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Full Length Research Paper

Genetic control of flag leaf area in wheat (*Triticum aestivum*) crosses

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Mixed inheritance analysis for flag leaf area (FLA) was carried out using joint segregation analysis of six basic generations (P_1, P_2, F_1, F_2, B_1 and B_2) in two wheat crosses in 2006 to 2007 and 2008 to 2009. The results indicated that the trait was mostly under control of one major gene in combination with polygenes (model D-2) for the two crosses during the first year. However, it was controlled by mixed epistasis of two major genes plus polygenes (model E-1) in cross 2 during the second year. Transgressive segregate on both upper and lower extremity of the trait in B_1, B_2 and F_2 indicated the presence of both favorable and reversed genes in the parents. Higher major gene heritability (9.6 to 71.0) for the trait was recorded than the polygenes heritability (4.8 to 38.9) in the segregating generations (B_1, B_2 and F_2). Moderate to high environmental variations (14.4 to 85.0) in the trait for segregating generations revealed that FLA is influenced by the environmental fluctuations. Predominant additive effect over all other types of genetic effects suggests the delay in selection for FLA until maximum favorable genes are accumulated in the individuals.

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

INTRODUCTION

Improved grain yield is the ultimate aim for cereal breeders and is based on the performance of yield components together with a conducive environmental condition (Sahin and Yildirim, 2006). Leaves being the sites of photosynthesis have an obvious relationship with grain yield (Monyo and Whittington, 1973). Compared to other leaves, the flag leaf contributes the most of photosynthetic assimilates in wheat; therefore, it assumes the greatest importance in association with grain yield (Lupton, 1973; Senthold et al., 2003). The dry mater contributed by the flag leaf to the kernel in wheat accounts for 41 to 43% and is the major photosynthetic site during the grain filling stage (Athwal, 1968; Berdhal et al., 1972). Leaf size is an important parameter for determining differences in dry weight yield and grain yield in cereals and is related to photosynthetic area above the flag-leaf node; therefore, FLA should be one of the major objectives of plant breeding programs (Thorne, 1965). Based on the conclusion of Sahin and Yildirim (2006), larger flag leaf area is correlated with higher assimilates in wheat kernel due to efficient photosynthesis.

All previous genetic studies relevant to the inheritance of flag leaf traits were either based on diallel analysis (Hsu and Walton, 1970; Jain and Singh, 1976; Ilyhchenko, 1977; Sahin and Yildirim, 2006) or generation means analysis (Bariga, 1980; Cristaldo et al., 1992; Simon, 1999; Saleem et al., 2005) which measure the trait only as the polygenic system without measuring the effect of individual genes (Wang, 2001). The statistical approach used in the present investigation has the power to determine individual effects up to two major genes as well as, the collective epistatic effects of polygenes (Wang et al., 2001). Because of the high cost of the molecular techniques, population and sample size restriction, and the interference of errors, QTL technique has limited applications in breeding (Gai and Wang,

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1998). Based on the efforts of Wang (1996), joint segregation analysis (JSA) is the segregation-analysis method used to identify the mixed inheritance model of QTLs and to estimate related genetic parameters; this takes large advantage of the sample size available for plant quantitative traits (Gai and Wang, 1998).

In light of the superiority of the JSA over the previous approaches, the present study was undertaken to find out (i) the genetic diversity for FLA among the genotypes to be used in cross combinations, (ii) genetic mechanism of FLA through hybridization between the parents of larger and smaller FLA and vice versa and (iii) the number and individual effects of major genes, and cumulative effect of the major as well as, polygenes involved in controlling the FLA.

MATERIALS AND METHODS

Genetically diverse parents (Tables 1, 2 and 3) were selected from wheat germplasm as reported by Irfaq et al. (2011) for hybridization. In cross 1(B-92 × Frontana), Frontana with smaller FLA as pollen donor while B-92 with larger FLA as pollen recipient, while in cross 2 (Inqilab-91 × FS), FS with larger FLA (pollen donor: P_2) and Inqilab-91 with smaller FLA (pollen recipient: P_1) were used to develop populations for JSA during November, 2004 to April, 2005. Six basic populations {P_1, F_1, P_2, B_1 (F_1 × P_1), B_2 (F_1 × P_2), and F_2} of each cross were developed during 2005 to 2006. The experiment for the populations of the two crosses were repeated for two years that is, 2006 to 2007 (Year 1) and 2008 to 2009 (Year 2). During each year, the populations of the crosses were planted as randomized complete block design (RCBD) in three replications. Keeping 5 m row length, two rows were planted on parents (P_1, P_2) and F_1 population, four rows on each of B_1 and B_2 and 8 rows on F_2 populations of both the crosses in each replication. The plant to plant and row to row spacing was maintained 10 and 30 cm, respectively. Seeds were sown at 2.5 cm depth at the rate of 2 seed per hill which were later thinned to single healthy seedling per hill after germination. Flag leaves from the selected plants of each of the populations were cut at the stage of dough (stage 83, Zadoks' scale, Zadoks et al., 1974) and were pressed over night in between two plane surfaces in order to remove the twist. Flag leaf area (cm^2) was then measured with USA made automatic light reflecting leaf area meter (Model Li-3100). Observations were recorded on 60 plants from each of the two homozygous parents (P_1 and P_2), 90 from each of first filial generation (F_1), 150 from each of the two backcrosses (B_1 and B_2), and 200 from each F_2 generation.

