Turkish Journal of Agriculture and Forestry

Volume 38 | Number 6 Article 5

1-1-2014

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KALIM ULLAH

NAQIB ULLAH KHAN

SHAH JEHAN KHAN

IMDAD ULLAH KHAN

MUHAMMAD IRFAQ KHAN

See next page for additional authors

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KALIM ULLAH, NAQIB ULLAH KHAN, SHAH JEHAN KHAN, IMDAD ULLAH KHAN, MUHAMMAD IRFAQ KHAN, REHMAT ULLAH KHAN, and SAMRIN GUL

TÜBİTAK

Turkish Journal of Agriculture and Forestry

http://journals.tubitak.gov.tr/agriculture/

Research Article

Turk J Agric For
(2014) 38: 807-819

doi:10.3906/tar-1403-87

Genetic analysis for grain filling duration in wheat using joint segregation analysis

Kalim ULLAH[1], Naqib Ullah KHAN[2,*], Shah Jehan KHAN[1], Imdad Ullah KHAN[1], Muhammad Irfaq KHAN[3], Rehmat Ullah KHAN[2], Samrin GUL[2]

[1]Faculty of Agriculture, Gomal University, Dera Ismail Khan, Pakistan
[2]The University of Agriculture, Peshawar, Pakistan
[3]Nuclear Institute for Food and Agriculture, Peshawar, Pakistan

Received: 16.03.2014 • **Accepted:** 06.06.2014 • **Published Online:** 31.10.2014 • **Printed:** 28.11.2014

Abstract: Mixed inheritance analysis using joint segregation analysis was investigated in 6 basic populations (P_1, F_1, P_2, BC_1, BC_2, and F_2) of 4 wheat crosses, i.e. Hashim-08 × LU-26, Farid-06 × Shafaq, Parula × Blue Silver, and TD-1 × D-97603, for grain filling duration during the crop season of 2011/2012. In cross Hashim-08 × LU-26, the duration of grain filling was controlled by 1 major gene and the additive-dominance-epistasis of polygenes (model D). In cross Farid-06 × Shafaq, the duration was controlled by additive-dominance-epistasis of 2 major genes (model B-1). However, in crosses Parula × Blue Silver and TD-1 × D-97603, the period of grain filling was under the control of 2 mixed groups of genes including additive-dominant-epistatic major genes plus the additive-dominant-epistasis of polygenes (model E and model E-1, respectively). In cross Hashim-08 × LU-26, the variation and heritability of the polygenes were greater than those of the major gene, whereas these components were low in cross Parula × Blue Silver. In crosses Farid-06 × Shafaq and TD-1 × D-97603, no polygenes were involved and the duration of grain filling was mainly under the influence of major genes. For the duration of grain filling, the maximum environmental variation revealed the influence of environment. Results suggested that due to its maximum heritability, early selection would be feasible in cross Hashim-08 × LU-26, while due to low heritability and variation in cross Parula × Blue Silver, delayed selection will be effective. Yield improvement based on duration of grain filling could be done through selection in later generations until the accumulation of the maximum favorable additive genes is achieved.

Key words: Additive-dominance-epistasis, environmental variation, grain filling duration, heritability, joint segregation analysis, major genes plus polygenes inheritance, *Triticum aestivum* L.

1. Introduction

Wheat grain yield is dependent on grains spike^{-1} and grain weight, which are the most important yield components of wheat, the latter being the product of the rate and the duration of grain filling (Gebeyehou et al., 1982; Van Sanford and Mackown, 1985; Bruckner and Frohberg, 1987). Grain filling duration is the period between flowering and physiological maturity (Przulj and Mladenov, 1999), and, in wheat, it is significantly affected by temperature and light (Sofield et al., 1977; Wiegand and Cuellar, 1981). Grain filling duration is influenced by environment as well as plant genotype (Metzger et al., 1984; Bauer et al., 1985), and significant genotypic differences have been reported for grain filling duration in spring wheat (Mou and Kronstad, 1994; Saadallah and Ghandorah, 2000; Talbert et al., 2001; Monpara, 2011). Hence, it could be an important trait in terminally heat-stressed environments (Al-Khatib and Paulsen, 1984). Under semiarid conditions, wheat lines with a longer grain filling duration produced lower yields if water stress and high temperature occurred during the grain filling period (Przulj and Mladenov, 1999). Therefore, wheat lines with a shorter grain filling duration should be produced in such environments (Wiegand and Cuellar, 1981), because after anthesis, the yield is mainly dependent on final grain weight, which is the product of the grain filling duration and the rate (Whan et al., 1996).

Multivariate analysis indicated that grain weight, rate, and duration of grain filling were equally important in characterizing the grain filling period of the wheat genotypes; however, the sequence of their significance varied in different years due to diverse environmental conditions (Brdar et al., 2008). Genetic variation has been reported for grain filling duration and rate in wheat, and multivariate analysis of variance proved to be a useful tool in examining grain filling curves (Darroch and Baker, 1990). Significant positive correlations have been observed between grain weight and the rate of filling (Calderini and Reynolds, 2000). The duration of grain filling and the time between anthesis and physiological maturity

* Correspondence: nukmarwat@yahoo.com

were positively correlated with grain yield in bread wheat (Monpara, 2011). An association between grain weight and duration of grain filling suggested that final grain weight is dependent on the period of grain filling, which is affected by environmental factors, especially temperature (Evans et al., 1975; Stone and Nicolas, 1994). However, a significant positive correlation was observed between grain filling parameters (duration and rate) and yield (Gebeyehou et al., 1982). Thus, a better understanding of the grain filling process may be helpful in breeding efforts to increase wheat grain yield. Various statistical methods have been used to describe the period of grain filling in wheat, including linear regression (Van Sanford, 1985), quadratic equations (Nass and Reiser, 1975; Bruckner and Frohberg, 1987), and a cubic equation (Gebeyehou et al., 1982). Multivariate analysis of variance has been recommended for analyzing model-derived variables when significant correlations exist among them (Keuls and Garretsen, 1982; Darroch and Baker, 1990).

Insufficient information is available about the inheritance of duration of grain filling and the rate of wheat grain filling. Better information on the factors involved in the duration of grain filling, including the gene effects controlling this trait, could result in the development of heat-tolerant or rapid grain filling wheat lines. Duration of grain filling is thought to be polygenically controlled because of the continuous variability for this trait in wheat (Xie and Zhang, 1981). Similarly, additive and dominant gene action associated with period of grain filling has been reported (Saadallah and Ghandorah, 2000; Yang et al., 2002). Mou and Kronstad (1994) observed additive gene action for duration of grain filling, even though nonadditive gene action also plays a vital role in certain crosses of wheat. Wong and Baker (1986) recorded low to intermediate heritability for period of grain filling and other developmental traits in spring wheat. Przulj and Mladenov (1999) reported additive and dominance effects, as well as epistatic interactions, that control the duration of grain filling, while both additive and dominant gene actions have been associated with period of grain filling under heat stress (Yang et al., 2002).

