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GENETIC EFFECTS IN CONTROLLING GRAIN FILLING DURATION IN WHEAT CROSSES

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ABSTRACT

Genetic effects for grain filling duration were determined in two bread wheat crosses (Bakhtawar-92 × Frontana: Cross-1; (Inqilab-91 × Fakhr-e-Sarhad: Cross-2) during 2006-07 and 2008-09. Joint segregation analysis (JSA), designed for six basic populations i.e. P_1, F_1, P_2, BC_1, BC_2 and F_2 was used as statistical approach. In both crosses, the grain filling duration was controlled by mixed additive and dominant effects of two major genes and several polygenes. Negative additive effects were found due to first and second major genes in the crosses during both years indicating that the major genes may affect the said trait adversely except in Bakhtawar-92 × Frontana during first year where the additive effect was positive due to the second major gene. However, the positive additive effects due to polygene were observed in the crosses during both years. Transgressive segregates for long and short grain filling duration indicated the dispersion of favorable and adverse genes in the parental genotypes. Major genes heritability for grain filling duration was higher than heritability due to polygene in BC_1, BC_2 and F_2 for the crosses with highest environmental influence. Additive genetic effects of the major and polygene were pronounced thus selection of desirable recombinants for both short and long grain filling duration may be delayed till the accumulation of maximum favorable genes in the subsequent advance generations.

Key words: Major genes + minor genes interaction— grain filling duration —Triticum aestivum L.

INTRODUCTION

The stages for growth and development in plant life cycle are under control of genetic factors and their interaction with the environment. Grain filling duration is the time from anthesis to physiological maturity which determines the accumulation of dry mater and its partition into grain. Whereas, grain weight is the outcome of grain filling duration and grain filling rate (Milka *et al.*, 2008) and physiological maturity is the dry matter accumulation in the seed (Przulj and Maldenov, 1999). Genetic variation for grain filling among wheat genotypes exists in response to water deficiency and terminal heat stress (Rawson, 1986; Wardlaw *et al.*, 1989a; b; Hunt *et al.*, 1991). Similarly, variations among wheat genotypes also exist for both rate and duration of grain filling (Nass and Reiser, 1975; Darroch and Baker, 1990).

Wheat breeders desire to have cultivars, genetically incorporated with shorter life cycle and shorter grain filling duration that can reach maturity before severe water deficit may occur in irrigated areas. However, it is an undesired trait when selection is needed for longer grain filling duration to give comparatively higher grain yield under drought condition. (Talbert *et al.*, 2001). Though positive correlation exists between grain filling duration and grain yield in corn (Daynard *et al.*, 1971; Daynard and Kannenberg, 1976) however, very few reports are available on relationship between significant grain filling duration and grain yield in wheat and other small grains (Bruckner and Frohberg, 1987; Metzger *et al.*, 1984; Nass and Reiser, 1975).

Genetic effects for controlling grain filling duration in terms of polygene in wheat have previously been determined using either diallel or generation mean analysis as statistical procedure. In the present study, the Joint Segregation Analysis proposed by Jiankang and Gai (2001), Gai and Wang (1998) and Gai *et al*. (2003) with special advantages and efficacy (Wang *et al*., 2001), as summarized by Irfaq *et al*. (2012) over all the previous analytical approaches of Kearsey and Jinks. (1968), Mather and Jinks. (1982) and Kearsey and Pooni. (1996) was used to determine the number of major genes with their individual effects and accumulative effect of the major genes as well as polygene on grain filling duration in wheat.

MATERIALS AND METHODS

Parental selection and development of six populations: Parental genotypes with contrast in grain filling duration were selected for crossing through cluster analysis of 45 bread wheat genotypes (Table 1) for 10 phenological traits with further ratification by genotyping of the same germplasm (Irfaq *et al*., 2011). Using parental genotypes with short grain filling duration (Bakhtawar-92 and Inqilab-91) as pollen recipients and

the genotypes with long grain filling duration (Frontana and Fakhr-e-Sarhad) as pollen donors, two cross combinations viz. Bakhtawar-92 × Frontana (Cross-1) and Inqilab-91 × Fakhr-e-Sarhad (Cross-2) were attempted to develop F_1. Including parental genotypes, six basic populations i.e. P_1, F_1, P_2, BC_1, BC_2 and F_2 of both the crosses were developed on the pattern of joint segregation analysis (Wang, 1996; Gai and Wang, 1998; Gai *et al.*, 2003 and Zhang *et al*., 2003) as practiced previously (Irfaq *et al*., 2009; 2012).

Experimental cite, design and years: During the cropping season 2006-2007 (Year 1), the populations for each cross were planted in three replications with randomized complete block (RCB) design in the experimental farm of Nuclear Institute for Food and Agriculture (NIFA), Peshawar. Each population was planted in 5 meters long rows but number of rows varied i.e. two rows for parental genotypes and F_1, four rows for each of BC_1 and BC_2 and 8 rows for 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 on thinned to single healthy seedling per hill after germination (Irfaq *et al.*, 2009). In order to understand the effects of seasonal fluctuations on the genetic behavior of grain filling duration, the experiment for the same populations was repeated during the cropping season 2008-2009 (Year 2).

Data collection and number of observations: The observations regarding grain filling duration on selected individual plants from each of the six populations were recorded by counting number of days from the date of anthesis to that of physiological maturity i.e. turning yellow (Przulj and Mladenov, 1999, Sharma and Sain, 2004). Data were recorded on 60 plants from each of two homozygous parental genotypes (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 of the F_2 generation of both the crosses.