Statistical approach

Number of major genes and their effects controlling FLA were determined by subjecting the data to the five groups consisting of 24 different genetic models described in Table 5 of the JSA specially designed for the six basic populations (Gai and Wang, 1998; Gai et al., 2003, 2007). Based on the assumptions of Wang (1996), Gai and Wang (1998), Gai and Zhang (2003) and Zhang et al. (2003) that is, diploid nuclear inheritance with no cytoplasmic effects, no linkage between major genes and polygenes, no selection and equal variances within the P_1, P_2 and F_1 populations as well as, normal distribution in any segregating generation due to the polygenic and environmental effects, suitable genetic models for each cross were determined by using maximum log of likelihood values (Dempster et al., 1977; McLachlan, 1988; Wang and Gai, 1997) and Akaike's information criterion (Akaike, 1977). As suggested (Gai and Wang, 1998; Zhang et al., 2003), further selection of the best fit model was made on the basis of all non-significant or least number of significant values of the three χ^2 statistics (Table 6) that is, U_1^2 =12 [$\Sigma\ Y_i - n/2]^2/n$, ~ χ^2 (1), to test whether the mean of Y_i is 1/2, U_2^2 = 45/4 ($\Sigma\ Y_i^2 - n/3)^2/n$, ~ χ^2 (1), to test whether the 2nd momentum of Y_i is 1/3 and U_3^2 = 180 [$\Sigma\ (Y_i - 1/2)^2/n$ -12/n]$^2/n$, ~ χ^2 (1), to test whether the variance of Y_i is 1/12. Where; AIC= (-2) log (Maximum likelihood) +2 (Number of independent parameters). Likelihood-ratio test (LRT) was used to choose the simplest type within the model group. Where; LRT = λ =2 log (La) -2 log (L_0). Where; L_a and L_0 are the maximum likelihoods under H_a and H_0, respectively. Two other important completely distribution free tests (Table 6) that is, Smirnov's statistics (nW^2) and Kolmogorove's statistics (D_n) where; D = Sup $|F_n(x) - F_o(x)|$ were used as goodness of fit tests to determine whether the selected model sufficiently explains the data. If, for a particular genetic model, none of these five statistics were significant, then the data adequately fit the model (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 B_1, B_2 and F_2 were worked out with the help of proposed formulae (Gai et al., 2003; Zhang et al., 2003) by using excel program of windows. Under the second order genetic parameters (Table 8), the phenotypic variation (σ_p^2) is partitioned into genetic and environmental variation (σ_e^2) for the two crosses. The genetic component of variation in turn is subdivided into variation due to major genes (σ_{mg}^2) and polygenes (σ_{pg}^2). Based on Mather and Jinks (1982), the values from μ_1 to μ_{69} of Table 7 indicate different means of component distributions (Wang and Gai, 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.

RESULTS

Frequency distribution and mean values

To determine the number of major genes, their individual effects, and combined effect due to polygenes, cross 1 and 2 were performed in the manner as given in the materials and methods under development of six populations. Mean FLA of each parent is presented in Tables 1 and 4. The frequency distribution of six populations (P_1, F_1, P_2, B_1, B_2 and F_2) along the range of FLA and mean values (Table 4) indicate that F_1s of the two crosses during the two years were tended towards the parents with larger FLA, except cross 2 during the first year which showed almost intermediate FLA (39.1 cm^2) to those of P_1 (46.6 cm^2) and P_2 (32.8 cm^2). The mean values and frequency distribution further indicated that B_1 and B_2 were tended towards their respective pollen donor parents during the both years. However, they showed larger FLA than the parents of smaller FLA. The situation is presented in Table 4, that is, in cross 1, it was 47.9 and 45.6 cm^2 for B_1 and B_2, respectively, during first year; 43.5 and 34.0 cm^2 for the same generations, respectively, during the second year. In case of cross 2,

Table 1. Origin, pedigree and mean values of ten different agronomic characters of 45 bread wheat (*Triticum aestivum L*) accessions.

Genotype	1	2	3	4	5	6	7	8	9	10	11	12
Frontana	Brazil	Fronteria/Mentana	124.5	121.8	173.4	51.6	24.8	21.0	63.1	32.4	16.8	2.1
B-92	CIMMYT	KAUZ 'S'	83.8	112.1	158.7	46.6	35.5	22.5	69.3	32.4	15.4	2.2
Saleem-2K	CIMMYT	CHAM-6//KITE/PGO	77.8	116.7	163.6	46.9	21.7	22.6	69.6	34.0	15.0	2.3
Tatara	CIMMYT	JUP/ALD "S"//RLT 'S'/3VEE 'S')	97.1	119.4	167.0	47.6	34.7	21.4	66.6	37.0	14.6	2.4
F. Sarhad	CIMMYT	PFAU 'S'/SERI/BOW 'S'	84.5	125.7	173.8	48.1	34.9	22.1	64.5	36.0	11.4	2.3
CT-02009	CIMMYT	PUNJAB-96-0PAK	94.7	121.4	164.6	43.2	20.3	20.6	76.1	26.0	14.3	2.0
CT-02019	CIMMYT	KAUZ//STAR/LUCO-M	94.1	122.9	165.3	42.4	21.2	20.3	45.1	45.0	12.2	2.1
CT-02081	CIMMYT	VEE/TRAP#1//ANGRA/3/PASTOR	94.1	122.9	165.3	42.4	21.2	20.3	45.1	45.0	12.2	2.1
CT-02192	CIMMYT	IRENA//CMH76.176/2*GEN/3/SNB/4/BORL95	92.2	121.1	162.4	41.3	22.6	21.0	46.6	37.9	11.7	1.8
CT-02266	CIMMYT	SW89.5181/KAUZ	97.2	123.5	168.9	45.4	24.3	22.5	48.7	37.5	11.1	1.8
CT-02267	CIMMYT	SW89.5181/KAUZ	97.6	124.6	169.1	44.5	24.1	21.8	49.2	35.3	10.6	1.7
CT-02204	CIMMYT	KAUZ/PASTOR	93.5	126.0	164.9	38.9	22.2	21.1	49.6	37.2	11.2	1.8
CT-02306	CIMMYT	CMH80A.542/CNO79	102.6	125.6	168.8	43.2	21.7	21.1	37.2	36.4	7.1	1.4
CT-02248	CIMMYT	ALTAR84/AE.SQUARROSA(219)//SERI	92.2	119.1	160.1	41.5	20.4	20.0	48.1	34.2	8.0	1.6
CT-02390	CIMMYT	FRET2	101.5	121.3	165.8	44.5	22.9	20.8	51.0	48.4	11.0	2.5
CT-01183	CIMMYT	SITTA/*SKUZ	96.0	124.2	161.0	36.8	20.3	20.2	63.3	31.7	10.0	2.0
CT-01084	CIMMYT	ATTILA/3*BCN	102.7	126.3	165.1	38.8	23.2	24.1	67.7	34.6	11.3	2.3
Inqilab-91	CIMMYT	WL 711/CROW 'S'	87.7	123.9	163.9	40.5	24.5	22.6	56.8	38.4	13.1	2.2
Karawan	CIMMYT	C182.2/C166.3/3/CNO/7C2*//CC//TOB/SWM6828	93.5	122.1	167.0	44.9	25.2	22.1	59.5	33.8	10.9	2.0
CT-99022	CIMMYT	URES/JUN//KAUZ	101.1	125.2	167.8	42.6	22.7	24.3	62.0	44.0	10.4	2.8
Metal Tail	India	ORE F_1 158/FDL//KAL/BB/3/NAC	108.2	112.5	150.5	38.2	21.9	20.8	51.7	34.1	13.3	1.8
V-84051	India	TAN'S'/3/TI/TOB//ALD	76.1	103.3	137.3	34.3	21.1	19.3	52.4	33.2	11.8	1.7
Soleman-96	CIMMYT	(Pedigree not available)	107.5	111.9	152.5	40.6	22.1	22.2	58.6	33.2	10.1	1.9
CB-61	CIMMYT	MILAN/HD.832 PK.3484-3A-3A-500A	86.8	103.6	133.2	29.6	25.6	20.5	44.7	38.1	10.0	1.7
CB-82	CIMMYT	SATLUJ 86CMT/YR//MON 'S'	111.5	129.7	171.0	41.3	29.6	22.3	67.7	39.4	8.6	2.1
CB-148	CIMMYT	WEAVER/TSC//WEAVER/3/WEAVER	108.7	125.8	169.2	43.4	31.1	25.1	65.6	32.6	15.9	2.1
CB-179	CIMMYT	GAMDOW-6/CM79515-044Y…	90.2	103.3	153.2	49.9	20.2	20.3	49.4	34.6	13.2	1.7
CB-185	CIMMYT	PASTOR-2/CM85295-0101TOPY--	65.4	96.7	138.0	41.3	18.3	18.1	43.1	28.9	16.0	2.1
CB-195	CIMMYT	MAYA74'S'/MON'S'	96.9	105.8	131.2	25.4	20.8	20.8	43.9	31.4	11.5	1.8
CB-196	CIMMYT	MAYA74 'S'/MON CM 29480-20Y0Y	96.9	105.8	131.2	25.4	20.8	20.8	43.9	38.6	12.3	1.7
CB-197	CIMMYT	PF70402/ALD'S'//PAT72/160//ALD'S'/3/PEW 'S'	88.8	112.5	152.5	40.1	20.1	22.5	51.0	35.7	13.3	1.8
CB-289	CIMMYT	BOW'S'*2/PRL'S'	111.5	118.8	157.7	38.9	31.9	22.9	68.5	38.6	16.8	2.6
UQAB-2K	CIMMYT	CROW'S'/NAC//BOW'S'PB 22138	103.4	125.4	165.4	40.1	33.0	23.3	68.6	37.1	14.8	2.5
CB-325	CIMMYT	TAN'S'/3/TI/TOB//ALD = V-84051	84.7	101.5	144.8	43.3	29.0	19.6	49.6	32.2	14.2	1.6
DRRM	India	PB-96/V-87094//MH-97	95.0	116.0	165.8	49.8	30.7	20.6	43.0	44.4	13.5	1.9
CM-03-04	India	PASTOR/3/VEE#5DOVE/BUC	90.9	123.5	166.6	43.1	26.5	22.4	47.5	40.6	13.0	1.9