The present investigations were based on joint segregation analysis (JSA) to identify the mixed inheritance model and related genetic parameters. In light of the superiority of the JSA over other approaches (Gai and Wang, 1998; Gai et al., 2003, 2007), the present study was undertaken to determine: 1) the genetic diversity for duration of grain filling among the genotypes to be used in cross combinations, 2) the genetic mechanism of duration of grain filling through hybridization between diverse parental lines, and 3) the number and individual effects of major genes, and the cumulative effect of the major genes as well as polygenes controlling period of grain filling.

2. Materials and methods

2.1. Breeding material and procedure

Eight genetically diverse wheat parents (Hashim-08, LU-26, Farid-06, Shafaq, Parula, Blue Silver, TD-1, and D-97603) were selected from wheat germplasm and crossed in the combinations of Hashim-08 × LU-26, Farid-06 × Shafaq, Parula × Blue Silver, and TD-1 × D-97603. Six basic populations (P_1, F_1, P_2, BC_1, BC_2, and F_2) of each cross were developed during the 2 crop seasons of 2009/2010 and 2010/2011. All the basic populations of each cross were planted in a randomized complete block design with 2 replications. The P_1, P_2, and F_1 populations and the back cross populations BC_1 and BC_2 were grown in 2 rows 4 m in length while 4 rows were used for the F_2 populations. The spaces within rows and between rows were 10 and 30 cm, respectively.

2.2. Trait measurement and statistical analysis

Data on duration of grain filling were recorded for each basic population and were calculated as the time between heading and physiological maturity. The data regarding period of grain filling were subjected to JSA designed for 6 basic populations as suggested by Gai and Wang (1998) and Gai et al. (2003, 2007) with 5 groups consisting of 24 different genetic models (Tables 1 and 2). Suitable genetic models for each cross combination were determined by maximum log of likelihood estimated through iterated expectation and conditional maximization (IECM) (Wang and Gai, 1997; McLachlan, 1988) and Akaike's information criterion (AIC) (Akaike, 1977) (Table 3). Further selection of a best-fit model was made on the basis of all nonsignificant or the least significant values of the 3 chi-square statistics U_1^2, U_2^2, and U_3^2. Two other important completely distribution-free tests, Smirnov's statistics (nW^2) and Kolmogorov's statistics (Dn), were used as goodness-of-fit tests to determine whether the selected model could sufficiently explain the data (Tables 4 and 5). If none of these 5 statistics were significant for a particular genetic model, then the data adequately fit the model (Gai and Wang, 1998). The data were analyzed using sin.exe software and the major gene–polygene mixed inheritance model to generate a joint analysis of multiple generations (Gai et al., 2003). In the case of the best-fit model, the values of the second-order genetic parameters as well as σ_{mg}^2 and σ_{pg}^2 for BC_1, BC_2, and F_2 were determined with the help of proposed formulae (Gai et al., 2003; Zhang et al., 2003). Under the second-order genetic parameters, the phenotypic variation (σ_p^2) was partitioned into genetic and environmental variation (σ_e^2) for each cross. The genetic component of variation in turn was subdivided into variation due to major genes (σ_{mg}^2) and variation due to polygenes (σ_{pg}^2). Based on Mather and Jinks (1982), the values from μ1 to μ69 exhibited different means of component distributions (Wang et al., 2001; Zhang et

Table 1. Estimable first-order genetic parameters in various genetic models (A-1 to E-6).

Models	Model groups, code, and implication of model type	First-order genetic parameters	
		Major genes	Polygenes
Group 1: 1 major gene			
A-1	Additive-dominant	*m*, *d*, *h*	σ^2
A-2	Additive	*m*, *d* (*h* = 0)	σ^2
A-3	Completely dominant	*m*, *d* (*h* = *d*)	σ^2
A-4	Completely negative-dominant	*m*, *d* (*h* = –*d*)	σ^2
Group 2: 2 major genes			
B-1	Additive-dominance-epistasis	*m*, *da*, *db*, *ha*, *hb*, *i*, *jab*, *jba*, *l*	σ^2
B-2	Additive-dominant	*m*, *da*, *db*, *ha*, *hb*, *i*, *jab*, *jba*, *l*	σ^2
B-3	Additive	*m*, *da*, *db* (*ha* = *hb* = 0)	σ^2
B-4	Equally additive	*m*, *d* (*da* = *db*, *ha* = *hb* = 0)	σ^2
B-5	Completely dominant	*m*, *da* (= *ha*), *db* (= *hb*)	σ^2
B-6	Equally dominant	*m*, *d* (= *da* = *db* = *ha* = *hb*)	σ^2
Group 3: Polygene			
C	Additive-dominant-epistasis	*M*	[d], [h], [*i*], [*j*], [l]
C-1	Additive-dominant	*M*	[d], [h]
Group 4: 1 major gene plus polygene			
D	Additive-dominant 1 major gene and additive-dominant-epistasis of polygene	*m*, *d*, *h*	[d], [h], [*i*], [*j*], [*l*]
D-1	Additive-dominant 1 major gene and additive-dominant polygene	*m*, *d*, *h*	[d], [h]
D-2	Additive 1 major gene and additive-dominant polygene	*m*, *d* (*h* = 0)	[d], [h]
D-3	Completely dominant 1 major gene and additive-dominant polygene	*m*, *d* (*h* = *d*)	[d], [h]
D-4	Completely negative-dominant 1 major gene and additive-dominant polygene	*m*, *d* (*h* = –*d*)	[d], [h]
Group 5: 2 major genes plus polygene			
E	Additive-dominant-epistatic of 2 major genes and additive-dominant-epistasis of polygene	*M1* ~ *m6*, *da*, *db*, *ha*, *hb*, *i*, *jab*, *jba*, *l*	[d], [h], [*i*], [*j*], [*l*]
E-1	Additive-dominant-epistasis of 2 major genes and additive-dominant polygene	*m*, *da*, *db*, *ha*, *hb*, *i*, *jab*, *jba*, *l*	[d], [h]
E-2	Additive-dominant 2 major genes and additive-dominant polygene	*m*, *da*, *db*, *ha*, *hb*, *i* = *jab* = *jba*, *l*	[d], [h]
E-3	Additive 2 major genes and additive-dominant polygene	*m*, *da*, *db*, *ha* = *hb* = 0	[d], [h]
E-4	Equally additive 2 major genes and additive-dominant polygene	*m*, *d* (= *da* = *db*), (*ha* = *hb* = 0)	[d], [h]
E-5	Completely dominant 2 major genes and additive-dominant polygene	*m*, *da* = *ha*, *db* = *hb*	[d], [h]
E-6	Equally dominant 2 major genes and additive-dominant polygene	*m*, *d* = *da* = *db* = *ha* = *hb*	[d], [h]