Statistical approach: Individual genetic effects due to major genes and commutative effects due to polygene for grain filling duration were determined by using joint segregation analysis (JSA) or mixed inheritance model with five different groups of 24 genetic models (Tables 3, 4 with certain assumptions of Wang (1996), Gai and Wang (1998), Gai *et al*. (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 1 degree of freedom (Gai and Wang, 1998). Likelihood-ratio test (LRT) was used to choose the simplest type within the model group. Where; 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 4) i.e. Smirnov's statistics (nW^2) and Kolmogorove's statistics (D_n) where; D: Sup $|F_n(x) - F_o(x)|$ (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 BC_1, BC_2 and F_2 were worked out with the help of proposed formulae (Gai *et al.*, 2003) by using Microsoft excel program of windows. Under the second order genetic parameters (Table 6), the phenotypic variation (σ_p^2) is partitioned into genetic and environmental variation (σ_e^2) for the 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} in Table 5 indicated different means regarding six generations which have to be used 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. $(\sigma_e^2/\sigma_p^2) \times 100$.

RESULTS AND DISCUSSION

Differences in parental means and segregation pattern of different generations: In cross of Bakhtawar-92 × Frontana and Inqilab-91× Fakhr-e-Sarhad, mean grain filling duration for parental genotypes i.e. Bakhtawar-92, Frontana, Inqilab-91, and Fakhr-e-Sarhad were 42.6, 51.6, 36.0, and 45.1 days, respectively (Table 1). As apparent from the range and mean grain filling duration values (Table 2), the F_1 in the crosses revealed intermediate co-dominance towards the parental genotypes with long grain filling duration for the trait during both the years. BC_1 (mean grain filling duration: 28.0, 39.3, 35.2, and 36.7) and BC_2 (mean grain filling duration: 24.2, 46.9, 45.5 and 46.5) in the crosses showed tendency towards their respective pollen donor parents, respectively, during the two years (Table 2). This trend indicates that the trait was under control of nuclear genes rather than the cytoplasmic factors. F_2 populations in the crosses were normally distributed between the ranges of

respective parents during the two years which indicated the polygenic nature of the trait in wheat. The values for F_2 populations outside the parental range on both the extremities represent transgressive segregates (Table 2). Occurrence of transgressive segregates in F_2 for both short and long grain filling duration, though very few plants for each cross, revealed the dispersion of genes for short and long grain filling duration in the parental genotypes (Table 2). As evident from the segregation pattern of BC_1, BC_2 and especially of F_2 populations for the two crosses (Table 2), grain filling duration being a quantitatively controlled trait is under the control of major genes and minor genes (polygene). In the previous investigations, transgressive segregates have also been reported for grain filling duration in F_2 of some wheat crosses (Sharma and Sain, 2004). The present results regarding mean grain filling duration (Table 2) for P_1, F_1, P_2 and F_2 of both the crosses in both experimental years also coincide with those of Kamaluddin *et al.* (2007) who found intermediate or closer grain filling duration of F_1 and F_2 to the average of the respective parental genotypes involved in the cross. Resistance and susceptible transgressive segregates have also been observed for stripe rust in F_2 population (Irfaq *et al*., 2009) as well as for flag leaf area ((Irfaq *et al*., 2012) in wheat. Whereas in barley, Zheng *et al*. (2008) reported both resistant and susceptible F_2 plants against fusarium head blight.

Selection of best fitting models and calculation of genetic effects: Based on maximum log of likelihood estimates (MLLE), Akaike's information criterion (AIC) proposed by Dempster *et al.* (1977) and Akaike (1977), respectively, and smallest number of least significant or non-significant values of five suggested goodness of fit tests (Gai and Wang, 1998) i.e. U_1^2, U_2^2, U_2^3, W^2 and D_n of Tables 3 and 4, the best fitting genetic models for cross Bakhtawar-92 × Frontana were E-2 and, E during first and second year, respectively. The models represent mixed action of two major additive dominant genes plus additive-dominant polygene and mixed action of two major additive dominant epistatic genes plus additive dominant epistasis of some polygene, respectively (Table 3). Negative additive gene interaction was observed due to both major genes during first year (-16.2, -2.5), representing the adverse effect of major genes on the trait (Table 6). According to 2nd year studies in the cross-1 (Bakhtawar-92 × Frontana), the negative additive effect was observed due to major gene A only, whereas, it was positive due to major gene B. The dominant effects due major genes during the first year was higher (h_a = 4.2, h_b = 6.5) but smaller and equal during the second year i.e. h_a = h_b: 1.6 (Table 6). The positive additive [*d*] and negative dominant [*h*] interaction due to polygene was recorded as 7.1 and -11.2, respectively. In case of model E for cross-1 (Bakhtawar-92 × Frontana) which was the best fit during second year, values for m_1 to m_6 represent mean grain filling duration of P_1, F_1, P_2, BC_1, BC_2 and F_2, respectively. Pronounced negative additive effect due to first major gene was -9.3, whereas, smaller positive additive effect due to second major gene was 1.7. Dominant effect due to the major genes was equal and positive (h_a = h_b = 1.6). The ratio of dominance to additiveness (*h*/*b*) due to first and second major gene was -0.2, 1.0, respectively. Smaller and positive additive × additive gene interaction due to major genes was 0.5 and negative dominant × dominant interaction was -3.8. The fitness of two different models i.e. 'E2' and 'E' for genetic analysis of grain filling duration in cross-1 (Bakhtawar-92 × Frontana) during the two years indicated that genetic constitution of the cross is highly influenced by the environmental conditions of the years. Sharma and Sain. (2004) explained this situation that the segregating population, composed of component distributions is mainly controlled by major genes whereas, the polygenic system of the cross tries to modify the effects due to major genes. In addition, this might have occurred due to involvement of parental genotypes with more variable genetic background in the cross (Zhang *et al*., 2003).