Table 1. Contd.

E-41	India	SH-88/PAK-81//MH-97	94.1	111.4	144.2	32.8	21.0	19.6	44.1	36.5	12.4	1.6
V-2156	India	Weaver/SH-88	106.6	125.9	167.4	41.5	32.3	23.3	70.6	32.6	14.7	2.2
V-03007	India	Pb-96/V-87094//MH-97	75.6	108.5	143.7	35.2	25.1	19.7	56.7	35.0	12.5	2.0
AS-2002	India	Pedigree not available	96.3	105.2	140.2	35	27.0	19.8	47.5	34.5	17.4	1.6
CB-145	India	CHOIX/STAR/3/HE1/3*CNO79//2*SERI	100.9	89.8	168.0	78.2	25.2	20.5	55.0	34.0	17.1	1.8
Mango	CIMMYT	RSK/AZ//PVN/CM 4170-9	106.2	125.9	163.3	37.4	23.0	20.5	57.3	36.8	18.5	2.1
BANA-4	India	(Pedigree not available)	75.0	130.0	164.4	34.4	24.1	21.3	56.8	33.9	15.6	1.9
CB-171	India	ABTIN-1ICW92-0717	85.2	106.1	140.5	34.4	23.4	21.0	56.2	33.8	17.4	1.9
E-29	India	SH-88/V-90A 204//MH-97	100.2	120.6	162.0	41.4	22.5	21.3	51.8	38.1	19.0	2.0

1) Origin; 2) Pedigree; 3) Plant height (cm): height of the fully mature plants from the soil surface to the top of the ear excluding awns length. days to 50% flowering; 4) Days to flowering: days from sowing to ears emergence; 5) Days to 50% maturity: days from date of sowing till the appearance of physiological maturity (when plants color turned yellow); 6) Grain filling duration (days): counting number of days from the date of heading to that of physiological maturity, that is, turning yellow (Przulj and Mladenov, 1999); 7) Flag leaf area (cm^2): calculated manually using the formula (length x breadth x 0.74); 8) Number of tillers $plant^{-1}$: productive tillers (ears) of individual selected plants were counted; 9) Number of spikelets $spike^{-1}$: the number of spikelets $spike^{-1}$ were counted by taking the main spikes of the selected plants; 10) Number of grains $spike^{-1}$: the same main spikes were hand threshed, separately, cleaned and their seed were manually counted; 11) 1000 grains weight (g): 1000 dry grains were manually counted from each selected plant and weight was determined by using electronic balance; 12) Grain yield $plant^{-1}$ (g): selected individual plants from each accession were hand threshed, separately, and their grains were weighed using electronic balance.

Table 2. Clusters vise mean values and standard deviations based on flag leaf area and 9 agronomic traits in 45 bread wheat (*Triticum aestivum* L.) accessions.

Trait	Group A			Group B	
	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
Flag leaf area (cm^2)	22.9±2.9	26.9±4.6	24.9±4. 7	22.5±2.6	25.5±5.9
Days to flowering	110.2±13.2	120. 8±7.8	121.9±4.5	111.6±9.00	118.4±5.7
Days to maturity	152.1±13.8	161.8±11.5	165.9±7.3	150.1±11.6	158.3±5.7
Plant height (cm)	86.2±11.6	100.9±8.5	96.1±10.9	94. 2±10.1	96.1±13.4
No. of spikes $plant^{-1}$	9.4±2.8	10.8±5.1	8.7±1.6	9.9±3.9	11.4±4.2
No. of spikelets $spike^{-1}$	20.4±1.2	22.4±1.5	21.4±1.2	20.5±0.9	22.7±0.2
No. of grains spike-1	53.8±8.8	57.5±12.8	56.7±9.5	50.4±5.2	58.8±8.9
1000 grain weight (g)	33.67±2.4	35.9±4.1	37.9±6.2	35. 7±2.4	37.5±1.6
Grain weight $spike^{-1}$ (g)	1.89±0.2	2.1±0.0	2. 2±0.3	1.8±0.2	2.2±0.4
Grain yield $plant^{-1}$ (g)	14.05±3.7	12.6±2.8	12.2±1.9	13.7±3.1	14.4±2.1

54.9 and 63.3 cm^2, FLA was recorded for B_1 and B_2 during the first year while 49.8 and 56.9 cm^2 during the second year. Few transgressive segregates were apparent on both upper and lower extremity along the range of FLA in F_2 generation of the crosses during both years. Moreover, F_2s were normally distributed among the respective pollen donor and pollen recipient parents with increased FLA (Table 4) than the

Table 3. Grouping based on different clusters for 45 bread wheat accessions evaluated during cropping season 2003 - 2004.

