



Original Research Article

Genetic analysis of flag leaf area in the crosses of wheat (*Triticum aestivum* L.)

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Using joint segregation analysis (JSA) technique for flag leaf area, mixed inheritance analysis was performed in six basic generations (P_1 , F_1 , P_2 , BC_1 , BC_2 and F_2) of four bread wheat crosses viz., Hashim-08 × LU-26, Farid-06 × Shafaq, Parula × Blue Silver and TD-1 × D-97603 at Nuclear Institute for Food and Agriculture (NIFA), Peshawar, Pakistan during cropping season 2011-12. Results revealed that flag leaf area in cross Hashim-08 × LU-26 was found to be controlled by additive, dominance and epistasis of two major genes (Model B-1). In cross Farid-06 × Shafaq and Parula × Blue Silver the flag leaf area was under the control of mixed action of two major additive dominant epistatic genes plus additive dominant polygenes (Model E-1). In cross TD-1 × D-97603 the flag leaf area was under the control of mixed one major gene and additive dominance polygenes (Model D-1). The major gene variation (σ_{mg}^2) and heritability (h_{mg}^2) was higher than the polygene variation (σ_{pg}^2) and heritability (σ_{pg}^2) in case of cross Farid-06 × Shafaq and Parula × Blue Silver. Polygene variation and polygene heritability was zero because no polygenes were involved in case of Hashim-08 × LU-26 and the trait was mainly under the influence of major genes. On the other hand, in cross TD-1 × D-97603, polygene variation and polygene heritability was higher compared to major gene variation and heritability. Higher environmental variation for the trait suggests that it was highly under the influence of environment. The trait (flag leaf area) suggests early selection in cross Hashim-08 × LU-26, Farid-06 × Shafaq, Parula × Blue Silver and delayed selection till the accumulation of maximum favorable genes in cross TD-1 × D-97603.

Key words: *Triticum aestivum* L., flag leaf area, major genes plus polygenes inheritance

INTRODUCTION

Improved grain yield is the ultimate aim of cereal breeders. Yield increase has direct association with yield components and other closely related traits. Leaves, being the site of photosynthesis, have an obvious relation with grain yield (Sharma et al., 2003). The flag leaf has a major contribution towards the grain yield (about 40 %) and it is major contributor in the photosynthetic assimilates in wheat (Berdhal et al., 1972). Therefore size of flag leaf is important for higher yield in wheat.

Previous genetic studies of the inheritance of flag leaf area were mostly based on diallel analysis and generation mean analysis thus give no clue on estimates of different non allelic interactions, and can inflate the measure of additive and dominance components. The current technique (Joint segregation analysis) used in the study is able to determine individual effects up to two major genes and the collective epistatic effects of polygenes (Wang et al., 2001). To breed physiologically productive and efficient wheat, knowledge

of the different epistatic interactions operating in the inheritance of the trait would be helpful (Sharma et al., 2003).

The present study was thus designed to evaluate the genetic behavior and inheritance pattern of flag leaf area, and to select the efficient genotypes in terms of photosynthesis, for future breeding strategies.

MATERIALS AND METHODS

Eight genetically diverse parents were selected 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 2009-10 and 2010-11. The six basic populations of each cross combination planted in randomized complete block (RCB) design using two replications. Two rows of four meters length were planted in case of parents (P_1 , P_2) and F_1 populations, whereas three rows each for back cross populations (BC_1 , BC_2) and four rows for F_2 populations in each replication. The plant to plant and row to row spacing was 10 and 30 cm, respectively.

Flag leaf area

From each basic population, the flag leaf area was measured with automatic light reflecting leaf area meter (model. Li-3100).

Data recording and analysis

The data related to flag leaf area were subjected to the five groups consisting of 24 different genetic models of the Joint Segregation Analysis (JSA) designed for the six basic populations using standard methods (Gai and Wang, 1998; Gai et al., 2003, 2007) (Table 1). Suitable genetic models for each cross combination determined by using maximum log of likelihood estimates (McLachlan, 1988; Wang and Gai, 1997) and Akaike's information criterion (Akaike, 1977). Further selection of best fit model was made on the basis of all non significant or least number of significant values of the three chi-square statistics i.e. U_1^2 , U_2^2 and U_3^2 (Table 4 and 5). Two other important completely distribution free tests i.e. Smirnov's statistics (nW^2) and Kolmogorove's statistics (Dn) were used as goodness of fit tests to determine whether the selected model sufficiently explains the data (Table 4 and 5). If, for a particular genetic model, none of these five statistics were significant, then the data adequately fit the model (Gai and Wang, 1998). The data were analyzed by using sin.exe software and the major gene-polygenes 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 worked out with