Same genetic model, i.e. E-1 was the best fit for cross-2 (Inqilab-91× Fakhr-e-Sarhad) during both the years. The model represents mixed action of two major additive dominant epistatic genes plus additive dominant epistasis of some polygene (Table 3). Almost equal but negative additive effects of the major genes (d_a = -1.7, d_b = -1.6 during first year, and d_a = -5.8, d_b = -5.2 during second year) were observed during both the years, representing the adverse effect of both major genes A and B on grain filling duration. The positive dominant effect of the major genes during the second year was pronounced in comparison to the first year. During first year, the ratio of dominance to additiveness due to the first major gene (A) was -0.3 and -1.0 whereas, due to second major gene (B), it was 3.2, and -1.1, respectively. Pronounced negative additive × additive interaction was found as -4.5 and -11.9 during first and second years, respectively (Table 6). Highest additive effect due to polygene [*d*] was recorded as 14.6 and 22.9 during first and second year, respectively (Table 6). The non allelic dominant effect [h] due to polygene was 6.6 and 1.5 during firs and second year, respectively (Table 6). The fitness of the same genetic model (E1) for Cross-2 i.e. Inqilab-91 × Fakhr-e-Sarhad during both the years indicated that the diverse environmental conditions of the two years have very little effect on the genetic constitution of the cross. It may probably be due to the higher additive polygenic effect [*d*] which was recorded as 14.6 and 22.9 during the first and 2nd year, respectively (Table 6). Another possibility may be due to the smaller genetic variability between the parental genotypes involved in the cross (Gai *et al*., 2007).

Estimates of heritability and environmental variation: Under the second order genetic parameters (Table 6), irrespective of the model group, higher major gene heritability (h_{mg}^2) was recorded for BC_1, BC_2, and F_2 of cross-1 (Bakhtawar-92 × Frontana) i.e. 65.7%, 36.1% and 87.5%, respectively, during first year, and 83.0%, 83.2% and 45.0%, respectively, during second year. Low polygene heritability (h_{pg}^2) was observed for the generations of cross-1was 0.0%, 24.4% and 0.0%, respectively during the first year, and 0.0%, 0.5% and 36.6%, respectively during the 2nd year. Similarly, major gene heritability was higher than the polygene heritability for these generations of cross-2 (Inqilab-91 × Fakhr-e-Sarhad) during both the years (Table 6). Highest variation due to environment (V_e) i.e. 23.1, 30.5, 34.3, 39.6, 58.0 and 62.5 (Table 6) was observed for segregating generations (BC_1, BC_2 and F_2) in the crosses during the two years (Table 6).

Under the mix interaction of both major as well as polygene for cross-1(Bakhtawar-92 × Frontana) during the second year, the negative signs of the epistatic effects (d_a, d_b, I, J_{ab} and J_{ba}) indicate the presence of reversed major genes for controlling grain filling duration among the parents. This suggests that progeny selection of genotypes for both long and short grain filling duration might be delayed to advanced generations ($F_5 \sim F_6$) till maximum favorable polygene may be accumulated (Jiankang *et al.*, 2007; Gai *et al.*, 2003; Jiankang and Gai, 2001).

Using generation mean analysis as statistical approach in the previous studies, additive-dominance model (absence of epistasis) digenic epistasis with predominant additive effect, significant additive × additive '*i*' and dominant × dominant '*l*' types of epistatic interaction for grain filling duration were reported in wheat crosses (May and Sanford, 1992; Beiquan and Kronstad, 1998; Przulj and Mladenov, 1999). Contrary to the investigation of these observers; in the present findings, environmental effect in back crosses and F_2 generations for cross-2 (Inqilab-91 × Fakhr-e-Sarhad) was pronounced during the second year i.e. 62.5, 58.0 (Table 6). However, the contradictions between the present and the previous results may be due to the statistical procedures, as outlined by Kearsey and Pooni. (1996) i.e. the diallel or generation mean analysis were used in the previous studies to measure the genetic effects as the polygenic system. These have no power to determine the effect of the individual major genes and aggregate polygenic effects (Wang *et al.*, 2001). Moreover, the difference in the genetic background of the material and different environmental conditions used in the present and past experimentations may further leads to the deviation in the results (Irfaq *et al.*, 2009).

Higher values of *Ve* indicated that the trait was highly influenced by environment (Zheng *et al.*, 2008). Using same statistical approach, higher heritability due to major genes but low for polygene due to more involvement of environmental influence for controlling resistance to yellow rust and flag leaf area have been reported in wheat (Irfaq *et al.*, 2009; 2012) and also for controlling resistance to Fusarium head blight in barley (Zheng *et al.*, 2008). The fitness of two different genetic models (E-2 and E) for cross-1 (Bakhtawar-92 × Frontana) during the separate experiments for the two years may be due to i.e. segregating populations composed of component distributions was under control of major gene(s) and which was modified by polygene system as well as variable environments of the experimental years (Sharma and Sain, 2004). The second may be as a theoretical procedure, JSA analyze the segregating data of quantitatively controlled trait like the Mendelian method and the best-fitting genetic model could be chosen according to Akaike's information criterion, a likelihood ratio test and tests for goodness of fit (Gai *et al*., 2007).