Group	Cluster	Frequency	Age (%)	Accessions with Euclidean distances							
A	1	9	20	Saleem-2K(6.6)	CT-02248(4.3)	CT-01183(6.7)	CB-61(8.4)	CB-185(8.6)	AS-2002(7.8)	CB-145(10.6)	BANA-4(16.2)
	2	11	24.4	CB-171(4.8) B-92(7.5)	CT-02306(5.9)	CT-01084(4.2)	Metal Tail(5.9)	CB-82(6.2)	CB-148(4.6)	CB-195(9.8)	UQAB-2K(6.4)
	3	13	28.9	DRRM 03(7.1) Frontana(13.7) CT-02204(3.4)	CM-03-04(5.4) Tatara(7.4) CT-02390(5.5)	V-2156(6.7) F-Sarhad(7.8) Karwan(2.8)	CT-02009(5.5) CT-99022(4.9)	CT02019(6.5) V-03007(8.5)	CT-02081(6.5)	CT-02266(2.4)	CT-02267(3.5)
B	4	9	20	CT-02192(5.2)	V-84051(7.1)	Soleman(4.4)	CB-179(6.9)	CB-196(6.5)	CB-325(4.4)	E-41(4.3)	Mango(6.3)
	5	3	6.7	E-29(5.9) Inqilab-91(6.5)	CB-197(9.8)	CB-289(5.8)					

In Parentheses is the Euclidian distance representing the separation/closeness among the lines including in the same cluster.

Table 4. Frequency distribution of plant population for flag leaf area (cm^2) in P_1, P_2, F_1, B_1, B_2 and F_2 of two bread wheat crosses during the two years.

Cross[1]	Year	PT[2]	Range of flag leaf area (cm^2)															Size[3]	M- FLA[4]	Var[5]	SD(±)[6]
			11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-90				
1	1	P_1					4	7	8	7	11	16	7						60	50.4	79.1	8.9
		F_1						7	9	14	14	17	16	12	1				90	55.1	80.8	9.0
		P_2		5	8	12	9	11	10	5									60	33.3	77.5	8.8
		B_1				14	15	18	15	25	15	30	16	2					150	47.9	135.0	11.6
		B_2		3	5	8	11	19	20	45	12	8	15	4					150	45.6	127.5	11.3
		F_2			3	15	11	9	27	17	15	23	32	23	18	7			200	53.5	210.0	14.5
1	2	P_1				2	10	7	8	10	10	7	6						60	46.6	98.9	9.9
		F_1		2	8	11	13	14	16	12	9	5							90	39.1	106.4	10.3
		P_2	2	5	8	12	10	9	7	5	2								60	32.8	99.0	10.0
		B_1			5	15	19	17	26	30	19	12	5	2					150	43.5	103.4	10.2
		B_2	11	11	15	19	23	23	20	20	8								150	34.0	126.4	11.2
		F_2	8	17	20	20	28	28	22	15	11	17	8	6					200	37.9	206.0	14.4
2	1	P_1						8	12	11	22	7							60	48.9	33.9	5.8
		F_1								9	19	34	8	19	1				90	58.7	38.4	6.2
		P_2								10	14	14	12	10					60	57.9	43.9	6.6
		B_1					7	6	15	27	24	20	19	23	9				150	54.9	109.2	10.5

Table 4. Contd.

		B_2					2	18	15	22	20	43	14	16		150	63.3	83.4	9.1
		F_2		10	13	17	24	22	29	18	27	17	10	12	1	200	53.6	196.8	14.0
		P_1				7	12	13	20	8						60	48.9	34.3	5.9
		F_1						10	23	31	14	11	1			90	58.0	35.9	6.0
2	2	P_2					3	10	21	21	5					60	58.6	33.6	5.8
		B_1		2	7	14	21	32	34	35	15					150	49.8	69.9	8.4
		B_2				1	19	16	40	28	16	18	9	3		150	56.9	81.5	9.0
		F_2	1	7	12	22	25	20	25	22	15	18	14	12	7	200	53.9	214.8	14.7

1) Cross 1= B-92 (P_1) x Frontana (P_2), Cross 2= Inqilab-91(P_1) x FS (P_2); 2) Population type; 3) Population size; 4) Mean flag leaf area; 5) Phenotypic variance; 6) Standard deviation.

Table 5. Akaike's information criterion (*AIC*) values for flag leaf area under five groups of 24 genetic models estimated through the iterated expectation and conditional maximization (IECM) algorithm.

Model group, code, and implication of model type	First order genetic parameters		Cross combination and *AIC* values			
	Major genes	Polygene	1st year		2nd year	
			Cross 1	Cross 2	Cross 1	Cross 2
Group 1: One major gene						
A-1: Additive-dominant	*m, d, h*	-	5537.6	5303.3	5494.0	5273.0
A-2: Additive	*m, d,* (*h=0*)	-	5607.7	5347.0	5492.0	5237.3
A-3: Completely dominant	*m, d* (*h = d*)	-	5563.1	5405.1	5520.0	5326.3
A-4: Completely negative dominant	*m, d* (*h = -d*)	-	5699.0	5295.3	5511.6	5277.7
Group 2: Two major genes						
B-1: Additive-dominance-epistasis	*m*, d_a, d_b, h_a, h_b, *i*, j_{ab}, j_{ba}, *l*	-	5469.6	5205.8	5483.5	5117.2
B-2: Additive-dominant	*m*, d_a, d_b, h_a, h_b, *i*, j_{ab}, j_{ba}, *l*	-	5471.5	5199.8	5481.5	5142.9
B-3: Additive	*m*, d_a, d_b (h_a=h_b= 0)	-	5721.4	5365.8	5478.9	5199.9
B-4: Equally additive	*m, d* (d_a= d_b, h_a=h_b=0)	-	5619.1	5373.2	5502.0	5304.0
B-5: Completely dominant	*m*, d_a (= h_a), d_b (=h_b)	-	5564.9	5340.3	5518.3	5257.4
B-6: Equally dominant	*m, d* (= d_a= d_b= h_a= h_b)	-	5565.8	5415.0	5525.7	5340.8
Group 3: Polygene						
C: Additive-dominant-epistasis	*m*	[d], [h], [*i*], [*j*], [l]	5479.9	5220.5	5487.8	5144.9
C-1: Additive-dominant	*m*	[d], [h]	5518.3	5255.0	5486.0	5159.8
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*]	5470.14	5193.6	5491.7	5133.0
D-1: Additive-dominant one major gene and additive-dominant polygene	*m, d, h*	[d], [h]	5461.6	5189.4	5470.8	5130.9
D-2: Additive one major gene and additive-dominant polygene	*m, d,* (*h* = 0)	[d], [h]	5459.6	5187.4	5468.8	5128.9

Table 5. Contd.