the help of proposed formulae (Gai et al., 2003; Zhang et al., 2003). Under the second order genetic parameters (Table 1), the phenotypic variation (σ_p^2) partitioned into genetic and environmental variation (σ_e^2) for each cross. The genetic component of variation in turn subdivided into variation due to major genes (σ_{mg}^2) and polygenes (σ_{pg}^2). Based on Mather and Jinks (1982), the values from μ_1 to μ_69 exhibited different means of component distributions (Wang et al., 2001; Zhang et al., 2003) regarding six generations which are to be put in the formulae as suggested by Gai et al. (2003) for calculating 1st and 2nd order genetic parameters (Table 6).

RESULTS

Occurance of flag leaf area in various crosses

The data of frequency distribution of plant population regarding flag leaf area in six generations of four different wheat crosses are presented in Table 2. Most of the plant population in four crosses and their six basic generations were recorded in the range of 36-40, 41-45 and 46-50 cm² flag leaf area, followed by 31-35 and 51-55 cm² in all the crosses. Less number of the plants of all the populations was observed in the range of 26-30 and 56-60 cm² flag leaf area. On average F_1 exhibited almost equal flag leaf area to P_1 and less than P_2 and other populations in cross Hashim-08 × LU-26. The F_1 in cross Hashim-08 × LU-26 and Parula × Blue Silver has slight tendency towards parent 1 with smaller flag leaf area, whereas in cross Farid-06 × Shafaq and TD-1 × D-97603, it was equally distributed between the corresponding parents. In cross TD-1 × D-97603, slight increases in the flag leaf area over both the parents was observed indicating that dominant genes may be involved in controlling the trait. BC_1 and BC_2 showed little tendency towards corresponding parents involved in cross Hashim-08 × LU-26 and Parula × Blue Silver, whereas in cross Farid-06 × Shafaq and TD-1 × D-97603, it was equally distributed among parents. F_2 was also equally distributed among the parents and transgressive segregation on both upper and lower extremity was found in all the crosses which explain that mixed type of interaction of major and polygenes are present in controlling the trait.

Genetic analysis of flag leaf area

The best fit genetic model according to the *maximum log of likelihood* values, *Akaike's information criterion* (Table 3) and *goodness of fit* tests (Table 4) for cross Hashim-08 × LU-26 was found to be model B-1 which indicates additive, dominance and epistasis of two major genes (Table 1). The first and second order genetic parameters calculated from component parameters (Table 6) are presented in Table 7. The population mean was estimated as 39.47. The additive effect due to the first major gene was negative and

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: One 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: Two 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: One major gene plus polygene			
D	Additive-dominant one major gene and additive-dominant-epistasis of polygene	m, d, h	$[d], [h], [i], [j], [l]$
D-1	Additive-dominant one major gene and additive-dominant polygene	m, d, h	$[d], [h]$
D-2	Additive one major gene and additive-dominant polygene	$m, d, (h = 0)$	$[d], [h]$
D-3	Completely dominant one major gene and additive-dominant polygene	$m, d (h = d)$	$[d], [h]$
D-4	Completely negative dominant one major gene and additive-dominant polygene	$m, d (h = -d)$	$[d], [h]$
Group 5: Two major genes plus polygene			
E	Additive-dominant-epistatic of two major genes and additive-dominant-epistasis of polygene	$m1 \sim m6, da, db, ha, hb, i, jab, jba, l$	$[d], [h], [i], [j], [l]$
E-1	Additive-dominant epistasis of two major genes and additive-dominant polygene	$m, da, db, ha, hb, i, jab, jba, l$	$[d], [h]$
E-2	Additive-dominant two major genes and additive-dominant polygene	$m, da, db, ha, hb, i = jab = jba, l$	$[d], [h]$
E-3	Additive two major genes and additive-dominant polygene	$m, da, db, ha = hb = 0$	$[d], [h]$
E-4	Equally additive two major genes and additive-dominant polygene	$m, d (= da = db, (ha = hb = 0))$	$[d], [h]$
E-5	Completely dominant two major genes and additive-dominant polygene	$m, da = ha, db = hb$	$[d], [h]$
E-6	Equally dominant two 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 \times additive component due to major gene(s) and polygenes, respectively. $jab: da \times hb$: First major gene with additive \times second major gene with dominant effect. $jba: db \times ha$: Second major gene with additive \times 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).