In spite of the facts that the model tests were polygenic in both years but still some values of the polygene variance (σ_{pg}^2) as well as polygene heritability (h_{pg}^2) for the segregating generations were equal to zero or very small, i.e. $h_{pg}^2 = 0.0$ for BC_1, F_2 during the first year and 0.0, 0.5 for BC_1 and BC_2 during the second year, respectively, for Bakhtawar-92 × Frontana (Table 6). Same situation was observed for segregating generations of cross-2 (Inqilab-91 × Fakhr-e-Sarhad) during both the years (Table 2). Jiankang and Gai (2001) mentioned the occurrence of smaller values for σ_{pg}^2 and h_{pg}^2 to be due to epistatic effects between the major and minor genes. The other possibility they described for this situation is that it is not appropriate to view environmental variance (σ^2) as the estimate of environmental variation in segregating generations.

The JSA with the capacity to find the genetic mechanism up to two major genes plus polygene was designed for the six basic populations (Gai *et al*., 2003). However, seven groups and 32 types of genetic models, including one major-gene, two major-genes, three-major genes, polygene, mixed one major-gene and polygene, mixed two major-genes and polygene, and a mixed three major-genes and polygene models have also been set up to determine the genetic effects in recombinant inbred lines (RIL) population (Gai *et al*., 2007). But it is still inadequate and requires gradation 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 (Gai *et al*., 2007).

From present investigations, it was concluded that two major genes plus several polygene are involved in controlling grain filling duration in wheat. Transgressive segregates in F_2 for both long and short grain filling duration may occur due to the accumulation of maximum favorable major and minor genes. The

tendency of BC_1 and BC_2 to their respective recurrent parents during both the experimental years indicates that the trait was under control of nuclear genes rather than the cytoplasmic factors. Different types of epistasis as well as additive genetic effects due to both major genes as well as polygene were pronounced in controlling the trait. However, due to apparent additive genetic effects of major genes plus polygene, the selection of desirable recombinants for both shot and along grain filling duration is desired to be delayed up to advance generations till maximum favorable genes are accumulated. Being a quantitatively controlled trait, grain filling duration is highly influenced by environmental fluctuations with higher major genes and low polygene heritability.

Table 1. Origin, pedigree and mean grain filling duration (GFD) of 45 wheat genotypes

Genotype	Origin	Pedigree	GFD (days)
Frontana	Brazil	Fronteria/Mentana	51.6
Bakhtawar-92	CIMMYT	KAUZ 'S'	42.6
Saleem-2000	CIMMYT	CHAM-6//KITE/PGO	46.9
Tatara	CIMMYT	JUP/ALD "S"//RLT 'S'/3VEE 'S')	47.6
Fakhre Sarhad	CIMMYT	PFAU 'S'/SERI/BOW 'S'	45.1
CT-02009	CIMMYT	PUNJAB-96-0PAK	48.2
CT-02019	CIMMYT	KAUZ//STAR/LUCO-M	42.5
CT-02081	CIMMYT	VEE/TRAP#1//ANGRA/3/PASTOR	44.5
CT-02192	CIMMYT	IRENA//CMH76.176/2*GEN/3/SNB/4/BORL95	41.3
CT-02266	CIMMYT	SW89.5181/KAUZ	45.4
CT-02267	CIMMYT	SW89.5181/KAUZ	44.4
CT-02204	CIMMYT	KAUZ/PASTOR	38.9
CT-02306	CIMMYT	CMH80A.542/CNO79	43.3
CT-02248	CIMMYT	ALTAR84/AE.SQUARROSA(219)//SERI	41.0
CT-02390	CIMMYT	FRET2	44.5
CT-01183	CIMMYT	SITTA/*SKUZ	36.9
CT-01084	CIMMYT	ATTILA/3*BCN	38.8
Inqilab-91	CIMMYT	WL 711/CROW 'S'	36.0
Karawan	CIMMYT	C182.2/C166.3/3/CNO/7C2*//CC//TOB/SWM6828	44.9
CT-99022	CIMMYT	URES/JUN//KAUZ	42.6
Metal Tail	India	ORE F_1 158/FDL//KAL/BB/3/NAC	38.0
V-84051	India	TAN'S'/3/TI/TOB//ALD	34.0
Soleman-96	CIMMYT	F6.74/BUN//SIS/3/VEE#7	40.6
CB-61	CIMMYT	MILAN/HD.832 PK.3484-3A-3A-500A	29.6
CB-82	CIMMYT	SATLUJ 86CMT/YR//MON 'S'	41.3
CB-148	CIMMYT	WEAVER/TSC//WEAVER/3/WEAVER	43.4
CB-179	CIMMYT	GAMDOW-6/CM79515-044Y…	49.9
CB-185	CIMMYT	PASTOR-2/CM85295-0101TOPY--	41.3
CB-195	CIMMYT	MAYA74'S'/MON'S'	25.4
CB-196	CIMMYT	MAYA74 'S'/MON CM 29480-20Y0Y	26.3
CB-197	CIMMYT	PF70402/ALD'S'//PAT72/160//ALD'S'/3/PEW 'S'	40.0
CB-289	CIMMYT	BOW'S'*2/PRL'S'	38.9
Uqab-2K	CIMMYT	CROW'S'/NAC//BOW'S'PB 22138	40.0
CB-325	CIMMYT	TAN'S'/3/TI/TOB//ALD = V-84051	43.3
DRRM	India	PB-96/V-87094//MH-97	49.8
CM-03-04	India	PASTOR/3/VEE#5DOVE/BUC	43.0
E-41	India	SH-88/PAK-81//MH-97	32.8
V-2156	India	Weaver/SH-88	41.5
V-03007	India	Pb-96/V-87094//MH-97	35.2
AS-2002	India	KHP/D31708//CN74A370/3/CIAN079/4/RL6043/*4NAC	35.0
CB-145	India	CHOIX/STAR/3/HE1/3*CNO79//2*SERI	48.2
Mango	CIMMYT	RSK/AZ//PVN/CM 4170-9	37.4
BANA-4	India	(Pedigree not available)	34.4
CB-171	India	ABTIN-1ICW92-0717	34.4
E-29	India	SH-88/V-90A 204//MH-97	41.4

Source: Irfaq *et al*. (2009)

Table 2. Frequency distribution of plant population for grain filling duration (days) in P_1, P_2, F_1, BC_1, BC_2 and F_2 of two bread wheat crosses during two years.