D-3: Completely dominant one major gene and additive-dominant polygene	*m*, *d* (*h* = *d*)	[d], [h]	5471.9	5214.9	5484.1	5148.0
D-4: Completely negative dominant one major gene and additive-dominant polygene	*m*, *d* (*h*= -*d*)	[d], [h]	5480.0	5209.5	5471.5	5160.1
Group 5: Two major genes plus polygene						
E: Additive-dominant-epistatic of two major genes and additive-dominant-epistasis of polygene.	m_1 ~ m_6, d_a, d_b, h_a, h_b , *i*, j_{ab}, j_{ba}, *l*	[d], [h], [*i*], [*j*], [*l*]	5470.6	5202.4	5494.8	5142.9
E-1: Additive-dominant epistasis of two major genes and additive-dominant polygene	*m*, d_a, d_b, h_a, h_b , *i*, j_{ab}, j_{ba}, *l*	[d], [h]	5474.0	5198.6	5491.8	5121.0
E-2: Additive-dominant two major genes and additive-dominant polygene	*m*, d_a, d_b, h_a, h_b , *i*= j_{ab}= j_{ba}, *l*	[d], [h]	5473.1	5197.8	5491.0	5151.6
E-3: Additive two major genes and additive-dominant polygene	*m*, d_a, d_b, h_a = h_b = 0	[d], [h]	5467.7	5205.6	5488.8	5140.0
E-4: Equally additive two major genes and additive-dominant polygene	*m*, *d* (= d_a = d_b , (h_a = h_b = 0)	[d], [h]	5475.0	5206.2	5487.8	5155.2
E-5: Completely dominant two major genes and additive-dominant polygene	*m*, d_a = h_a, d_b = h_b,	[d], [h]	5513.8	5216.9	5489.1	5154.9
E-6: Equally dominant two major genes and additive-dominant polygene	*m*, *d* = d_a = d_b = h_a = h_b	[d], [h]	5556.4	5389.6	5667.9	5508.9

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. $j_{ab:}$ d_a × $h_{b:}$ First major gene with additive × second major gene with dominant effect. $j_{ba:}$ d_b × $h_{a:}$ 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 6. Tests for goodness-of-fit regarding flag leaf area for suitable models in two wheat crosses.

First year							Second year						
Crosses 1: Bakhtawar-92 × Frontana													
Model	**Population**	U_1^2	U_2^2	U_2^3	$_nW^2$	**D_n**	**Model**	**Population**	U_1^2	U_2^2	U_2^3	$_nW^2$	**D_n**
D-2	P_1	4.66*	7.30**	6.05**	0.77(>0.05)	0.23(>0.05)	D-2	P_1	0.02(0.88)	0.10(0.75)	3.46(0.06)	0.12(>0.05)	0.11*
	F_1	3.65*	5.84**	5.13**	0.53(>0.05)	013*		F_1	0.05(0.82)	0.17(0.68)	6.21*	0.16(>0.05)	0.08*
	P_2	.05(0.82)	.35(0.55)	2.25(0.13)	0.09*	0.09*		P_2	0.05(0.82)	0.01(0.92)	1.67(0.20)	0.06(>0.05)	0.07*
	B_1	9.42**	8.35**	0.11(0.74)	0.93*	0.12(>0.05)		B_1	0.13(0.72)	0.26(0.61)	0.40(0.53)	0.06(>0.05)	0.05*
	B_2	0.09(0.76)	0.22(0.64)	0.49(048)	0.30(>0.05)	0.11(>0.05)		B_2	0.28(0.59)	0.42(0.52)	0.27(0.60)	0.09(>0.05)	0.05*
	F_2	0.41(0.52)	0.05(0.81)	2.38(0.12)	0.17(>0.05)	0.8*		F_2	0.08(0.77)	0.21(0.65)	0.51(0.48)	0.06(>0.05)	0.04*
D-1	P_1	4.66*	7.29**	5.96**	0.77(>0.05)	0.23(>0.05)	D-1	P_1	0.02(0.88)	0.10(0.75)	3.46(0.06)	0.12(>0.05)	0.11*
	F_1	3.65*	5.84**	5.12**	0.53(>0.05)	0.13*		F_1	0.05(0.82)	0.17(0.68)	6.21*	0.16(>0.05)	0.08*
	P_2	0.05(0.82)	0.35(0.55)	2.25(0.13)	0.09*	0.08*		P_2	0.05(0.82)	0.01(0.92)	1.67(0.20)	0.06(>0.05)	0.07*
	B_1	9.42***	8.35***	0.11 (0.74)	0.93(>0.05)	0.12*		B_1	0.13(0.72)	0.26(0.61)	0.40(0.53)	0.06(>0.05)	0.05*
	B_2	0.09(0.76)	0.22(0.64)	0.49(0.48)	0.30(>0.05)	0.11*		B_2	0.28(0.59)	0.42(0.52)	0.27(0.60)	0.09(>0.05)	0.05*
	F_2	0.40(0.53)	0.05(0.82)	2.38*	0.17(>0.05)	0.08*		F_2	0.08(0.77)	0.21(0.65)	0.51(0.48)	0.06(>0.05)	0.04*
E-3	P_1	2.22(0.13)	4.08*	4.52*	0.51(>0.05)	0.20(>0.05)	D-4	P_1	0.03(0.86)	0.02(0.87)	1.62(0.20)	0.09(>0.05)	0.09*
	F_1	0.00(0.95)	0.16(0.69)	3.35*	0.13*	0.07*		F_1	0.05(0.82)	0.05(0.82)	3.24(0.07)	0.11(>0.05)	0.08*
	P_2	2.25(0.13)	1.05(0.30)	2.89(0.09)	0.30(>0.05)	0.13*		P_2	0.04(0.83)	0.00(0.99)	0.57(0.45)	0.04(>0.05)	0.06*

Table 6. Contd.