estimated as -6.80, whereas that of second major gene was positive and recorded as 3.89. The additive \times additive (i) epistatic interaction was estimated as 0.88. The dominant \times dominant non allelic interaction (l) was negative and recorded as -1.70. The dominant \times additive interaction due to the first and second major gene i.e. J_{ab} and J_{ba} was recorded as 0.61 and -5.46, respectively. The major gene heritability estimated in segregating generations BC₁, BC₂ and F₂ was 39.24, 16.60 and 13.14, respectively, whereas the polygene variation and heritability was zero because no polygenes were involved according to the best fit genetic model B-1.

In case of cross, Farid-06 \times Shafaq and cross Parula \times Blue Silver, E-1 was the best fit model according to the maximum log of likelihood values, Akaike's information

criterion (Table 3) and goodness of fit tests (Table 4). Model E-1 represented mixed two major additive-dominance epistatic genes plus additive-dominant polygenes (Table 1). It is apparent from the first order genetic parameters (calculated from component parameters (Table 6)) that the additive effect (d_a & d_b) on flag leaf area due to first and second major gene (A & B) was 3.30 & -0.7 in cross Farid-06 \times Shafaq and -2.6 and -5.6 in cross Parula \times Blue Silver (Table 7). The favorable dominant effect (h_a & h_b) due to the two major genes (A & B) was 5.7 and 2.4 in case of cross Farid-06 \times Shafaq, whereas negative dominant effect was observed and estimated as -4.0 and -7.7 in case of cross Parula \times Blue Silver (Table 7). Negative additive \times additive interaction by the major genes was recorded as -6.9 and -11.2 for cross Farid-06 \times Shafaq and cross Parula \times Blue

Table 2. Frequency distribution of plant population of flag leaf area in P₁, F₁, P₂, BC₁, BC₂ and F₂ of four bread wheat crosses

Cross	Generation	Range of flag leaf area										Size	Mean	Variance
		20-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70			
Hashim-08 × LU-26	P ₁	-	5	15	24	16	-	-	-	-	-	60	56.33	53.58
	F ₁	-	13	22	30	25	-	-	-	-	-	90	44.15	120.98
	P ₂	-	-	-	16	24	20	-	-	-	-	60	39.93	81.11
	BC ₁	-	27	33	55	35	-	-	-	-	-	150	53.9	76.88
	BC ₂	-	-	16	44	62	28	-	-	-	-	150	42.71	98.58
	F ₂	7	23	40	48	52	22	8	-	-	-	200	41.23	260.41
Farid-06 × Shafaq	P ₁	-	-	-	15	20	15	10	-	-	-	60	58.68	50.11
	F ₁	-	-	-	21	34	20	15	-	-	-	90	49.03	73.65
	P ₂	-	-	-	10	17	25	8	-	-	-	60	51.16	53.12
	BC ₁	-	-	-	23	37	45	38	7	-	-	150	49.24	82.97
	BC ₂	-	-	-	23	40	60	27	-	-	-	150	48.31	68.84
	F ₂	-	-	13	34	46	57	23	13	14	-	200	49.69	132.06
Parula × Blue Silver	P ₁	-	-	13	21	16	10	-	-	-	-	60	63.23	42.92
	F ₁	-	-	15	25	31	19	-	-	-	-	90	60.82	68.23
	P ₂	-	-	-	12	18	20	10	-	-	-	60	66.81	75.71
	BC ₁	-	13	24	36	42	35	-	-	-	-	150	63.24	66.34
	BC ₂	-	-	-	21	39	32	38	20	-	-	150	69.61	59.98
	F ₂	-	9	25	38	37	29	21	20	11	10	200	64.92	81.95
TD-1 × D-97603	P ₁	-	-	-	14	22	18	6	-	-	-	60	52.73	25.01
	F ₁	-	-	-	19	10	23	27	11	-	-	90	62.58	186.13
	P ₂	-	-	-	10	20	21	9	-	-	-	60	62.66	56.42
	BC ₁	-	-	8	28	34	47	33	-	-	-	150	51.74	84.61
	BC ₂	-	-	-	27	33	45	30	15	-	-	150	63.51	76.89
	F ₂	-	-	10	35	41	54	30	18	12	-	200	61.51	81.31