Cross[1]	Year	Generation[2]	Range of grain filling duration (days)													Size[3]	M-GFD[4]	Variance[5]	SD(±)[6]
			18-20				33-35	36-38	39-41	42-44	45-47	48-50	51-53	54-56	57-59				
1	1st year	P_1					6	5	8	33	8					60	41.7	11.2	3.4
		F_1						4	12	28	30	13	3			90	44.8	8.7	2.9
		P_2								1	24	16	10	6	3	60	49.2	12.9	3.6
		BC_1			1	8	7	14	21	22	41	36				150	28.0	28.0	5.3
		BC_2								8	47	50	17	5	12	11	150	24.2	24.2	4.9
		F_2			3	10	13	11	8	6	7	28	23	59	22	10	200	43.3	77.0	8.8
1	2nd year	P_1							3	11	38	8					60	42.5	4.1	2.0
		F_1							1	4	13	51	20	1			90	46.6	5.7	2.4
		P_2									5	14	30	11			60	49.1	7.4	2.7
		BC_1			3	12	15	18	22	19	36	23	2				150	39.3	37.1	6.1
		BC_2								7	35	45	27	17	13	6	150	46.9	29.2	5.0
		F_2		1	7	6	9	25	29	35	28	23	17	10	7	3	200	41.6	85.6	9.3
2nd	2nd year	P_1			1	5	10	28	16								60	33.8	8.0	2.8
		F_1					1	15	50	18	6						90	37.0	5.9	2.4
		P_2							13	21	13	10	3				60	41.6	10.9	3.3
		BC_1		2	7	14	17	31	29	39	11						150	35.2	24.4	4.9
		BC_2				3	4	5	4	12	22	34	46	13	7		150	45.5	34.2	5.8
		F_2		3	7	13	14	13	33	26	23	27	24	10	6	1	200	40.3	60.7	7.8
2nd	2nd year	P_1		4	10	13	14	9	10								60	32.1	23.6	4.9
		F_1			1	7	21	28	23	8	2						90	35.0	13.3	3.6
		P_2					7	17	17	5	6	3	2	3			60	37.7	30.9	5.6
		BC_1		5	4	5	5	31	41	40	11	6	2				150	36.7	26.1	5.1
		BC_2					3	6	6	6	13	40	50	16	9	1	150	46.5	42.2	5.3
		F_2	2	4	6	9	11	23	36	30	21	16	16	13	10	3	200	40.0	70.7	8.5

1, 2: Cross 1= Bakhtawar-92 (P_1) × Frontana (P_2) and cross 2 = Inqilab-91 (P_1) × Fakhr-e-Sarhad (P_2). 3: Sample size.
4: Mean grain filling duration. 5: Phenotypic variance. 6: Standard deviation.

Table 3. Maximum log of likelihood estimates (MLLE) and Akaike's information criterion (*AIC*) values for Grain filling duration under 24 genetic models estimated through the Iterated Expectation and Conditional Maximization (IECM) algorithm

Model group, code, and implication of model type	Cross combination									
	Year 1				Year 2					
	Cross 1		Cross 2				Cross 1		Cross 2	
	MLLE	*AIC*	MLLE	*AIC*			MLLE	*AIC*	MLLE	*AIC*
Group 1: One major gene										
A-1: additive and dominant			-2236.3	4480.6	-2207.5	4423.0	-2280.3	4568.7	-2358.3	4724.6
A-2: additive			-2232.3	4471.8	-2216.6	4439.2	-2291.4	4588.8	-2366.2	4738.4
A-3: dominance			-2283.1	4572.2	-2220.0	4446.2	-2339.6	4685.3	-2354.6	4715.2
A-4: negative dominance			-2264.8	4535.7	-2257.9	4521.9	-2295.9	4597.9	-2360.5	4727.0
Group 2: Two major genes										
B-1: additive dominance and epistasis			-2097.8	4215.7	-2121.2	4262.5	-2126.0	4272.0	-2236.5	4493.0
B-2: additive and dominance			-2123.3	4258.6	-2131.9	4275.7	-2116.8	4245.5	-2296.8	4605.6
B-3: additive			-2165.4	4338.8	2136.9	4281.9	-2135.5	4279.1	-2398.9	4805.8
B-4: equal additive			-2268.4	4542.9	-2247.7	4501.3	-2316.2	4638.4	-2376.5	4759.1
B-5: dominance			-2289.8	4587.5	-2182.8	4373.6	-2338.1	4684.2	-2299.5	4607.0
B-6: equal dominance			-2289.8	4585.6	-2260.9	4527.8	-2339.5	4685.1	-2382.3	4770.7