	B_1	14.21***	12.70***	0.12(0.73)	1.38*	0.14(>0.05)		B_1	0.12(0.73)	0.29(0.59)	0.67(0.41)	0.07(>0.05)	0.05*
	B_2	1.36(0.24)	0.57(0.45)	2.27(0.13)	0.54(>0.05)	0.13(>0.05)		B_2	0.15(0.69)	0.52(0.47)	1.83(0.17)	0.11(>0.05)	0.05*
	F_2	27.86***	33.79***	7.89**	3.10***	0.21*		F_2	0.32(0.57)	0.66(0.42)	1.14(0.28)	0.11(>0.05)	0.05*
						Cross 2: Inqilab-91 × Fakhre Sarhad							
	P_1	0.06(0.81)	0.00(0.95)	0.5(0.48)	0.14(>0.05)	0.09*		P_1	0.03(0.86)	0.36(0.55)	2.80(0.09)	0.16(>0.05)	0.11*
	F_1	1.09(0.29)	0.35(0.56)	2.84(0.09)	0.37(>0.05)	0.13*		F_1	0.03(0.85)	0.21(0.64)	1.27(0.26)	0.06(>0.05)	0.06*
D-2	P_2	0.01(0.90)	0.18(0.67)	4.67*	0.14(>0.05)	0.09*	B-1	P_2	2.38(0.12)	2.36(0.12)	0.03(0.86)	0.41(>0.05)	0.15*
	B_1	0.87(0.35)	0.86(0.35)	0.01(0.91)	0.15(>0.05)	0.07*		B_1	1.82(0.17)	1.44(0.23)	0.18(0.67)	0.21(>0.05)	0.07*
	B_2	2.41(0.12)	2.33(0.12)	0.01(0.92)	0.43(>0.05)	0.11(>0.05)		B_2	4.24*	4.72**	0.52(0.47)	0.58(>0.05)	0.12(>0.05)
	F_2	0.36(0.54)	0.16(0.69)	0.57(0.45)	0.09(>0.05)	0.04*		F_2	0.05(0.83)	0.52(0.47)	13.96***	0.38(>0.05)	0.08*
	P_1	0.06(0.81)	0.00(0.95)	0.5(0.48)	0.14(>0.05)	0.09*		P_1	0.00(0.98)	0.20(0.65)	2.84(0.09)	0.15(>0.05)	0.10*
	F_1	1.09(0.29)	0.35(0.56)	2.84(0.09)	0.37(>0.05)	0.13*		F_1	0.11(0.74)	0.00(0.99)	1.53(0.22)	0.08(>0.05)	0.06*
D-1	P_2	0.01(0.90)	0.18(0.67)	4.67*	0.14(>0.05)	0.09*	E-1	P_2	1.24(0.26)	1.14(0.28)	0.00(0.96)	0.27(>0.05)	0.13*
	B_1	0.87(0.35)	0.86(0.35)	0.01(0.91)	0.15(>0.05)	0.07*		B_1	2.49(0.11)	2.71(0.10)	0.22(0.64)	0.31(>0.05)	0.08*
	B_2	2.41(0.12)	2.33(0.12)	0.01(0.92)	0.43(>0.05)	0.11(>0.05)		B_2	0.05(0.82)	0.18(0.67)	0.68(0.41)	0.08(>0.05)	0.05*
	F_2	0.36(0.54)	0.16(0.69)	0.57(0.45)	0.09(>0.05)	0.04*		F_2	1.27(0.26)	0.32(0.57)	4.37*	0.28(>0.05)	0.08*
	P_1	0.12(0.72)	0.32(0.57)	0.84(0.36)	0.18(>0.05)	0.12*		P_1	4.06*	5.71**	3.04(0.08)	0.55*	0.18(>0.05)
	F_1	0.23(0.63)	0.01(0.93)	2.33(0.12)	0.25(>0.05)	0.11*		F_1	2.17(0.14)	2.48(0.11)	0.34(0.55)	0.22(>0.05)	0.09*
D	P_2	0.00(0.99)	0.30(0.58)	4.86**	0.14*	0.09*	D-2	P_2	1.26(0.26)	0.95(0.33)	0.21(0.65)	0.29(>0.05)	0.13*
	B_1	0.01(0.93)	0.00(0.95)	0.01(0.94)	0.07*	0.05*		B_1	8.92***	8.44***	0.00(0.95)	0.80*	0.10*
	B_2	1.99(0.15)	1.61(0.20)	0.15(0.70)	0.39(>0.05)	0.10*		B_2	3.81*	3.47*	0.01(0.91)	0.57*	0.13*
	F_2	0.76(0.38)	0.35(0.55)	1.02(0.31)	0.15(>0.05)	0.06*		F_2	0.00(0.97)	0.12(0.73)	2.39(0.12)	0.11(>0.05)	0.05*

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.

parents with smaller FLA.

Selection of alternative and best fit models

Based on maximum likelihood values (not shown) estimated through IECM algorithm and smallest Akaike's information criterion (*AIC*) for different genetic models presented in Table 5; B-1, D, D-2, D-4, E-1 and E-3 were the most suitable genetic models for the crosses during both years. As described in the materials and methods under statistical procedure, based on non-significant or least number of significant values of five χ^2 statistics (U_1^2, U_2^2, U_3^2, ${}_nW^2$ and D_n) of LRT presented in Table 6, D-2 representing one major gene with additive effect and polygenes with additive-dominance effect (Table 5) was the best fit model for crosses 1 and 2 during both years whereas, model E-1 representing the mixture of two major additive-dominant-epistatic genes plus additive-dominant polygenes (Table 5) was the best fit for cross 2 during the second year.

First order genetic effects according to the best fit models

The first and second order genetic parameters

Table 7. Maximum likelihood estimate of component parameters regarding flag leaf area for two wheat crosses in their respective best fit models.