m: Population mean. *d*, [d]: Additive effect due to major gene(s) and polygenes, respectively. *h,* [h]: Dominant component due to major gene(s) and polygenes, respectively. *i*, [*i*]: Additive × additive component due to major gene(s) and polygenes, respectively. *jab*: *da* × *hb*: First major gene with additive × second major gene with dominant effect. *jba*: *db* × *ha*: Second major gene with additive × first major gene with dominant effect. [*j*]: Additive-dominance-epistasis. Source of different model groups and model types (Gai and Wang, 1998; Gai et al., 2003; Zhang et al., 2003).

Table 2. Frequency distribution of plant population in P_1, F_1, P_2, B_1, B_2, and F_2 for grain filling duration in 4 wheat crosses.

Crosses	Populations	Ranges of grain filling duration (days)								Size	Mean	Variance
		11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90			
Hashim-08 × LU-26	P_1	–	–	1	8	33	16	2	–	60	56.33	53.58
	F_1	3	8	20	35	17	7	–	–	90	44.15	120.98
	P_2	–	11	22	20	5	2	–	–	60	39.93	81.11
	BC_1	–	–	10	46	59	29	6	–	150	53.9	76.88
	BC_2	–	22	34	61	28	5	–	–	150	42.71	98.58
	F_2	14	55	33	34	37	21	5	1	200	41.23	260.41
Farid-06 × Shafaq	P_1	–	–	–	10	19	31	–	–	60	58.68	50.11
	F_1	–	–	18	30	35	7	–	–	90	49.03	73.65
	P_2	–	–	7	17	32	4	–	–	60	51.16	53.12
	BC_1	–	5	21	54	55	13	2	–	150	49.24	82.97
	BC_2	–	1	29	55	56	9	–	–	150	48.31	68.84
	F_2	–	7	35	66	61	22	6	2	200	49.69	132.06
Parula × Blue Silver	P_1	–	–	–	–	24	25	10	1	60	63.23	42.92
	F_1	–	–	1	10	29	39	11	–	90	60.82	68.23
	P_2	–	–	–	2	14	18	25	1	60	66.81	75.71
	BC_1	–	–	–	7	52	61	27	3	150	63.24	66.34
	BC_2	–	–	–	1	19	52	71	7	150	69.61	59.98
	F_2	–	–	2	12	41	94	44	7	200	64.92	81.95
TD-1 × D-97603	P_1	–	–	2	14	40	4	–	–	60	52.73	25.01
	F_1	–	–	4	13	30	9	24	10	90	62.58	186.13
	P_2	–	–	–	2	26	22	10	–	60	62.66	56.42
	BC_1	–	–	26	36	60	26	2	–	150	51.74	84.61
	BC_2	–	–	–	11	41	65	33	–	150	63.51	76.89
	F_2	–	–	1	20	79	66	31	3	200	61.51	81.31

al., 2003) regarding 6 generations, which were put in the formulae as suggested by Gai et al. (2003) for calculating first- and second-order genetic parameters (Tables 6 and 7).

3. Results

3.1. Duration of grain filling in wheat crosses

The frequency distribution of the plant population regarding duration of grain filling in 6 basic populations is presented in Table 2. For duration of grain filling, most of the populations derived from 4 crosses (Hashim-08 × LU-26, Farid-06 × Shafaq, Parula × Blue Silver, and TD-1 × D-97603) were in the ranges of 41–50, 51–60, and 61–70 days. However, these populations were followed by ones in the ranges of 31–40 days (Hashim-08 × LU-26 and Farid-06 × Shafaq) and 71–80 days (Parula × Blue Silver and TD-1 × D-97603). Few plants of all 6 populations were observed in the ranges of 11–20, 21–30, and 81–90 days for duration of grain filling. On average, in the cross Hashim-08 × LU-26, F_1 took fewer days than P_1 and BC_1 for grain filling, and more days than the other populations (P_1, BC_2, and F_2). In Farid-06 × Shafaq, the F_1 hybrid completed grain filling in fewer days than P_1 and P_2; however, it was the same as BC_1, BC_2, and F_2. In Parula × Blue Silver, the F_1 hybrid took fewer days than all other populations for grain filling. In the fourth cross, TD-1 × D-97603, the period of grain filling was equivalent to P_2, BC_2, and F_2; however, it took more days than P_1 and BC_1. In terms of the variance, the F_2 population in crosses Hashim-08 × LU-26, Farid-06 × Shafaq, and Parula × Blue Silver had the highest variance (81.95–260.41), which may have been due to segregation. However, in cross TD-1 × D-97603, F_1 (186.13) attained maximum variance above all other populations.

In crosses Hashim-08 × LU-26, Farid-06 × Shafaq, and Parula × Blue Silver, the F_1 hybrids were equally owned by the parental lines. However, in the F_1 from cross TD-1 × D-97603, the duration slightly increased over the parents'

Table 3. Maximum log of likelihood values and AIC values for grain filling duration under various genetic models estimated through the IECM algorithm*.