Group 3: Polygene								
C: additive dominance and epistasis	-2177.1	4374.2	-2134.5	4289.0	-2141.1	4302.2	-2246.3	4512.6
C-1: additive and dominance	-2196.7	4407.5	-2193.4	4400.7	-2194.2	4402.5	-2364.7	4743.5
Group 4: One major gene plus polygene								
D: mixed one major-gene and additive-dominance-epistasis polygene	-2138.6	4301.4	-2127.5	4279.0	-2068.5	4161.1	-2246.3	4516.6
D-1: mixed one major-gene and additive-dominance polygene	-2140.2	4298.5	-2127.8	4273.7	-2164.2	4346.5	-2262.7	4543.5
D2: mixed one additive major gene and additive-dominance polygene	-2140.2	4296.5	-2127.8	4271.7	-2164.2	4344.5	-2262.9	4541.8
D-3: mixed one dominance major gene and additive-dominance polygene	-2193.8	4403.5	-2134.8	4285.7	-2177.6	4371.2	-2263.2	4542.3
D-4: mixed one negative dominance major gene and additive-dominant polygenes	-2140.3	4296.6	-2131.8	4279.7	-2176.3	4368.6	-2263.0	4542.1
Group 5: Two major genes plus polygene								
E: mixed two major additive-dominance epistatic genes plus additive –dominant-epistasis of polygene.	-2130.2	4296.5	-2108.9	4253.8	-2063.7	4163.4	-2219.8	4475.6
E-1: mixed two major additive-dominance epistatic genes plus additive-dominant polygene	-2127.0	4284.0	-2107.6	4245.3	-2077.8	4185.7	-2233.4	4496.9
E-2: mixed two major additive-dominant genes plus additive-dominant polygene	-2118.9	4259.8	-2132.5	4287.0	-2107.5	4237.0	-2276.5	4575.1
E-3: mixed two major additive genes plus additive-dominant polygene	-2175.3	4368.6	-2135.4	4288.8	-2137.8	4293.6	-2250.4	4518.8
E-4: mixed two major equal additive genes plus additive-dominant polygene	-2196.1	4408.2	-2171.1	4358.2	-2176.1	4368.2	-2365.4	4746.7
E-5: mixed two major dominant genes plus additive-dominant polygene	-2196.8	4411.5	-2132.6	4283.1	-2190.6	4399.4	-2283.8	4585.7
E-6: mixed two major equal dominant genes plus additive-dominant polygene	-2399.1	4814.3	-2202.7	4421.5	-2386.5	4789.1	-2351.6	4719.2

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

Table 4. Tests for goodness-of-fit regarding grain filling duration for suitable genetic models in two wheat crosses

		Year 1							Year 2				
						Crosses 1							
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**
B-1	P_1	0.01(0.77)	0.02(0.88)	0.06(0.79)	0.39(>0.05)	0.17*	D	P_1	0.51(0.70)	0.02(0.87)	4.67**	0.43(>0.05)	0.19(>0.05)
	F_1	0.00(0.95)	0.00(0.96)	0.00(0.96)	0.11*	0.09**		F_1	0.48(0.49)	0.07(0.78)	2.50(0.11)	0.46(>0.05)	0.21(>0.05)
	P_2	0.43(0.51)	0.01(0.93)	4.81***	0.11*	0.09**		P_2	0.05(0.83)	0.29(0.59)	1.72(0.19)	0.19(>0.05)	0.13*
	BC_1	10.23***	7.85***	1.39(0.24)	1.4(>0.05)	0.18(>0.05)		B_1	5.30**	4.69**	0.00(0.99)	0.93(>0.05)	0.15(>0.05)
	BC_2	21.66***	15.43***	5.33***	1.44(>0.05)	0.17(>0.05)		B_2	36.41***	32.86***	0.19(0.66)	4.23(>0.05)	0.30(>0.05)
	F_2	43.12***	60.30***	31.71***	5.95(>0.05)	0.31(>0.05)		F_2	0.61(0.43)	2.08(0.15)	7.4***	0.35(>0.05)	0.09(>0.05)
B-2	P_1	4.06(0.04)	4.38**	0.33(0.56)	1.03(>0.05)	0.28(>0.05)	E	P_1	0.19(0.66)	0.00(0.97)	2.47(0.11)	0.38(>0.05)	0.20(>0.05)
	F_1	0.06(0.80)	0.26(0.61)	1.20(0.27)	0.14(>0.05)	0.10*		F_1	0.59(0.44)	0.29(0.59)	0.71(0.40)	0.42(>0.05)	0.20(>0.05)
	P_2	3.30(0.07)	1.60(0.21)	3.86*	0.70(>0.05)	0.22(>0.05)		P_2	0.06(0.80)	0.55(0.46)	3.93*	0.23(>0.05)	0.15*
	BC_1	19.08***	30.80***	27.90***	3.00(>0.05)	0.32(>0.05)		B_1	1.57(0.21)	0.93(0.33)	0.98(0.32)	0.31(>0.05)	0.10*
	BC_2	6.63**	5.92**	0.06 (0.81)	1.78(>0.05)	0.22>(0.05)		B_2	2.18(0.14)	2.76(0.09)	0.86(0.35)	0.39(>0.05)	0.11(>0.05)
	F_2	1059***	14.29***	6.34**	2.39(>0.05)	0.21(>0.05)		F_2	0.32(0.56)	1.67(0.20)	0.86(0.35)	0.35(>0.05)	0.09*
E-2	P_1	1.30(0.25)	1.31(0.25)	0.02(0.86)	0.66(>0.05)	0.23(>0.05)	E-1	P_1	0.46(0.49)	0.05(0.82)	2.96(0.08)	0.43(>0.05)	0.21(>0.05)
	F_1	0.00(0.99)	0.02(0.87)	0.32(0.56)	0.12*	0.11*		F_1	0.24(0.62)	0.68(0.41)	1.91(0.17)	0.36(>0.05)	0.15(>0.05)
	P_2	1.37(0.24)	0.41(0.52)	3.94*	0.49(>0.05)	0.19(>0.05)		P_2	1.65(0.20)	0.70(0.40)	2.71(0.09)	0.33(>0.05)	0.19(>0.05)
	BC_1	18.96***	32.45**	35.4***	3.22(>0.05)	0.33(>0.05)		B_1	0.54(0.46)	0.19(0.66)	1.22(0.27)	0.22(>0.05)	0.09*
	BC_2	5.25**	4.83**	0.01(0.93)	1.58(>0.05)	0.22(>0.05)		B_2	0.09(0.75)	0.36(0.55)	1.41(0.23)	0.31(>0.05)	0.10*
	F_2	3.83**	13.45***	9.79***	1.75(>0.05)	0.19(>0.05)		F_2	2.19(0.14)	3.67*	3.73*	0.38(>0.05)	0.10(>0.05)
						Cross 2							