Parameter	Cross 1: Bakhtawar-92 × Frontana		Cross 2: Inqilab-91 × Fakhre Sarhad	
	First year	Second year	First year	Second year
	Model type: D-2	Model type: D-2	Model type: D-2	Model type: E-1
	Estimate	Estimate	Estimate	Estimate
μ_1 :	48.4	49.3	46.9	49.2
μ_2 :	53.5	59.1	39.4	58.0
μ_3 :	32.9	57.9	32.9	58.4
μ_{41} :	59.6	46.2	47.4	49.7
μ_{42} :	42.2	62.3	38.9	39.9
μ_{43} :	-	-	-	48.4
μ_{44} :	-	-	-	57.5
μ_{51} :	48.0	54.9	40.6	47.5
μ_{52} :	44.0	69.5	27.0	54.3
μ_{53} :	-	-	-	57.3
μ_{54} :	-	-	-	69.0
μ_{61} :	66.4	38.2	55.5	44.7
μ_{62} :	57.5	53.7	34.5	34.9
μ_{63} :	35.9	70.4	26.0	75.1
μ_{64} :	-	-	-	43.4
μ_{65} :	-	-	-	52.5
μ_{66} :	-	-	-	59.3
μ_{67} :	-	-	-	75.1
μ_{68} :	-	-	-	62.3
μ_{69} :	-	-	-	74.0
σ^2 :	73.4	35.4	87.9	30.9
σ_4^2 :	81.1	43.8	93.5	37.2
σ_5^2 :	123.0	39.4	102.3	41.5
σ_6^2 :	85.6	62.1	115.2	62.3

σ2: Phenotypic variance of P1, F1 and P2; σ42: polygenic + environmental variance of B1; σ52: polygenic + environmental variance of B2; σ62: polygenic + environmental variance of F2.

(Table 8) for best fit model of each cross were worked out from the component parameters of the respective models given in Table 7. Under the first order genetic parameters the additive effect that is, *d* due to single major gene was recorded 13.7, the collectively additive effect of the polygenes [*d*] was -7.0, whereas the dominant effect due to the polygenes [*h*] was 14.5 for cross 1 during year 1 (Table 8). Under the same best fit genetic model that is, D-2 for cross 1 during year 2; *d* (additive effect of single major gene), [*d*] (additive action of the polygenes) and [*h*] (Dominant action of the polygenes) were estimated at 13.5, -5.7 and -1.0, respectively (Table 8).

In the case of cross 2, two different models that is, D-2 and E-1 were the best fitting during the first and second year, respectively. Under model D-2, the first order genetic parameters that is, *d* (additive effect of single major gene), [*d*] (additive action of the polygene) and [*h*] (dominant action of the polygenes) for cross 2 during the second year were recorded as -15.9, 10.3 and 5.6, respectively (Table 8). For the same cross during the second year, the additive 'd_a' and dominant 'h_a' effects due to first (A) and second (B) major genes were -7.3 and -15.9, respectively, under model E-1. The same estimates (d_b, h_b) were recorded as -11.5 and -18.6 for the second major gene, respectively. The additive × additive epistatic effect that is, *i* due to the two major genes was -7.9.

Additive × dominant and dominant × additive epistatic effects for the two major genes were -6.4 and -0.6, respectively. The dominant × dominant epistatic effect due to the two major genes i.e. *l* was pronounced and estimated to be 19.8 (Table 8). Pronounced additive [*d*] and dominant [*h*] effects due to the polygene system were 30.6 and 11.1, respectively (Table 8). The values of '*m*' represent the average of parental means involved in the cross (Table 8).

Estimates of heritability and environmental variation (second order parameters)

Under the second order genetic parameters of Table 8,

Table 8. Estimates of first and second order genetic parameters for flag leaf area (cm^2) in two bread wheat crosses.

First experimental year						Second experimental year					
Cross 1: Bakhtawar-92 × Frontana						Cross 1: Bakhtawar-92 × Frontana					
Model type: D -2						Model type: D-2					
1st order parameters	Estimates	2nd order parameters	Estimates			1st order parameters	Estimates	2nd order parameters	Estimates		
			B_1	B_2	F_2				B_1	B_2	F_2
m =	42.3	σ_p^2=	135.0	127.5	210.0	m =	39.4	σ_p^2=	103.4	126.4	206.9
d=	13.7	σ_{mg}^2=	53.9	4.6	124.4	d=	13.5	σ_{mg}^2=	9.9	24.1	91.7
[d] =	-7.0	σ_e^2=	73.4	73.4	73.4	[d] =	-5.7	σ_e^2=	87.9	87.9	87.9
[h] =	14.5	σ_{pg}^2=	7.8	49.6	12.2	[h] =	-1.0	σ_{pg}^2=	5.6	14.4	27.3
		h_{mg}^2 (%)	39.9	38.9	59.3			h_{mg}^2 (%)	9.6	19.1	44.3
		h_{pg}^2 (%)	5.8	3.6	5.8			h_{pg}^2 (%)	5.4	11.4	13.2
		V_e =	54.3	57.5	34.9			V_e =	85.0	69.5	42.5
Cross 2: Inqilab-91 × Fakhre Sarhad (Model type: D -2)						Cross 2: Inqilab-91 × Fakhre Sarhad (Model type: E -1)					
m =	53.7	σ_p^2=	109.2	83.4	196.8	m	61.7	σ_p^2=	69.9	81.5	214.8
d=	-15.9	σ_{mg}^2=	65.4	44.0	134.7	d_a=	-7.3	σ_{mg}^2=	32.7	40.0	152.5
[d] =	10.3	σ_e^2=	35.4	35.4	35.4	d_b=	-11.5	σ_e^2=	30.9	30.9	30.9
[h] =	5.6	σ_{pg}^2=	8.4	4.0	26.7	h_a=	-15.9	σ_{pg}^2=	6.3	10.6	31.4
		h_{mg}^2 (%)	59.9	52.8	68.4	h_b=	-18.6	h_{mg}^2 (%)	46.8	49.1	71.0
		h_{pg}^2 (%)	7.7	4.8	13.6	h_a/d_a	2.2	h_{pg}^2 (%)	9.0	13.0	14.6
		V_e =	32.4	42.4	18.0	h_b/d_b	1.6	V_e =	44.2	37.9	14.4
						i =	-7.9				
						j_{ab} =	-6.4				
						j_{ba} =	-0.6				
						l =	19.8				
						[d]	30.6				
						[h]	11.1				

d_a, d_b: additive effect due to major gene A and B, respectively; h_a, h_b: dominant effect due to major gene A and B, respectively; h_a/d_a, h_b/d_b: ratio of dominance to additiveness due to major gene A and B, respectively; *i*: additive x additive component due to major genes; $j_{ab} = d_a \times h_b$: first major gene with additive x second major gene with dominant effect; $j_{ba} = d_b \times h_a$: second major gene with additive x first major gene with dominant effect; *l*: dominant x dominant component/effect due to major; [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.

irrespective of the model group, higher major gene heritability (h_{mg}^2) for B_1, B_2, and F_2 of cross 1 was recorded as 39.9, 38.9 and 59.3%, respectively, during first year, and 9.6, 19.1 and 44.3%, respectively, during the second year. Low polygene heritability (h_{pg}^2) for these generations of the cross were 5.8, 3.6 and 5.8%, respectively, during the first years, and 5.4, 11.4 and13.2%, respectively, during the second year. Similarly,

major gene heritability (59.9, 52.8, 68.4, respectively, during year 1 and 46.8, 49.1, 71.0, respectively, during year 2) was higher than the polygene heritability (7.7, 4.8, 13.6, respectively, during year 1 and 9.0, 13.0, 14.6, respectively, during year 2) for these generations of cross 2 (Table 8). Low (14.4) to high (85.0) variation for the trait due to environment (V_e) that is, 54.3, 57.5, 34.9, 85.0, 69.5, 42.5, 32.4, 42.4, 18.0, 44.2, 37.9 and 14.4 was observed for the segregating generations in the crosses during the two years (Table 8).