Cross 1: Hashim-08 × Lu-26			Cross 2: Farid-06 × Shafaq		
Models	Max. log of likelihood	AIC	Models	Max. log of likelihood	AIC
A-1	–2183.08	4374.16	A-1	–2183.06	4374.13
A-2	–2183.49	4372.99	A-2	–2184.15	4374.30
A-3	–2251.05	4508.13	A-3	–2183.61	4373.23
A-4	–2241.5	4489.08	A-4	–2184.44	4374.88
B-1	–2173.02	4366.04	B-1	–2134.06	4288.13
B-2	–2179.92	4371.85	B-2	–2145.04	4302.08
B-3	–2185.71	4379.42	B-3	–2161.05	4330.11
B-4	–2183.81	4373.63	B-4	–2184.20	4374.41
B-5	–2248.73	4505.47	B-5	–2168.72	4345.44
B-6	–2248.73	4503.47	B-6	–2183.76	4373.53
C	–2170.92	4361.84	C	–2142.02	4304.04
C-1	–2181.74	4377.49	C-1	–2153.30	4320.60
D	–2170.92	4365.84	D	–2142.01	4308.03
D-1	–2173.66	4365.33	D-1	–2146.75	4311.51
D-2	–2173.66	4363.33	D-2	–2146.76	4309.52
D-3	–2173.68	4363.37	D-3	–2152.27	4320.54
D-4	–2173.67	4363.35	D-4	–2146.68	4309.36
E	–2165.69	4367.39	E	–2132.50	4301.03
E-1	–2167.91	4365.82	E-1	–2133.58	4297.16
E-2	–2180.63	4383.24	E-2	–2145.63	4313.27
E-3	–2181.33	4380.67	E-3	–2143.75	4305.51
E-4	–2180.9	4377.81	E-4	–2153.05	4322.11
E-5	–2181.63	4381.27	E-5	–2153.28	4324.56
E-6	–2361.13	4738.26	E-6	–2728.68	5473.37
Cross 3: Parula × Blue Silver			Cross 4: TD-1 × D-97603		
Models	Max. log of likelihood	AIC	Models	Max. log of likelihood	AIC
A-1	–2134.45	4276.91	A-1	–2247.85	4503.71
A-2	–2152.37	4310.74	A-2	–2262.09	4530.18
A-3	–2133.68	4273.36	A-3	–2276.95	4559.91
A-4	–2165.92	4337.84	A-4	–2250.15	4506.31
B-1	–2107.30	4234.61	B-1	–2243.51	4507.01
B-2	–2124.33	4260.66	B-2	–2247.61	4507.23
B-3	–2177.78	4363.57	B-3	–2288.40	4584.81
B-4	–2156.71	4319.43	B-4	–2261.55	4529.11
B-5	–2123.59	4255.19	B-5	–2276.71	4561.43
B-6	–2145.87	4297.74	B-6	–2276.71	4559.43
C	–2111.95	4243.91	C	–2239.67	4499.34
C-1	–2140.73	4295.47	C-1	–2246.28	4506.57
D	–2112.43	4248.86	D	–2246.06	4508.12

Table 3. (Continued).

D-1	–2106.36	4230.72	D-1	–2245.33	4508.67
D-2	–2106.36	4228.72	D-2	–2245.33	4506.67
D-3	–2112.43	4240.87	D-3	–2245.61	4507.23
D-4	–2112.43	4240.87	D-4	–2245.61	4507.21
E	–2105.62	4247.24	E	–2242.06	4520.13
E-1	–2106.36	4242.72	E-1	–2242.34	4514.69
E-2	–2123.12	4268.25	E-2	–2247.60	4517.20
E-3	–2125.34	4268.68	E-3	–2247.41	4512.82
E-4	–2141.48	4298.97	E-4	–2247.64	4511.28
E-5	–2124.33	4266.66	E-5	–2247.63	4513.27
E-6	–2850.16	5716.33	E-6	–2363.40	4742.81

*AIC = Akaike's information criterion (Akaike, 1977). IECM = Iterated expectation and conditional maximization.

duration, which revealed that some parental-line dominant genes were responsible for the longer duration of this cross. The BC_1 and BC_2 populations showed a slight tendency towards their respective parents in all the crosses, whereas F_2 was equally distributed between the parental genotypes in all the crosses in segregating generations, indicating a mixed type of gene action by major and minor genes.

3.2. Genetic analysis of duration for grain filling in wheat crosses

According to the maximum log of likelihood values (Table 3) and goodness-of-fit tests (Table 4), model D was selected as the best-fit model for the cross Hashim-08 × LU-26. Model D showed a mix of 1 major gene and additive-dominance-epistasis of polygenes. As evident from the first-order genetic parameters (Tables 6 and 7), the population mean was 55.22. Positive additive effects (1.11) and dominant effects (0.82) observed in the cross revealed that the duration of grain filling was controlled by additive gene action with partial dominance by the major genes; however, no epistasis was found in this cross. The second-order genetic parameters revealed the phenotypic variation for duration of grain filling in segregating populations, i.e. BC_1, BC_2, and F_2 (Tables 6 and 7). The phenotypic variance was divided into genetic and environmental variances, while genetic variation was further subdivided into variation due to major genes and polygenes. In cross Hashim-08 × LU-26, the variation values due to polygenes for BC_1, BC_2, and F_2 were 0.00, 13.18, and 174.53, respectively. However, the variation values due to major genes were 6.90, 1.61, and 1.09 for BC_1, BC_2, and F_2, respectively. Similarly, for segregating generations including BC_1, BC_2, and F_2, the polygene heritabilities were 0.00%, 13.37%, and 67.02%, while the major gene heritabilities were 8.99%, 1.63%, and 0.80%, respectively (Table 7).

For the cross Farid-06 × Shafaq, the suitable model was B-1, which was selected on the basis of its maximum log of likelihood values, smallest values of AIC (Table 3), and goodness-of-fit tests (Table 4). The B-1 model indicates that duration of grain filling is controlled by additive-dominance-epistasis of 2 major genes. The mean value of the population was estimated as 53.48. The additive effect of the major genes was positive (10.46), whereas the additive effect due to a second major gene was negative (–6.89). Negative dominant effects due to major genes A and B were estimated as –12.25 and –1.57, respectively. The first major gene ratio was dominant and negative, whereas a positive and dominant ratio was observed for the second major gene. The additive × additive and dominant × dominant nonallelic interaction values were positive, i.e. 1.12 and 9.42, respectively. As evident from the second-order parameters, both the polygene variation and polygene heritability were zero because no polygenes were involved in controlling the duration of grain filling. Maximum dominant × dominant nonallelic interaction (9.42) and positive additive effects were observed due to major gene A (10.46), revealing that gene A has the maximum contribution in the additive-type control of the duration of grain filling. Moderate major gene heritabilities of 31.87%, 17.88%, and 57.19% were observed for BC_1, BC_2, and F_2, respectively, whereas the environmental variation was higher, indicating that the period of grain filling was under the influence of the environment and may vary in different environments (Tables 6 and 7).

In cross Parula × Blue Silver, the best-fit model for duration of grain filling was E, which was preferred on the basis of its maximum log of likelihood values, smallest

Table 4. Test for goodness-of-fit regarding grain filling duration of models C, D, and E. Asterisks represent statistical significance.