Silver, respectively. The dominant × dominant interaction in both the crosses was positive and estimated as 1.705 and 3.6 in cross Farid-06 × Shafaq and cross Parula × Blue Silver, respectively. The additive and dominant effects due to polygenes i.e. [d] and [h] were recorded as 16.5 and 0.1 for cross Farid-06 × Shafaq, whereas for cross Parula × Blue Silver these were 20.0 and -4.7, respectively. As apparent from the second order genetic parameters (Table 7), the major gene heritability in segregating generations BC₁, BC₂ and F₂ was estimated as 31.6, 11.6, 47.0% and 39.6, 40.4, 77.9% for cross Farid-06 × Shafaq and Parula × Blue Silver, respectively. The major gene variation (σ_{mg}^2) and heritability (h_{mg}^2) was higher than the polygene variation (σ_{pg}^2) and heritability (σ_{pg}^2) in case of cross Farid-06 × Shafaq and cross Parula × Blue Silver.

The best fit genetic model for flag leaf area in cross TD-1 × D-97603 was D-1 indicating mixed one major-gene and additive-dominance polygenes (Table 1). The population mean estimated for this cross was 45.01. The 1st and 2nd order genetic parameters (Table 7) were calculated from the component parameters given in Table 6. Negative additive (*d*) and dominant (*h*) effect due to single major gene was estimated as -4.15 and -2.42, respectively. Both the additive[d] and dominant [h] effects due to polygene were positive and estimated as 3.29 and 5.27, respectively. The second order genetic parameters explain the

phenotypic variance in segregating generations BC₁, BC₂ and F₂. This phenotypic variation is divided into environmental and genetic variation, while the genetic variation is further divided into variation due to major genes and polygenes. From the second order genetic parameters it is evident that polygene variation and polygene heritability was higher compared to major gene variation and heritability (Table 7).

DISCUSSION

The gene action regarding flag leaf area was determined in four crosses of bread wheat. In cross Hashim-08 × LU-26, flag leaf area was controlled by additive, dominance and epistasis of two major genes (model B-1). According to the best fit model, no polygenes were involved in the expression of the trait. The trait was mainly contributed by the additive × additive digenic epistatic type of gene action with the over dominance effect of gene A and additive effect of gene B. Partial dominance with additive type of gene action has also been reported by Munis et al., 2012 which revealed that selection in early generations may lead to significant improvement in this traits. In previous research Saleem et al., 2005 also reported additive type of gene action with partial dominance which is in close accordance

Table 3. Maximum log likelihood values and AIC values for flag leaf area under various genetic models estimated through 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	-2240.53	4489.07	A-1	-2291.96	4591.92
A-2	-2246.61	4499.22	A-2	-2292.08	4590.16
A-3	-2240.58	4487.16	A-3	-2292.09	4590.18
A-4	-2272.59	4551.19	A-4	-2290.96	4587.92
B-1	-2214.82	4449.65	B-1	-2261.59	4543.18
B-2	-2222.89	4457.79	B-2	-2264.71	4541.42
B-3	-2298.31	4604.62	B-3	-2275.78	4559.56
B-4	-2251.28	4508.57	B-4	-2292.08	4590.16
B-5	-2241.009	4490.01	B-5	-2283.38	4574.77
B-6	-2241.84	4489.69	B-6	-2292.09	4590.18
C	-2215.61	4451.23	C	-2258.17	4536.35
C-1	-2220.58	4455.17	C-1	-2264.03	4542.06
D	-2215.69	4455.39	D	-2258.2	4540.41
D-1	-2216.63	4451.26	D-1	-2258.15	4534.3
D-2	-2216.63	4449.26	D-2	-2258.15	4532.3
D-3	-2216.64	4449.28	D-3	-2258.2	4532.4
D-4	-2215.57	4447.14	D-4	-2261.43	4538.87
E	-2212.89	4461.78	E	-2258.2	4552.41
E-1	-2213.29	4456.59	E-1	-2255.34	4540.68
E-2	-2220.52	4463.04	E-2	-2263.98	4549.97
E-3	-2220.41	4458.82	E-3	-2257.7	4533.41
E-4	-2220.6	4457.2	E-4	-2264.08	4546.16
E-5	-2220.61	4459.21	E-5	-2264.08	4546.16
E-6	-2414.16	4844.32	E-6	-2426.2	4868.41
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	-2421.86	4851.73	A-1	-2330.08	4668.17
A-2	-2429.96	4865.92	A-2	-2338.2	4682.4
A-3	-2424.29	4854.59	A-3	-2340.26	4686.52
A-4	-2437.13	4880.27	A-4	-2334.86	4675.73
B-1	-2360.39	4740.79	B-1	-2318.35	4656.71
B-2	-2383.14	4778.28	B-2	-2324.04	4660.09
B-3	-2408.08	4824.17	B-3	-2375.23	4758.46
B-4	-2438.89	4883.78	B-4	-2338.86	4682.72
B-5	-2398.51	4805.03	B-5	-2336.47	4680.95
B-6	-2438.78	4883.56	B-6	-2340.26	4686.52
C	-2369.76	4759.52	C	-2321.11	4662.22
C-1	-2398.86	4811.73	C-1	-2321.44	4656.88
D	-2369.76	4763.52	D	-2321.11	4666.21
D-1	-2358.003	4734.006	D-1	-2318.88	4655.77
D-2	-2358.001	4732.003	D-2	-2318.88	4653.77
D-3	-2369.94	4755.89	D-3	-2321.21	4658.43
D-4	-2368.85	4753.71	D-4	-2321.21	4658.43
E	-2360.56	4757.13	E	-2317.37	4670.75
E-1	-2357.55	4745.11	E-1	-2317.86	4665.72
E-2	-2385.42	4792.85	E-2	-2320.27	4662.54
E-3	-2376.28	4770.56	E-3	-2321.42	4660.85
E-4	-2398.81	4813.63	E-4	-2321.44	4658.88
E-5	-2389.13	4796.27	E-5	-2320.68	4659.36
E-6	-2510.71	5037.42	E-6	-2440.17	4896.34