E-1	P_1	0.073(0.79)	0.03(0.86)	0.12(0.73)	0.19(>0.05)	0.15*	E	P_1	0.74(0.39)	2.74(0.10)	10.90***	0.61(>0.05)	0.21(>0.05)
	F_1	0.71(0.39)	2.17(0.14)	6.89**	0.50(>0.05)	0.19(0.05)		F_1	0.08(0.78)	0.02(0.89)	0.29(0.59)	0.12*	0.09*
	P_2	0.82(0.36)	0.01(0.91)	9.28**	0.41(>0.05)	0.17(>0.05)		P_2	1.982(0.15)	0.52(0.47)	6.60**	0.62(>0.05)	0.23(>0.05)
	BC_1	1.72(0.19)	1.51(0.22)	0.02(0.87)	0.33(>0.05)	0.11(>0.05)		B_1	4.06*	1.04(0.31)	13.79***	1.16(>0.05)	0.19(>0.05)
	BC_2	6.27**	3.82*	3.53(0.06)	0.87(>0.05)	0.16(>0.05)		B_2	3.74*	1.17(0.27)	9.96***	0.85(>0.05)	0.17(>0.05)
	F_2	0.50(0.48)	0.39(0.53)	0.06(0.80)	0.14(>0.05)	0.08*		F_2	0.14(0.71)	0.03(0.85)	0.48(0.48)	0.11(>0.05)	0.07*
E	P_1	0.53(0.47)	0.45(0.50)	0.02(0.88)	0.27(>0.05)	0.17*	B-1	P_1	0.86(0.35)	2.43(0.12)	6.99**	0.55(>0.05)	0.21(>0.05)
	F_1	0.03(0.86)	0.71(0.40)	7.22**	0.43*	0.17*		F_1	2.22(0.14)	3.17(0.07)	1.83(0.18)	0.30(>0.05)	0.13*
	P_2	0.44(0.51)	0.01(0.92)	8.60**	0.35(>0.05)	0.16*		P_2	7.78**	3.51(0.06)	10.95***	1.31(>0.05)	0.29(>0.05)
	BC_1	0.50(0.48)	0.32(0.57)	0.23(0.63)	0.19(>0.05)	0.09*		B_1	2.57(0.11)	0.86(0.35)	6.23**	0.92(>0.05)	0.16(>0.05)
	BC_2	3.36(0.07)	1.75(0.18)	3.27(0.07)	0.57(>0.05)	0.14(>0.05)		B_2	40.84***	32.07***	4.41**	5.32(>0.05)	35(>0.05)
	F_2	0.03(0.86)	0.11(0.74)	0.38(0.53)	0.56(>0.05)	0.14(>0.05)		F_2	0.01(0.92)	0.00(0.96)	0.04(0.84)	0.09*	0.07*
B-1	P_1	0.00(0.93)	0.04(0.83)	1.37(0.24)	0.21(>0.05)	0.13*	E-1	P_1	1.26(0.26)	3.52(0.06)	9.98**	0.64(>0.05)	0.22(>0.05)
	F_1	0.10(0.75)	0.32(0.57)	12.17**	0.56(>0.05)	0.17(>0.05)		F_1	1.13(0.29)	1.62(0.20)	0.94(0.33)	19(>0.05)	0.11*
	P_2	4.18**	1.72(0.18)	7.12***	0.72(>0.05)	0.22(>0.05)		P_2	8.82***	3.71*	14.43***	1.4(>0.05)	0.31(>0.05)
	BC_1	1.89(0.17)	1.59(0.21)	.083(0.77)	0.37(>0.05)	0.12(>0.05)		B_1	0.89(0.35)	0.00(0.99)	13.59***	0.85(>0.05)	0.16(>0.05)
	BC_2	9.37**	7.35**	0.98(0.13)	1.36(>0.05)	0.19(>0.05)		B_2	39.95***	26.99***	5.95**	4.32(>0.05)	31(>0.05)
	F_2	2.84(0.09)	2.67(0.10)	0.00(0.99)	0.36(>0.05)	0.09*		F_2	0.01(0.93)	0.03(0.86)	0.10(0.32)	0.17(>0.05)	0.09(>0.05)

P: Population type. In parenthesis is the probability value. *, **, *** represents the 0.05, 0.01, 0.001significance levels respectively. U_1^2, U_2^2, U_2^3 : χ^2 statistics with 1 degree of freedom; ${}_nW^2$: Smirnov's statistics; D_n: Kolmogorov's statistics. The model with least number of significant values relevant to the five statistics is the best fit in each cross.