Cross 1 = Hashim-08 × Lu-26						
Models	Populations	U_1^2	U_2^2	U_3^2	nW^2	Dn
D	P_1	0.005 (0.94)	0.26 (0.61)	5.42*	0.18	0.13
	F_1	0.13 (0.71)	0.72 (0.39)	3.94*	0.12	0.08
	P_2	0.02 (0.88)	0.03 (0.84)	0.04 (0.83)	0.03	0.05
	BC_1	0.001 (0.97)	0.001 (0.98)	0.001 (0.97)	0.02	0.03
	BC_2	0.19 (0.66)	0.23 (0.62)	0.06 (0.79)	0.15	0.08
	F_2	0.23 (0.62)	0.004 (0.95)	4.54*	0.42	0.10
E	P_1	0.006 (0.94)	00.22 (0.63)	4.81*	0.17	0.13
	F_1	0.14 (0.71)	0.82 (0.36)	4.74*	0.13	0.08
	P_2	0.02 (0.88)	0.02 90.87)	0.003 (0.95)	0.03	0.05
	BC_1	0.001 (0.97)	0.001 (0.96)	0.07 (0.77)	0.02	0.03
	BC_2	0.08 (0.76)	0.04 (0.82)	0.07 (0.78)	0.11	0.07
	F_2	0.24 (0.62)	0.002 (0.96)	4.34*	0.42	0.10
E-1	P_1	0.04 (0.83)	0.52 (0.46)	4.39*	0.16	0.11
	F_1	0.007 (0.93)	0.42 (0.51)	5.17*	0.12	0.09
	P_2	0.09 (0.76)	0.07 (0.78)	0.005 (0.94)	0.03	0.06
	BC_1	1.47 (0.22)	1.22 (0.26)	0.07 (0.77)	0.16	0.06
	BC_2	2.86 (0.09)	2.54 (0.11)	0.03 (0.86)	0.48	0.12
	F_2	10.29**	6.55*	4.75*	1.39	0.15
Cross 2 = Farid-06 × Shafaq						
Models	Populations	U_1^2	U_2^2	U_3^2	nW^2	Dn
B-1	P_1	1.24 (0.26)	1.21 (0.27)	0.006 (0.93)	0.45	0.17
	F_1	0.14 (0.70)	0.78 (0.37)	4.34*	0.24	0.11
	P_2	0.36 (0.54)	0.26 (0.60)	0.07 (0.79)	0.15	0.11
	BC_1	0.35 (0.55)	1.05 (0.30)	3.29 (0.06)	0.21	0.09
	BC_2	0.29 (0.58)	0.29 (0.58)	0.004 (0.95)	0.07	0.06
	F_2	0.89 (0.34)	1.67 (0.19)	2.28 (0.13)	0.21	0.10
E	P_1	0.31 (0.57)	0.17 (0.67)	0.24 (0.62)	0.33	0.14
	F_1	0.17 (0.67)	0.71 (0.39)	3.11 (0.07)	0.22	0.11
	P_2	0.19 (0.66)	0.07 (0.77)	0.33 (0.56)	0.14	0.11
	BC_1	0.001 (0.97)	0.03 (0.84)	0.76 (0.38)	0.10	0.06
	BC_2	0.002 (0.96)	0.05 (0.81)	0.56 (0.45)	0.06	0.06
	F_2	0.008 (0.92)	0.006 (0.93)	0.002 (0.96)	0.07	0.06
E-1	P_1	0.54 (0.45)	0.41 (0.51)	0.08 (0.77)	0.36	0.15
	F_1	0.32 (0.56)	1.08 (0.29)	3.83*	0.25	0.12
	P_2	0.22 (0.63)	0.12 (0.72)	0.20 (0.64)	0.14	0.11
	BC_1	0.07 (0.78)	0.26 (0.61)	1.01 (0.31)	0.11	0.07
	BC_2	0.002 (0.96)	0.004 (0.94)	0.18 (0.66)	0.05	0.05
	F_2	0.02 (0.87)	0.06 (0.79)	0.19 (0.66)	0.07	0.07

***,**,*= Significant at $P \leq 0.001$, $P \leq 0.01$ and $P \leq 0.05$, respectively.

Table 5. Test for goodness of fit regarding grain filling duration of models C, D, E, E-1, and B-1. Asterisks represent statistical significance.

Cross 3 = Parula × Blue Silver						
Models	Populations	U_1^2	U_2^2	U_3^2	nW^2	Dn
D-1	P_1	0.09 (0.75)	0.41 (0.52)	1.82 (0.17)	0.13	0.12
	F_1	0.08 (0.77)	0.30 (0.57)	1.17 (0.27)	0.09	0.09
	P_2	0.47 (0.48)	1.17 (0.27)	2.74 (0.09)	0.34	0.16
	BC_1	0.11 (0.74)	0.11 (0.73)	0.008 (0.93)	0.10	0.07
	BC_2	0.27 (0.59)	0.24 (0.62)	0.006 (0.93)	0.20	0.10
	F_2	0.08 (0.77)	0.01 (0.90)	2.59 (0.11)	0.21	0.07
E	P_1	0.10 (0.75)	0.39 (0.53)	1.63 (0.20)	0.12	0.12
	F_1	0.08 (0.76)	0.33 (0.56)	1.39 (0.23)	0.09	0.09
	P_2	0.49 (0.48)	1.23 (0.26)	3.01 (0.08)	0.35	0.16
	BC_1	0.10 (0.74)	0.17 (0.67)	0.14 (0.69)	0.11	0.07
	BC_2	0.27 (0.59)	0.25 (0.61)	0.001 (0.96)	0.20	0.10
	F_2	0.05 (0.82)	0.02 (0.87)	2.23 (0.13)	0.19	0.07
E-1	P_1	0.20 (0.65)	0.37 (0.54)	0.49 (0.48)	0.12	0.12
	F_1	0.10 (0.74)	0.02 (0.88)	3.35 (0.06)	0.12	0.08
	P_2	0.008 (0.92)	0.33 (0.56)	3.77*	0.27	0.15
	BC_1	0.02 (0.86)	0.01 0.92)	0.06 (0.80)	0.09	0.06
	BC_2	3.13 (0.07)	2.06 (0.15)	1.22 (0.26)	0.56	0.14
	F_2	0.14 (0.69)	0.45 (0.49)	1.45 (0.22)	0.19	0.08
Cross 4 = TD-1 × D-97603						
Models	Populations	U_1^2	U_2^2	U_3^2	nW^2	Dn
E	P_1	12.10***	6.04*	13.25***	2.05	0.34
	F_1	2.51 (0.11)	10.30**	44.79***	1.23	0.26
	P_2	0.14 (0.70)	0.03 (0.86)	4.64*	0.19	0.13
	BC_1	11.40***	10.14**	0.11 (0.73)	1.11	0.65
	BC_2	0.18 (0.66)	0.18 (0.66)	0.004 (0.94)	0.16	0.07
	F_2	0.05 (0.82)	0.02 (0.88)	0.08 (0.77)	0.19	0.07
E-1	P_1	1.11 (0.29)	0.03 (0.84)	23.58***	0.90	0.23
	F_1	0.007 (0.93)	3.60 (0.05)	62.75***	1.42	0.21
	P_2	0.35 (0.54)	0.94 (0.32)	2.49 (0.11)	0.21	0.12
	BC_1	4.002*	3.84*	0.009 (0.92)	0.44	0.11
	BC_2	0.16 (0.68)	0.15 (0.69)	0.009 (0.99)	0.15	0.07
	F_2	3.56 (0.05)	2.42 (0.11)	1.17 (0.27)	0.47	0.09
C	P_1	0.008 (0.92)	1.73 (0.18)	31.51***	1.004	0.21
	F_1	0.07 (0.77)	1.68 (0.19)	39.49***	1.03	0.18
	P_2	0.06 (0.80)	0.80 (0.36)	6.84**	0.27	0.12
	BC_1	0.02 (0.86)	0.12 (0.72)	0.54 (0.45)	0.13	0.08
	BC_2	0.16 (0.68)	0.50 (0.47)	1.64 (0.19)	0.24	0.08
	F_2	0.05 (0.81)	0.00 (0.99)	0.86 (0.35)	0.22	0.08