Table 4. Test for goodness of fit regarding flag leaf area of models C, D and E

Cross-1 = Hashim-08 × Lu-26						
Models	Generations	U_1^2	U_2^2	U_3^2	nW^2	Dn
E	P ₁	0.064 (0.80)	0.53 (0.46)	3.82*	0.15 (>0.05)	0.12 (>0.05)
	F ₁	0.12 (0.71)	1.31 (0.25)	10.21**	0.29 (>0.05)	0.11 (>0.05)
	P ₂	0.003 (0.95)	0.012 (0.91)	0.43 (0.50)	0.04*	0.06*
	BC ₁	0.15 (0.69)	0.22 (0.63)	0.14 (0.70)	0.15 (>0.05)	0.08*
	BC ₂	0.10 (0.75)	0.03 (0.86)	0.28 (0.59)	0.11 (>0.05)	0.08*
	F ₂	0.02 (0.87)	0.01 (0.97)	0.21 (0.64)	0.09*	0.06*
E-1	P ₁	0.07 (0.77)	0.57 (0.44)	3.83 (0.052)	0.16 (>0.05)	0.12 (>0.05)
	F ₁	0.15 (0.69)	1.37 (0.24)	10.22**	0.29 (>0.05)	0.11*
	P ₂	0.004 (0.94)	0.010 (0.91)	0.44 (0.50)	0.04*	0.06*
	BC ₁	0.004 (0.94)	0.017 (0.89)	0.07 (0.78)	0.12 (>0.05)	0.07*
	BC ₂	0.009 (0.92)	0.001 (0.97)	0.25 (0.61)	0.09*	0.07*
	F ₂	0.19 (0.66)	0.34 (0.55)	0.40 (0.52)	0.107*	0.07*
B-1	P ₁	0.03 (0.85)	0.43 (0.51)	3.78*	0.15	0.12 (>0.05)
	F ₁	0.09 (0.75)	1.19 (0.27)	10.15**	0.28	0.1 (>0.05)
	P ₂	0.06 (0.79)	0.007 (0.93)	0.42 (0.51)	0.05*	0.07*
	BC ₁	0.17 (0.67)	0.31 (0.57)	0.35 (0.55)	0.13 (>0.05)	0.08*
	BC ₂	0.00 (0.99)	0.08 (0.76)	1.52 (0.21)	0.11 (>0.05)	0.07*
	F ₂	0.24 (0.61)	0.004 (0.94)	2.78 (0.09)	0.19 (>0.05)	0.09*
Cross-2 = Farid-06 × Shafaq						
Models	Generations	U_1^2	U_2^2	U_3^2	nW^2	Dn
E-1	P ₁	0.12 (0.72)	0.03 (0.85)	4.44*	0.19 (>0.05)	0.11 (>0.05)
	F ₁	0.28 (0.59)	0.01 (0.91)	6.16*	0.33 (>0.05)	0.12 (>0.05)
	P ₂	0.00 (0.99)	0.07 (0.78)	1.31 (0.25)	0.08*	0.1 (>0.05)
	BC ₁	0.004 (0.95)	0.03 (0.86)	0.20 (0.65)	0.13 (>0.05)	0.07*
	BC ₂	0.04 (0.84)	0.03 (0.84)	0.00 (0.98)	0.21 (>0.05)	0.1 (>0.05)
	F ₂	0.10 (0.74)	0.20 (0.65)	0.28 (0.59)	0.14 (>0.05)	0.06*
E-3	P ₁	1.08 (0.29)	0.18 (0.66)	5.35*	0.3 (>0.05)	0.15 (>0.05)
	F ₁	0.34 (0.55)	0.005 (0.94)	6.47*	0.34 (>0.05)	0.12*
	P ₂	0.43 (0.51)	0.90 (0.34)	1.56 (0.21)	0.13*	0.13*
	BC ₁	2.32 (0.12)	2.17 (0.14)	0.00 (0.99)	0.34 (>0.05)	0.11*
	BC ₂	0.44 (0.50)	0.55 (0.45)	0.15 (0.69)	0.22 (>0.05)	0.13*
	F ₂	0.10 (0.74)	0.04 (0.82)	0.14 (0.69)	0.17 (>0.05)	0.09*
C	P ₁	0.05 (0.81)	0.01 (0.91)	1.78 (0.18)	0.13 (>0.05)	0.1*
	F ₁	0.12 (0.72)	0.002 (0.96)	2.43 (0.11)	0.23 (>0.05)	0.11*
	P ₂	0.003 (0.95)	0.02 (0.86)	0.21 (0.64)	0.05*	0.09*
	BC ₁	0.003 (0.95)	0.16 (0.68)	1.98 (0.15)	0.19 (>0.05)	0.11*
	BC ₂	0.13 (0.71)	0.23 (0.62)	0.27 (0.60)	0.24 (>0.05)	0.1*
	F ₂	0.32 (0.57)	0.29 (0.58)	0.001 (0.98)	0.23 (>0.05)	0.1*