Table 5. Maximum likelihood estimates of component parameters regarding grain filling duration for two wheat crosses in their respective best fit models

Parameter	Cross 1		Cross 2	
	Year 1 Model: E-2 Estimate	Year 2 Model: E Estimate	Year 1 Model: E-1 Estimate	Year 2 Model: E-1 Estimate
μ_1 :	41.7	42.5	33.9	32.1
μ_2 :	44.9	46.1	37.6	34.8
μ_3 :	49.3	49.1	41.7	37.8
μ_{41} :	32.5	30.0	37.5	27.4
μ_{42} :	41.4	44.3	28.1	37.9
μ_{43} :	45.2	44.3	39.2	37.9
μ_{44} :	54.1	37.0	34.0	38.8
μ_{51} :	47.0	46.8	34.7	36.6
μ_{52} :	43.0	43.7	48.4	48.3
μ_{53} :	51.3	43.7	48.4	48.3
μ_{54} :	47.3	55.8	44.7	48.1
μ_{61} :	29.0	33.8	37.9	26.2
μ_{62} :	37.9	48.0	28.4	36.6
μ_{63} :	33.9	29.4	45.3	37.1
μ_{64} :	41.6	48.0	39.6	36.6
μ_{65} :	50.5	39.9	34.3	37.6
μ_{66} :	46.5	36.9	48.0	49.3
μ_{67} :	45.9	51.2	45.5	38.2
μ_{68} :	54.8	36.7	48.0	49.3
μ_{69} :	50.8	48.8	44.3	49.1
σ^2 :	9.6	4.8	7.4	16.3
σ_4^2 :	9.6	4.8	7.4	16.3
σ_5^2 :	15.5	4.8	13.9	16.3
σ_6^2 :	9.6	36.4	15.4	20.6

σ^2: Phenotypic variance of P_1, F_1 and P_2; σ_4^2: polygenic + environmental variance of BC_1; σ_5^2: polygenic + environmental variance of BC_2; σ_6^2: polygenic + environmental variance of F_2

Table 6. Estimates of first and second order genetic parameters for GFD (days) in two bread wheat crosses under two experimental years.

Year 1: 2006-2007						Year 2: 2008-2009					
Cross 1: Bakhtawar-92 × Frontana											
Model type: E -2						Model type: E					
1st order parameters	Estimates	2nd order parameters	Estimates			1st order parameters	Estimates	2nd order parameters	Estimates		
			BC_1	BC_2	F_2				BC_1	BC_2	F_2
m =	45.5	σ_p^2=	28.0	24.2	77.0	m_1=	49.0	σ_p^2=	28.0	29.2	85.6
d_a=	-16.2	σ_{mg}^2=	18.4	8.7	67.4	m_2=	46.7	σ_{mg}^2=	23.2	24.3	38.6
d_b=	-2.5	σ_e^2=	9.6	9.6	9.6	m_3=	41.0	σ_e^2=	4.8	4.8	4.8
h_a=	4.2	σ_{pg}^2=	0.0	5.9	0.0	m_4=	37.2	σ_{pg}^2=	0.0	0.2	31.6
h_b=	6.5	h_{mg}^2 (%)	65.7	36.1	87.5	m_5=	47.6	h_{mg}^2 (%)	83.0	83.2	45.0
[d] =	7.1	h_{pg}^2 (%)	0.0	24.4	0.0	m_6=	38.3	h_{pg}^2 (%)	0.0	0.5	36.9
[h] =	-11.2	V_e =	34.3	39.6	12.5	d_a=	-9.3	V_e =	17.0	16.3	5.6
						d_b=	1.7				
						h_a=	1.6				
						h_b=	1.6				
						h_a/d_a	-0.2				
						h_b/d_b	1.0				
						i =	0.5				
						j_{ab} =	14.8				

						j_{ba} =	3.9				
						l	-3.8				
Cross 2: Inqilab-91 × Fakhr-e-Sarhad											
Model type: E -1						Model type: E -1					
m=	40.0	σ_p^2=	24.4	34.2	60.7	m=	36.6	σ_p^2=	26.1	28.2	70.7
d_a=	-1.7	σ_{mg}^2=	18.1	31.5	3.6	d_a=	-5.8	σ_{mg}^2=	9.8	11.8	50.2
d_b=	-1.6	σ_e^2=	7.4	7.4	7.4	d_b=	-5.2	σ_e^2=	16.3	16.3	16.3
h_a=	0.6	σ_{pg}^2=	0.0	6.5	7.9	h_a=	5.7	σ_{pg}^2=	0.0	0.0	4.2
h_b=	-5.0	h_{mg}^2 (%)	74.2	92.2	5.9	h_b=	5.7	h_{mg}^2 (%)	37.5	42.0	70.9
h_a/d_a	-0.3	h_{pg}^2 (%)	0.0	18.9	13.0	h_a/d_a	-1.0	h_{pg}^2 (%)	0.0	0.0	6.0
h_b/d_b	3.2	V_e =	30.5	21.7	12.3	h_b/d_b	-1.1	V_{e} =	62.5	58.0	23.1
i =	-2.2					i =	-0.3				
j_{ab} =	-8.1					j_{ab} =	-1.4				
j_{ba} =	-2.7					j_{ba} =	-1.9				
l =	-4.5					l =	-11.9				
[d]	14.6					[*d*]	22.9				
[h]	6.6					[*h*]	1.5				

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 × additive component due to major genes; $J_{ab} = d_a \times h_b$: first major gene with additive × second major gene with dominant effect; $J_{ba} = d_b$ x h_a: second major gene with additive × first major gene with dominant effect; l: mixed dominant × dominant component/effect due to major as well as polygene; [d]: additive component/effect 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; σ_{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.

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