***,**,*= Significant at $P \leq 0.001$, $P \leq 0.01$ and $P \leq 0.05$, respectively.

Table 6. Maximum likelihood estimates of component parameters regarding grain filling duration in 4 wheat crosses in their respective best fit model.

Variables	Hashim-08 × Lu-26	Farid-06 × Shafaq	Parula × Blue Silver	TD-1 × D-97603
	Model type: D	Model type : B-1	Model type: E	Model type: E-1
M_1	56.33	58.16	63.23	51.83
M_2	44.15	49.08	60.82	62.18
M_3	39.93	51.03	66.81	62.96
μ_{41}	54.04	58.16	61.82	57.47
μ_{42}	53.75	50.97	58.41	49.84
μ_{43}	–	40.85	65.05	50.01
μ_{44}	–	49.08	67.72	56.54
μ_{51}	43.67	49.08	68.11	65.46
μ_{52}	41.73	52.84	70.11	65.55
μ_{53}	–	41.61	70.11	65.61
μ_{54}	–	51.03	70.18	59.68
μ_{61}	41.93	58.16	59.99	61.93
μ_{62}	41.64	50.97	56.57	54.31
μ_{63}	39.73	69.71	67.71	68.87
μ_{64}	–	40.85	63.23	54.48
μ_{65}	–	49.08	65.89	61.08
μ_{66}	–	52.85	67.89	61.09
μ_{67}	–	35.03	67.71	69.46
μ_{68}	–	41.61	67.91	61.15
μ_{69}	–	51.03	67.97	55.22
Σ^2	83.79	56.53	59.36	80.93
σ_4^2	83.79	56.53	59.36	80.93
σ_5^2	96.97	56.53	59.36	80.93
σ_6^2	258.32	56.53	65.75	80.93

values of AIC (Table 3), and goodness-of-fit tests (Table 5). The model indicates a mix of 2 additive-dominant-epistatic major genes plus the additive-dominant-epistasis of polygenes. In this cross, the additive effects of both genes had the same negative value (–1.99). The dominant effects contributed by major genes A and B were estimated to be –0.29 and –3.61, respectively. The dominance ratios of genes A and B in this cross were 0.14 and 1.81, respectively (partial dominance due to major gene A and overdominance due to major gene B). The additive × additive effects of the major genes plus polygenes were recorded with a value of –1.87. The additive × dominant effects of gene A over gene B and of B over A were –3.67 and –0.34, respectively. The dominant × dominant type of nonallelic interaction value was 3.94. The second-order genetic parameters indicated that for duration of grain filling, phenotypic variation was observed in the segregating generations, i.e. BC_1, BC_2, and F_2. This phenotypic variance divided into genetic and environmental variance while genetic variation was further subdivided into variation due to major genes and polygenes. For BC_1, BC_2, and F_2, the variation values due to major genes were 12.20, 0.77, and 14.59, respectively, while the values due to polygenes were 5.21, 0.15, and 8.00, respectively. Similarly, maximum major gene heritabilities of 18.38%, 1.29%, and 17.80% were observed for segregating populations BC_1, BC_2, and F_2, respectively (Tables 6 and 7).

According to the maximum log of likelihood values (Table 3) and the goodness-of-fit tests (Table 5), the selected best-fit model for the cross TD-1 × D-97603 was E-1. The model revealed a mix of 2 major additive-dominance-epistatic genes plus additive-dominant polygenes. The population mean was recorded with the value of 62.69. The additive effects of the first and second

Table 7. Estimates of first- and second-order genetic parameters for grain filling duration in 4 wheat crosses.

Cross 1: Hashim-08 × LU-26 (model D)							
First-order parameter				Second-order parameter			
					BC_1	BC_2	F_2
m_1	55.22	D	1.11	σ_p^2	76.88	98.58	260.41
m_2	43.33	H	0.82	σ_{mg}^2	6.9	1.61	2.09
m_3	41.04			σ_e^2	83.79	83.79	83.79
m_4	52.93			σ_{pg}^2	0.00	13.18	174.53
m_5	42.84			h_{mg}^2(%)	8.99	1.63	0.80
m_6	40.82			h_{pg}^2(%)	0.00	13.37	67.02
Cross 2: Farid-06 × Shafaq (model B-1)							
First-order parameter				Second-order parameter			
					BC_1	BC_2	F_2
M	53.48	I	1.12	σ_p^2	82.97	68.84	132.06
d_a	10.46	j_{ab}	–11.4	σ_{mg}^2	26.4	12.31	75.53
d_b	–6.89	j_{ba}	6.51	σ_e^2	56.53	56.53	56.53
h_a	–12.25	L	9.42	σ_{pg}^2	0.00	0.00	0.00
h_b	–1.57			h_{mg}^2(%)	31.87	17.88	57.19
h_a/d_a	–1.17			h_{pg}^2(%)	0.00	0.00	0.00
h_b/d_b	0.23						
Cross 3: Parula × Blue Silver (model E)							
First-order parameter				Second-order parameter			
m_1	69.08	h_a	–0.29		BC_1	BC_2	F_2
m_2	60.77	h_b	–3.61	σ_p^2	66.34	60.0	82.00
m_3	64.69	h_a/d_a	0.14	σ_{mg}^2	12.2	0.77	14.59
m_4	67.67	h_b/d_b	1.81	σ_e^2	59.36	59.36	59.36
m_5	68.06	I	–1.87	σ_{pg}^2	5.21	0.15	8.00
m_6	61.21	j_{ab}	–3.67	h_{mg}^2(%)	18.38	1.29	17.80
d_a	–1.99	j_{ba}	–0.34	h_{pg}^2(%)	7.86	0.25	9.76
d_b	–1.99	L	3.94				
Cross 4: TD-1 × D-97603 (model E-1)							
First-order parameter				Second-order parameter			
					BC_1	BC_2	F_2
M	62.69	I	–5.30	σ_p^2	84.61	76.89	81.31
d_a	1.53	j_{ab}	–4.95	σ_{mg}^2	3.70	4.04	0.38
d_b	–2.96	j_{ba}	–5.13	σ_e^2	80.93	80.93	80.93
h_a	–6.09	L	9.36	σ_{pg}^2	0.00	0.00	0.00
h_b	–6.14	[d]	17.25	h_{mg}^2(%)	4.35	5.25	0.47
h_a/d_a	–3.89	[h]	2.36	h_{pg}^2(%)	0.00	0.00	0.00
h_b/d_b	2.07						

