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Inheritance of flag-leaf angle, flag-leaf area and flag-leaf area duration in four wheat crosses

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Abstract Flag-leaf angle (FLAngle), flag-leaf area (FLarea) and flag-leaf area duration (FLADuration) are important traits in determining yield in wheat (*Triticum aestivum* L). Genetic studies on these traits are very few. The objective of this study was to determine the gene action controlling those traits in four wheat crosses. Six generations were available for each cross: parents (P_1 and P_2), F_1, F_2 and backcrosses ($BC_{(F_1 \times P_1)}$ and $BC_{(F_1 \times P_2)}$). The joint scaling test described by Mather and Jinks was used to test goodness of fit to eight genetic models. Models including additivity, dominance and interallelic interactions best fitted the data for the three traits and the four crosses. Additive effects were most prevalent for FLAngle. They were also significant for FLArea and FLADuration. Dominance and epistatic gene action were also found, but the degree and direction was both trait- and genotype-specific. Heritabilities values were intermediate. Genetic progress, although slow, can be expected when selecting for these traits; however, selection would be most effective if delayed to later generations because of dominance and epistatic effects.

Key words *Triticum aestivum* · Wheat · Morphophysiological traits · Inheritance · Flag-leaf characters

Introduction

The importance of some morphophysiological traits as flag-leaf angle(FLAngle), flag-leaf area (FLArea) and flag-leaf area duration (FLADuration) in determining grain yield in wheat has been studied by several researchers.

The advantages of erect leaves in increasing both the growth rate of the crop and grain yield has been demonstrated in wheat (Maksimchuk 1966). In dense canopies with a leaf area index (LAI) over 5, horizontal positioning of the leaves leads to shading, which in turn causes a premature drying of the bottom leaves and reductions in photosynthetic activity (Thorne 1971; Borojevic et al. 1980). Conversely, an erect positioning of the leaves facilitates the penetration of sunlight to bottom leaves, thereby enhancing the activity of photosynthesis (Loomis and Williams 1969; Duncan 1971). De Witt (1965) calculated theoretically that the erect leaf position increases the activity of photosynthesis by 15% over the horizontal leaf position at a LAI level of 5; the increase reaches 50% at a LAI level of 10.

Previous research has shown that FLADuration is correlated with grain yield$\cdot$m^{-2} (Fischer and Kohn 1966; Lupton et al. 1974; Mohiuddin and Croy 1980). Watson (1952) pointed out that leaf size was an important determinant of differences in dry weight yield and that FLArea should be one of the major objectives of plant breeding programs. Thorne (1966) concluded that grain yield of cereals was related to photosynthetic area above the flag-leaf node. Thorne (1963, 1965) also reported that the CO_2 absorbed after ear emergence by the part of the shoot above the flag-leaf node, including the ear, accounted for most of the dry weight of grain for wheat.

Genetic studies of flag-leaf characters have been very few. Nigam and Srivastava (1976) found that the expression of FLAngle was under the control of additive gene effects and partial dominance. Borojevic and Kraljevic-Balalic (1984) also found a preponderance of additive effects. Hsu and Walton (1970) reported a preponderance of additive genetic effects for flag-leaf length and flag-leaf breadth. There is a lack of information regarding the inheritance of FLADuration,

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although Mou and Kronstad (1994) studied the inheritance of the duration and rate of grain filling in wheat, finding a preponderance of additive gene action, but also dominance genetic effects. Yap and Harvey (1972) reported that FLADuration in barley was controlled mainly by additive gene action, although dominance effects were also observed.

Considering the small number of reports on the inheritance of those flag-leaf characters and since they are relatively easy traits to be evaluated in breeding programs, the aim of the work presented here was to investigate the gene action controlling FLAngle, FLArea and FLADuration.

Materials and methods

F_1 and F_2 populations as well as backcrosses to each parent ($BC_{(F_1 \times P_1)}$ and $BC_{(F_1 \times P_2)}$) were developed for four crosses: the cross of two Argentinian cultivars ('Buck Pucará' and 'Chasicó INTA') and the three possible crosses among the Mexican cultivars 'Star'S'', 'Ciano 79' and 'Parula'. Parents were chosen on the basis of their contrasting flag-leaf characteristics (differences in FLAngle, FLArea and FLADuration). They were selected from a previous trial using accessions from Argentina and CIMMYT. Parents, F_1, F_2, $BC_{(F_1 \times P_1)}$ and $BC_{(F_1 \times P_2)}$ were planted in the field. The experimental layout was a randomised complete block design with three replications. Seeds were planted in rows, 20 × 4 cm apart. Between 15 and 60 seeds per generation and replication for each cross were planted. The larger number was used for the segregating generations (One row per plot for parents and F_1, four rows per F_2 and two rows for backcrosses were used). Soil type was a typical argiudol. Mean temperature during the growing season was 16.1°C. Mean humidity was 80.7% and total amount of precipitation during the growing season was 483 mm. N and P fertiliser was applied at sowing .