with these findings. In cross Farid-06 × Shafaq and Parula × Blue Silver the flag leaf area was under the control of mixed two major additive-dominance epistatic genes plus additive-dominant polygenes (model E-1). In cross Farid-06 × Shafaq, favorable dominant effects due to major gene A and B and additive effects due to polygenes [d] shows that flag leaf area is controlled by epistasis with over dominance type of gene action. Over dominance type of gene action was also reported by Ajmal et al., 2011. In cross Parula ×

Blue Silver, flag leaf area was mainly under the influence of additive effects due to polygenes [d]. The major gene heritability and variation in cross Farid-06 × Shafaq and Parula × Blue Silver was higher than polygene variation and heritability. This is because of epistasis of major genes and minor genes with the maximum contribution of major genes. In cross TD-1 × D-97603, flag leaf area was controlled by mixed one major gene and additive dominance polygenes (model D-1). The additive [d] and

Table 5. Test for goodness of fit regarding flag leaf area of models C, D, E, E-1 and B-1.

Cross-3 = Parula × Blue silver						
Models	Generations	U_1^2	U_2^2	U_3^2	nW^2	Dn
E-1	P ₁	0.03 (0.84)	0.17 (0.67)	5.86*	0.22	0.13
	F ₁	0.05 (0.81)	0.83 (0.35)	7.64**	0.24	0.11
	P ₂	0.02 (0.88)	0.22 (0.63)	1.78 (0.18)	0.08*	0.1
	BC ₁	0.68 (0.40)	0.83 (0.36)	0.21 (0.64)	0.17	0.09*
	BC ₂	0.00 (0.98)	0.00 (0.99)	0.005 (0.94)	0.08*	0.05*
	F ₂	1.40 (0.23)	0.80 (0.37)	1.02 (0.31)	0.21	0.08*
D-1	P ₁	0.02 (0.88)	0.45 (0.50)	4.49*	0.18	0.12*
	F ₁	0.20 (0.64)	1.13 (0.28)	6.22 (0.01)	0.23	0.12
	P ₂	0.007 (0.93)	0.12 (0.72)	1.20 (0.27)	0.07*	0.1*
	BC ₁	0.02 (0.88)	0.004 (0.95)	0.10 (0.74)	0.09*	0.06*
	BC ₂	0.03 (0.85)	0.004 (0.94)	0.18 (0.66)	0.09*	0.06*
	F ₂	0.002 (0.96)	0.01 (0.90)	0.41 (0.52)	0.05*	0.05*
D-2	P ₁	0.02(0.88)	0.44 (0.50)	4.42*	0.18	0.12
	F ₁	0.20 (0.65)	1.11 (0.29)	6.11*	0.22	0.12
	P ₂	0.007 (0.93)	0.12 (0.72)	1.16 (0.27)	0.07*	0.1*
	BC ₁	0.02(0.88)	0.003 (0.95)	0.11 (0.73)	0.09*	0.06*
	BC ₂	0.03 (0.86)	0.003 (0.95)	0.19 (0.65)	1	0.06*
	F ₂	0.002 (0.96)	0.01 (0.90)	0.41 (0.51)	0.05*	0.05*
Cross-4 = TD-1 × D-97603						
Models	Generations	U_1^2	U_2^2	U_3^2	nW^2	Dn
E	P ₁	0.01 (0.91)	0.002 (0.96)	0.05 (0.81)	0.05*	0.07*