major genes were positive (1.53) and negative (–2.96), respectively. The dominant effects contributed by major genes A and B were estimated to be –6.09 and –6.14, respectively, indicating that no dominance was involved in controlling the duration of grain filling in this cross. The additive × additive epistatic and dominant × dominant components were –5.30 and 9.36, respectively. Under the mixed epistatic effect, and due to the major genes as well as the polygenes, the additive × dominant effects of the first and second major genes were –4.95 and –5.13, respectively. The additive and dominant effects of the polygenes were 17.51 and 2.36, respectively. In the second-order genetic parameters, for segregating populations BC_1, BC_2, and F_2, the major gene variation values were 3.70, 4.04, and 0.38, respectively. The major gene heritabilities (4.35%, 5.25%, and 0.47%, respectively) were higher than those of the polygenes, which were zero or close to zero (Tables 6 and 7).

4. Discussion

The frequency distribution of the plant population of the different populations of all the crosses shows that F_1, F_2, BC_1, and BC_2 were equally distributed in the parental lines. In cross Hashim-08 × LU-26, the duration of grain filling was under the genetic control of a mix of 1 major gene and the additive-dominance-epistasis of polygenes, indicating that period of grain filling was controlled by additive gene action with partial dominance of the single major gene. Additive gene action with partial dominance gene action has been reported for duration of grain filling in wheat (Sharma and Pawar, 2000; Kamaluddin et al., 2007b; Zare-Kohan and Heidari, 2012). Results suggested that yield improvement based on duration of grain filling can be improved using the existing genetic variability present in the germplasm and selection for period of grain filling could be done in later generations until the accumulation of the maximum favorable additive genes is achieved. Work by Kamaluddin et al. (2007a) showed that progress could be achieved through selection in the wheat crosses for either long or short periods of grain filling. In cross Farid-06 × Shafaq, the duration of grain filling was under the control of additive-dominance-epistasis of 2 major genes. Maximum dominant × dominant nonallelic interaction and positive additive effects were observed due to major gene A, revealing its maximum additive contribution in controlling duration of grain filling. Duration of grain filling is polygenically controlled because of the continuous variability in genotypes for period of grain filling in wheat (Xie and Zhang, 1981); however, additive and dominant gene action associated with duration of grain filling has been reported (Saadallah and Ghandorah, 2000; Yang et al., 2002). In previous studies, findings suggested a prominent role of additive genetic effects, although the dominance and epistasis effects were also involved in the expression of the duration of grain filling and other yield traits in wheat (Kamaluddin et al., 2007a).

A mix of 2 additive-dominant-epistatic major genes plus additive-dominant-epistasis of polygenes controlled the duration of grain filling in cross Parula × Blue Silver. Partial dominance due to major gene A and overdominance due to major gene B was recorded for the duration of grain filling in this cross. These observations are in complete accordance with the previous findings of Zare-Kohan and Heidari (2012) and Akram et al. (2008), as they also reported partial dominance and overdominance. Though the period of grain filling was controlled dominantly, selection in early generations may be useful for improvement of grain weight by effective grain filling. However, Kamaluddin et al. (2007b) mentioned that the magnitude of additive effects was lower than for dominance × dominance epistasis, which suggests that selection for a shorter duration of grain filling might be difficult. In contrast, the positive dominance effects might mean that such selections could be effective, and when the dominance and dominance × dominance estimates have a similar sign or different sign, the interaction is considered complementary or duplicate, respectively (Mather and Jinks, 1982). Przulj and Mladenov (1999) observed the presence of additive and dominance as well as epistatic interactions in the expression of duration of grain filling in wheat. Yang et al. (2002) reported that both additive and dominance gene effects were associated with duration of grain filling in wheat plants subjected to heat stress. In cross TD-1 × D-97603, the duration of grain filling was controlled by a mix of 2 major additive-dominance-epistatic genes plus additive dominant polygenes. The additive and dominant effects of the polygenes revealed that period of grain filling was mainly controlled by the epistatic behavior of major and minor genes. The polygene variation and heritability was negligible, almost zero. The environmental variation was high, indicating that period of grain filling was under the influence of the environment and may vary in different environments. However, in previous studies, minor environmental effects were reported for the expression of duration of grain filling in wheat (Mou and Kronstad, 1994; Kamaluddin et al., 2007b). The period of grain filling indicated the presence of an overdominance gene action that controlled this trait and other yield attributes (Akram et al., 2008). Stone and Nicolas (1994) also concluded that the period of grain filling was affected by environmental factors, especially temperature.

In this study, considerable variations were observed among the parental genotypes for duration of grain filling. The genotypes with the same physiological maturity differed in their grain filling duration because of differences

in time to anthesis. All the crosses demonstrated the importance of both additive and dominance gene effects, as well as epistasis. Due to segregation, the F_2 populations of all the crosses were leading in terms of maximum variance over the other populations, and the selection for duration of grain filling could be done in later generations until the accumulation of the maximum favorable additive genes is reached. The existing variation in wheat populations regarding period of grain filling indicates the possibility for breeding exploitation for the purpose of increasing yield; however, other factors such as leaf area, anthesis, spike density, and grains per spike should also be kept under consideration. Yield improvement based on duration of grain filling could be done by using the existing genetic variability found in the present populations and selection in later generations until the accumulation of the maximum favorable additive genes is achieved. However, the influence of the environment may vary and cannot be avoided.

References

Akaike H (1977). On the entropy maximum principle. In: Krishnaiah, PR, editor. Applications of Statistics. Amsterdam, the Netherlands: North-Holland, pp. 27–41.