DISCUSSION

The normal distribution pattern of F_2s among their respective pollen donor and pollen recipient parents (Table 4) is the indication that FLA is a quantitatively controlled trait with pronounced additive type of gene action (Table 8) of the major genes (13.7, 13.5, -15.9 and -11.5) as well as minor genes (-7.0, -5.7, 10.3 and 30.6). Using generation means, diallel and QTL analysis, significant additive gene effect on FLA has been reported in the previous investigations (Simon, 1999; Sahin and Yildirim, 2006; Saleem et al., 2005; Xue et al., 2008). This indicates that successful progeny selection could be practiced for the trait in advanced generations till maximum genes are accumulated in the individual recombinants. The quite opposite additive effect due to the major genes for the two crosses may be either due to the fact that cross-1 is between larger FLA × smaller FLA and cross-2 is between smaller FLA × larger FLA (Wang and Gai, 2001; Zhang et al., 2003) or due to difference in the genetic back ground of the two crosses where the polygenic system of the genotypes may have interaction with major genes involved in controlling a quantitative trait (Wang and Gai, 2001). Occurrence of transgressive segregates in F_2s and some of the back cross generations of the crosses on both the upper and lower limit along the range of FLA (Table 4) reveals that both favorable and adverse genes for FLA are dispersed among the parents. Positive mid-parent and better parent heterosis were observed for the trait in wheat (Inamullah et al., 2006), whereas both positive and negative transgressive segregates in barley were also reported by Xue et al. (2008). The tendency of F_1s, B_1s, B_2s and F_2s to the parents of their respective larger FLA indicates that increased flag leaf area has dominance over the reduced FLA. However, as suggested by Sahin and Yildirim (2006), the trait might be under the influence of recessive genes with significant dominance variance component for flag leaf width.

Higher major genes heritability as compared to that of polygene indicates higher contribution of the major genes than the polygenes to control the trait. As compared to the first year, lower major genes heritability was recorded during the second year for both crosses while the environmental variance was higher than that of the first year. It may because that FLA being a quantitatively controlled trait is highly influenced by several environmental factors that is, soil nature, drought, heat stress, planting time and latitude/altitude etc (Ashraf et al., 2003). Secondly, it may also be due to involvement of polygenes system in controlling the trait. Using the same statistical approach designed for six basic generations (Gai and Wang, 1998; Gai et al., 2003) and five multiple generations (Zhang et al., 2003), higher major gene heritability in B_1, B_2 and F_2 generations has also been observed for fusarium head blight resistance in barley (Zheng et al., 2008), stripe rust resistance in wheat (Irfaq et al., 2009) and in F_2, F_2: F_3 generations of soybean for resistance to agromyzid bean fly (Wang and Gai, 2001; Zhang et al., 2003).

Low to high values (14.4 to 85.0) of environmental variation (V_e) of Table 8 regarding the segregating generations during the two years indicate that the trait is highly influenced by the environment. However, moderately low environmental variation has also been suggested by Simon (1999). This deviation in the results might be due to the different genetic background of the material and environments as well as, different statistical approach used in the past and present experimentation.

The fitness of two different genetic models that is, D-2, E-1 regarding cross-2 during the second year may be due to the two reasons. First, segregating population composed of component distributions is under control of the major genes and this is modified by polygenes system as well as, environments. Secondly, JSA is a theoretical procedure on which the segregating data of quantitatively controlled trait is analyzed like the Mendelian method and the best-fitting genetic model can be chosen according to Akaike's information criterion, a likelihood ratio test and tests for goodness of fit (Gai et al., 2007). The present approach with the capacity to find the genetic mechanism up to two major genes plus polygenes was designed for the six basic populations (Gai et al., 2003). However, seven groups and 32 types of genetic models, including one major-gene, two major-genes, three-major genes, polygenes, mixed one major-gene and polygenes, mixed two major-genes and polygenes, and a mixed three major-genes and polygenes models have also been set up to determine genetic effects in recombinant inbred line (RIL) population (Gai et al., 2007). But it is still inadequate and requires to be upgraded up to four major genes for better understanding of linkage between more than two genes and to resolve more estimates of genetic parameters in more segregating generations (Gai et al., 2007).

The present approach has the merits over the previous procedures (diallel, triple test cross and generation means analysis) because it determines the number of individual major genes, their individual effects as well as, collective effects of the polygenes involved in controlling quantitative traits (Wang and Gai, 2001). Unlike quantitative trait locus (QTL) mapping, it neither can

identify many QTLs nor locate the position of the major genes on a particular chromosome (Gai et al., 2007) while designing breeding experiments for the improvement of quantitative traits, selecting parents for crosses, progeny selection and gene pyramiding, etc. It is strongly recommended for plant breeders to exercise the JSA as a simple and useful technique to know the number of major genes, their kinds of genetic effects, heritability values as well as, genetic information on all kinds of genetic effects and heritability value of whole polygenes without any extra requirements on lab conditions except a precise experiment (Gai et al., 2007). JSA can also be used as a check for QTLs mapping and it should be conducted before QTL mapping is performed so that plant breeders can have a first impression on the genetic system of the involved trait (Gai et al., 2007).

As the outcome of the present study, one to two major genes and polygenes/minor genes in cumulative manner are involved in controlling the FLA. Additive interaction of the major gene/genes as well as, polygenes is pronounced to control the trait. Both favorable and reversed genes for the trait may be dispersed in the parents. The major gene heritability is higher than that of the polygenes to control the trait. The environmental conditions have influence on the trait. Because of its additively controlled nature, progeny selection for FLA may be delayed up to advanced generations till the favorable genes may attain the level of maximum homozygosity.

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