	F ₁	0.14 (0.70)	2.29 (0.13)	21.09***	0.51	0.15
	P ₂	0.007 (0.93)	0.04 (0.83)	0.26 (0.60)	0.05	0.1
	BC ₁	0.21 (0.64)	0.21 (0.64)	0.005 (0.94)	0.14	0.007*
	BC ₂	0.01 (0.89)	0.05 (0.81)	0.20 (0.65)	0.08*	0.07*
	F ₂	0.06 (0.80)	0.008 (0.92)	0.37 (0.53)	0.07*	0.06*
E-1	P ₁	0.26 (0.60)	0.24 (0.62)	0.00 (0.98)	0.07*	0.09*
	F ₁	0.02 (0.88)	1.42 (0.23)	17.77***	0.43	0.15
	P ₂	0.00 (0.99)	0.03 (0.85)	0.55 (0.45)	0.06*	0.09*
	BC ₁	1.17 (0.27)	1.42 (0.23)	0.35 (0.55)	0.3	0.11
	BC ₂	0.15 (0.69)	0.12 (0.72)	0.01 (0.90)	0.1	0.08*
	F ₂	0.04 (0.82)	0.11 (0.73)	0.25 (0.61)	0.07*	0.05*
D-1	P ₁	0.02 (0.87)	0.001 (0.97)	0.53 (0.46)	0.05*	0.07*
	F ₁	0.26 (0.61)	1.81 (0.17)	11.6***	0.36	0.13
	P ₂	0.00 (0.98)	0.12 (0.72)	1.85 (0.17)	0.09	0.1
	BC ₁	0.14 (0.70)	0.33 (0.56)	0.71 (0.39)	0.21	0.08
	BC ₂	0.03 (0.84)	0.007 (0.93)	1.16 (0.28)	0.11	0.07*
	F ₂	0.003 (0.95)	0.01 (0.90)	0.06 (0.79)	0.08	0.06*

dominant [h] effect due to polygenes was positive showing epistatic type of gene action between major and minor genes. Partial dominance with additive type of gene action was also previously reported by Munis et al., 2012 which

revealed that selection in early generations may lead to effective improvement in this trait. The environmental variation in all the crosses was higher indicating that the trait is highly influenced by environmental fluctuations.

Table 6. Maximum likelihood estimates of component parameters regarding flag leaf area in four 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: B-1	Model Type : E-1	Model Type: E-1	Model Type: D-1
μ ₁	37.44	44.92	39.82	44.007
μ ₂	36.89	44.9	41.05	47.99
μ ₃	43.25	45.99	45.42	45.54
μ ₄₁	37.44	48.55	36.27	45.43
μ ₄₂	30.54	45.7	35.24	46.56
μ ₄₃	39.77	52.3	42.8	
μ ₄₄	36.89	41.28	44.61	
μ ₅₁	36.89	48.46	42.16	46.42
μ ₅₂	42.91	46.42	52.26	47.64
μ ₅₃	42.91	46.42	52.26	
μ ₅₄	43.25	42.43	44.31	
μ ₆₁	37.44	52.14	35.04	43.94
μ ₆₂	30.54	49.29	34.01	44.05
μ ₆₃	27.91	41.75	62.69	55.21
μ ₆₄	39.77	55.89	41.58	
μ ₆₅	36.89	44.87	43.39	
μ ₆₆	42.91	42.83	53.49	
μ ₆₇	49.28	41.75	62.69	
μ ₆₈	42.91	42.83	53.49	
μ ₆₉	43.25	38.84	45.53	
σ ²	19.46	21.78	23.21	32.41
σ ₄ ²	19.46	21.78	23.21	36.68
σ ₅ ²	19.46	21.78	23.21	36.69
σ ₆ ²	19.46	33.02	23.21	34.86

Table 7. Estimates of first and second order genetic parameters for flag leaf area in four wheat crosses.

