashraf *et al.*, [17] which exhibited that selection in early generations may enhance in these characters. The normal distribution pattern of F_2s among their respective pollen donor and pollen recipient parents (Fig. 1-8) is the indication that 1000-GW is a quantitatively controlled trait with pronounced additive type of gene action (Table 6) of the major genes (13.7, 13.5, -15.9 and -11.5) as well as minor genes (-7.0, -5.7, 10.3 and 30.6). Using generation means, diallel and QTL analysis, significant additive gene effect on1000-GW has been reported in the previous investigations [18-20]. This indicates that successful progeny selection could be practiced for the trait in advanced generations till maximum genes are accumulated in the individual recombinants.

The quite opposite additive effect due to the major genes for the two crosses may be either due to the fact that cross-1 is between larger 1000-GW × smaller 1000-GW and cross-2 is between smaller 1000-GW × larger 1000-GW [8, 11] or due to difference in the genetic back ground of the two crosses where the polygenic system of the genotypes may have interaction with major genes involved in controlling a quantitative trait [9, 10]. Occurrence of transgressive segregates in F 2s and some of the back cross generations of the crosses on both the upper and lower limit along the range of 1000-GW (Table 4) reveals that both favorable and adverse gene for 1000-GW is dispersed among the parents. Positive mid-parent and better parent heterosis were observed for the trait in wheat [16], whereas both positive and negative transgressive segregates in barley were also reported by Xue *et al.*, [21]. The tendency of F_1s, B_1s, B_2s and F_2s to the parents of their respective larger FLA indicates that increased flag leaf area has dominance over the reduced 1000-GW. However, as suggested by Sahin and Yildirim [1], the trait might be under the influence of recessive genes with significant dominance variance component for flag leaf width. Higher major genes heritability as compared to that of polygene indicates

higher contribution of the major genes than the polygenes to control the trait. As compared to the first year, lower major genes heritability was recorded during the second year for both crosses while the environmental variance was higher than that of the first year. It may because that 1000-GW being a quantitatively controlled trait is highly influenced by several environmental factors that is, soil nature, drought, heat stress, planting time and latitude/altitude *etc*. [17]. Secondly, it may also be due to involvement of polygenes system in controlling the trait. Using the same statistical approach designed for six basic generations [9-11] and five multiple generations (Zhang *et al*., 2003), higher major gene heritability in B_1, B_2 and F_2 generations has also been observed for fusarium head blight resistance in barley [22], stripe rust resistance in wheat (Irfaq *et al*., 2009) and in F_2, F_2: F_3 generations of soybean for resistance to agromyzid bean fly [8, 10, 13]. Low to high values (14.4 to 85.0) of environmental variation (Ve) of Table 8 regarding the segregating generations during the two years indicate that the trait is highly influenced by the environment. However, moderately low environmental variation has also been suggested by Simon [20]. This deviation in

the results might be due to the different genetic background of the material and environments as well as, different statistical approach used in the past and present experimentation.   The fitness of two different genetic models that is, D-2, E-1 regarding cross-2 during the second year may be due to the two reasons. First, segregating population composed of component distributions is under control of the major genes and this is modified by polygenes system as well as, environments. Secondly, JSA is a theoretical procedure on which the segregating data of quantitatively controlled trait is analyzed like the Mendelian method 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 [7]. The present approach with the capacity to find the genetic mechanism up to two major genes plus polygenes was designed for the six basic populations [9]. However, seven groups and 32 types of genetic models, including one major-gene, two major- genes, three-major genes, polygenes, mixed one major- gene and polygenes, mixed two major-genes and polygenes, and a mixed three major-genes and polygenes models have also been set up to determine genetic effects in recombinant inbred line (RIL)

population [7]. But it is still inadequate and requires to be upgraded up to four major genes for better understanding of linkage between more than two genes and to resolve more estimates of genetic parameters in more segregating generations [7]. The present approach has the merits over the previous procedures (diallel, triple test cross and generation means analysis) because it determines the number of individual major genes, their individual effects as well as, collective effects of the polygenes involved in controlling quantitative traits [9]. Unlike quantitative trait locus (QTL) mapping, it neither canidentify many QTLs nor locate the position of the major genes on a particular chromosome [7, 8] while designing breeding experiments for the improvement of quantitative traits, selecting parents for crosses, progeny selection and gene pyramiding, etc. It is strongly recommended for plant breeders to exercise the JSA as a simple and useful technique to know the number of major genes, their kinds of genetic effects, heritability values as well as, genetic information on all kinds of genetic effects and heritability value of whole polygenes without any extra requirements on lab conditions except a precise experiment [7, 22]. JSA can also be used as a check for QTLs mapping and it

should be conducted before QTL mapping is performed so that plant breeders can have a first impression on the genetic system of the involved trait [9, 11]. As the outcome of the present study, one to two major genes and polygenes/minor genes in cumulative manner are involved in controlling the 1000-GW. Additive interaction of the major gene/genes as well as, polygenes is pronounced to control the trait. Both favorable and reversed genes for the trait may be dispersed in the parents. The major gene heritability is higher than that of the polygenes to control the trait. The environmental conditions have influence on the trait. Because of its additively controlled nature, progeny selection for 1000-GW may be delayed up to advanced generations till the favorable geans may attain the level of maximum homozygosity.

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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