Akram Z, Ajmal SU, Munir M, Shabir G (2008). Genetic determination of yield related attributes in bread wheat. Sarhad J Agric 24: 431–438.

Al-Khatib K, Paulsen GM (1984). Mode of high temperature injury to wheat during grain development. Physiol Plantarum 61: 363–368.

Bauer A, Frank AB, Black AL (1985). Estimation of spring wheat grain dry matter assimilation from air temperature. Agron J 77: 743–752.

Brdar MD, Kraljeviã-Balaliã MM, Kobiljski BD (2008). Grain filling parameters in high-yielding NS wheat cultivars. Proc Nat Sci Matica Srpska Novi Sad 114: 53–58.

Bruckner PL, Frohberg RC (1987). Rate and duration of grain fill in spring wheat. Crop Sci 27: 451–455.

Calderini DF, Reynolds MP (2000). Changes in grain weight as a consequence of de-graining treatments at pre- and post-anthesis in synthetic hexaploid lines of wheat (*T. durum* × *T. Tauschii*). Aust J Plant Physiol 27: 183–191.

Darroch BA, Baker RJ (1990). Grain filling in three spring wheat genotypes: statistical analysis. Crop Sci 30: 525–529.

Evans LT, Wardlaw IF, Fischer RA (1975). Wheat. In: Evans LT, editor. Crop Physiology: Some Case Histories. Cambridge, UK: Cambridge University Press, pp. 101–149.

Gai JY, Wang JK (1998). Identification and estimation of QTL model and its effects. Theor Appl Genet 97: 1162–1168.

Gai JY, Yonguin W, Xiaolei W, Shouyi C (2007). A comparative study on segregation analysis and QTL mapping of quantitative traits in plants with a case in soybean. Front Agric China 1: 1–7.

Gai JY, Zhang Y, Wang J (2003). Mixed genetic model for two major genes plus multi genes. In: Gai JY, editor. Genetic System of Quantitative Traits in Plants. 1st ed. Beijing, China: Science Press, pp. 277–285.

Gebeyehou G, Knott DR, Baker RJ (1982). Rate and duration of grain filling in durum wheat cultivars. Crop Sci 22: 337–340.

Kamaluddin, Singh RM, Abdin MZ, Khan MA, Alam T, Khan S, Prasad LC, Joshi AK (2007a). Inheritance of grain filling duration in spring wheat (*Triticum aestivum* L. em Thell). J Plant Biol 50: 504–507.

Kamaluddin, Singh RM, Prasad LC, Abdin MZ, Joshi AK (2007b). Combining ability analysis for grain filling duration and yield traits in spring wheat (*Triticum aestivum* L. em. Thell.). Genet Mol Biol 30: 411–416.

Keuls M, Garretsen F (1982). Statistical analysis of growth curves in plant breeding. Euphytica 31: 51–64.

Mather K, Jinks JL (1982). Biometrical Genetics. 2nd ed. London, UK: Chapman and Hall.

McLachlan GJ (1988). Mixture Models: Inference and Applications to Clustering. New York, NY, USA: Marcel Dekker.

Metzger DD, Czplewski SJ, Rasmusson DC (1984). Grain fill duration and yield in spring barley. Crop Sci 24: 1101–1105.

Monpara BA (2011). Grain filling period as a measure of yield improvement in bread wheat. Crop Improv 38: 1–5.

Mou B, Kronstad WE (1994). Duration and rate of grain filling in selected winter wheat populations. I. Inheritance. Crop Sci 34: 833–837.

Nass HG, Reiser B (1975). Grain filling and grain yield relationships in spring wheat. Can J Plant Sci 55: 673–678.

Przulj N, Mladenov N (1999). Inheritance of grain filling duration in spring wheat. Plant Breed 118: 517–521.

Saadallah MM, Ghandorah MO (2000). Inheritance of grain fill parameters in wheat under wheat stressful and non-stressful environments. Arab Univ J Agric Sci 8: 137–153.

Sharma PK, Pawar IS (2000). Genetic architecture of some wheat crosses through triple test cross method. Indian J Genet Plant Breed 48: 45–48.

Sofield I, Evans LT, Cook MG, Wardlaw IF (1977). Factors influencing the rate and duration of grain filling in wheat. Aust J Plant Physiol 4: 785–797.

Stone PJ, Nicolas ME (1994). Wheat cultivars vary widely in their responses of grain yield and quality to short periods of post-anthesis heat stress. Aust J Plant Physiol 21: 887–900.

Talbert LE, Lanning SP, Murphy RL, Martin JM (2001). Grain fill duration in twelve hard red spring wheat crosses: genetic variation and association with other agronomic traits. Crop Sci 41: 1390–1395.

Van Sanford DA (1985). Variation in kernel growth characters among soft red winter wheats. Crop Sci 25: 626–630.

Van Sanford DA, Mackown CT (1985). Cultivar differences in nitrogen remobilization during grain-fill in soft red winter wheat. Crop Sci 27: 295–300.

Wang J (1996). Studies on identification of major-polygene mixed inheritance of quantitative traits and estimation of genetic parameters. PhD, Nanjing Agricultural University, Nanjing, China.

Wang J, Gai JY (1997). Identification of major gene and polygene mixed inheritance and estimation of genetic parameters in F_2 progeny. Chin J Genet 24: 181–190.

Wang J, Podlich DW, Cooper M, DeLacy IH (2001). Power of the joint segregation analysis method for testing mixed major gene and polygene inheritance models of quantitative traits. Theor Appl Genet 103: 804–816.

Whan BR, Carlton GP, Anderson WK (1996). Potential for increasing rate of grain growth in spring wheat. I. Identification of genetic improvements. Aust J Agric Res 47: 17–31.

Wiegand CL, Cuellar JA (1981). Durations of grain filling and kernel weight as affected by temperature. Crop Sci 21: 95–101.

Wong ISL, Baker RJ (1986). Selection for time to maturity in spring wheat. Crop Sci 26: 1171–1175.

Xie RS, Zhang ZH (1981). Investigation of the genetic control of earliness in wheat based upon character correlation and heritability. Sci Agric Sin 3: 16–24.

Yang J, Sears RG, Gill BS, Paulsen GM (2002). Quantitative and molecular characterization of heat tolerance in hexaploid wheat. Euphytica 126: 275–282.

Zare-Kohan M, Heidari B (2012). Estimation for genetic parameters for maturity and grain yield in diallel crosses of five wheat cultivars using two different models. J Agric Sci 4: 74–85.

Zhang YM, Gai JY, Yang YH (2003). The EIM algorithm in the joint segregation analysis of quantitative traits. Genet Res 81: 157–163.