Cross-1: Hashim-08 × LU-26 (model B-1)							
First order parameter				2nd order parameter			
					BC ₁	BC ₂	F ₂
M	39.47	i	0.88	σ _p ²	29.0	21.5	54.1
d _a	-6.80	j _{ab}	0.61	σ _{mg} ²	11.4	3.57	7.10
d _b	3.89	j _{ba}	-5.46	σ _e ²	19.46	19.46	19.46
h _a	1.87	l	-1.70	σ _{pg} ²	0.00	0.00	0.00
h _b	-2.75			h _{mg} ² (%)	39.24	16.60	13.14
				h _{pg} ² (%)	0.00	0.00	0.00

Cross-2: Farid-06 × Shafaq (model E-1)							
First order parameter				2nd order parameter			
					BC ₁	BC ₂	F ₂
M	43.6	i	1.9	σ _p ²	31.8	24.6	62.3
d _a	3.3	j _{ab}	-0.1	σ _{mg} ²	10.1	2.9	29.3
d _b	-0.7	j _{ba}	3.2	σ _e ²	21.8	21.8	21.8
h _a	5.7	l	-6.9	σ _{pg} ²	0.0	0.0	11.2
h _b	2.4	[d]	16.5	h _{mg} ² (%)	31.6	11.6	47.0
h _a /d _a	1.7	[h]	0.1	h _{pg} ² (%)	0.0	0.0	18.0
h _b /d _b	-3.4						

Cross-3: Parula × Blue Silver (Model E-1)							
First order parameter				2nd order parameter			
					BC ₁	BC ₂	F ₂
M	53.8	i	-11.2				
d _a	-2.6	j _{ab}	-7.1	σ _p ²	38.6	39.1	105.7
d _b	-5.6	j _{ba}	-3.3	σ _{mg} ²	15.3	15.8	82.4

Table 7. Contin.

h_a	-4.0	l	3.6	σ_e^2	23.3	23.3	23.3
h_b	-7.7	$[d]$	20.0	σ_{pg}^2	0.0	0.0	0.0
h_a/d_a	1.5	$[h]$	-4.7	$h_{mg}^2(\%)$	39.6	40.4	77.9
h_b/d_b	1.4			$h_{pg}^2(\%)$	0.0	0.0	0.0
Cross-4: TD-1 × D-97603 (Model D-1)							
First order parameter				2nd order parameter			
M	45.01			σ_p^2	BC ₁	BC ₂	F ₂
D	-4.15			σ_{mg}^2	37.22	37.31	58.66
H	-2.42			σ_e^2	0.54	0.62	23.80
$[d]$	3.29			σ_{pg}^2	32.41	32.41	32.41
$[h]$	5.87			$h_{mg}^2(\%)$	4.27	4.28	2.45
				$h_{pg}^2(\%)$	1.45	1.66	40.57
					11.47	11.47	4.18

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 : $da \times hb$: First major gene with additive × second major gene with dominant effect. jba : $db \times ha$: Second major gene with additive × first major gene with dominant effect. $[j]$: Additive-dominance epistasis. (Gai and Wang, 1998; Gai *et al.*, 2003; Zhang *et al.*, 2003).

Conclusions

In cross Hashim-08 × LU-26 the flag leaf area was controlled by additive, dominance and epistasis of two major genes (Model B-1). According to the best fit genetic model no polygenes were involved in the trait and were mainly controlled by additive × additive epistatic interaction of two major genes. In cross Farid-06 × Shafaq and Parula × Blue Silver the flag leaf area was under the control of mixed action of two major additive dominant epistatic genes plus additive dominant polygenes (Model E-1). In both the crosses, flag leaf area was mainly under the influence of additive epistatic effect due to polygenes. In cross TD-1 × D-97603 was controlled by mixed one major gene and additive dominance polygenes (Model D-1). The additive and dominant effects of single major gene were negative and the trait was under the influence of additive effect of polygenes.

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