All measurements for the following characters were made on an individual plant basis:

1) FLAngle: angle between the flag leaf and the stem, measured with a protractor at flowering (stage 61, Zadoks' scale, Zadoks et al. 1974) on main tiller.
2) FLArea: measured with a Licor area meter at flowering on main tiller.
3) FLADuration: calculated by multiplying the FLArea by the flag-leaf duration. Flag-leaf duration was visually estimated as the time between heading (stage 59, Zadoks' scale) and when the flag leaves on the remaining primary tillers (except the main tillers, because its leaf had been removed for the flag-leaf area determination) were 50% dried.

Data analysis

A generation mean analysis was performed using the joint scaling test described by Mather and Jinks (1977) which estimates the mid-parent, genetic components and digenic interaction genetic variance components. These estimates were used to fit the data to genetic models. Main genetic components consisted of additive variance (d) and dominance variance (h). Interaction components were additive × additive variance (i), additive × dominance variance (j) and dominance × dominance variance (l). Goodness of fit to eight different genetic models was tested by estimating m, [d], [h] and a maximum of two interaction components in order to retain at least one degree of freedom. The fit to the six-parameter model could not be tested because of the lack of degrees of freedom. In spite of that, individual genetic components were tested. Individual genetic components were also tested for the best model for each trait and cross using Student's *t*-test. Genetic components estimated to be different from zero at $P < 0.05$ were considered to contribute to the model. Broad-sense heritability values were estimated using Allard's (1960) approach, and the standard error of the equations were calculated.

Results and discussion

Flag-leaf duration was estimated visually when the average of the whole plot was 50% dried (Mohiuddin and Croy 1980) because at this moment the grain filling was completed. This value was multiplied by the individual values of leaf area. The mean values and standard errors for FLAngle, FLArea and FLADuration for the four crosses are shown in Table 1. The goodness of fit to eight genetic models for each trait and cross is shown in Table 2. The simplest subsets of variables m, [d], [h], [i], [j] and [l] showing the best fit were selected for each cross and are presented in Table 3.

For the three traits and the four crosses, models including additive and dominance effects as well as

Table 1 Mean values and standard errors for flag-leaf angle (FLAngle), flag-leaf area (FLArea) and flag-leaf area duration (FLADuration) for four wheat crosses

Generation[a]	FLAngle (°)	FLArea (cm^2)	FLADuration ($cm^2 \cdot$ days)
	Mean ± SE	Mean ± SE	Mean ± SE
Pucará × Chasicó			
P_1	25.2 ± 1.78	24.6 ± 0.85	975.0 ± 34.2
P_2	18.8 ± 1.21	26.1 ± 0.72	1058.6 ± 29.0
F_1	29.4 ± 2.29	30.5 ± 1.23	1253.9 ± 50.5
$BC_{(F_1 \times P_1)}$	21.8 ± 0.80	27.9 ± 1.04	978.1 ± 36.6
$BC_{(F_2 \times P_2)}$	21.7 ± 0.98	26.8 ± 1.05	1062.2 ± 41.7
F_2	20.1 ± 1.16	28.2 ± 1.11	1113.9 ± 44.0
Ciano × Parula			
P_1	24.8 ± 0.55	28.4 ± 1.47	1350.4 ± 69.8
P_2	21.7 ± 0.58	15.0 ± 0.88	643.5 ± 37.9
F_1	25.0 ± 0.81	22.9 ± 1.27	1111.1 ± 38.2
$BC_{(F_1 \times P_1)}$	24.5 ± 0.57	23.3 ± 1.12	1176.3 ± 45.1
$BC_{(F_2 \times P_2)}$	22.3 ± 0.51	21.9 ± 1.15	888.7 ± 35.2
F_2	25.6 ± 0.90	30.5 ± 1.04	1706.9 ± 53.0
Star × Ciano			
P_1	28.0 ± 1.14	22.2 ± 1.66	1131.0 ± 84.7
P_2	24.8 ± 0.55	28.4 ± 1.47	1350.4 ± 69.8
F_1	27.5 ± 0.75	27.2 ± 1.37	1267.3 ± 63.6
$BC_{(F_1 \times P_1)}$	25.8 ± 0.85	30.1 ± 1.25	1480.2 ± 61.5
$BC_{(F_1 \times P_2)}$	28.5 ± 0.91	30.9 ± 1.84	1438.9 ± 85.5
F_2	25.3 ± 0.58	28.0 ± 1.87	1512.6 ± 101.0
Star × Parula			
P_1	28.0 ± 1.14	22.2 ± 1.66	1131.0 ± 84.7
P_2	21.7 ± 0.58	15.0 ± 0.88	643.5 ± 37.9
F_1	27.5 ± 0.82	21.5 ± 0.97	991.1 ± 45.8
$BC_{(F_1 \times P_1)}$	27.0 ± 0.63	24.0 ± 1.05	1174.3 ± 51.6
$BC_{(F_1 \times P_2)}$	21.0 ± 0.73	16.8 ± 0.84	826.4 ± 41.6
F_2	24.1 ± 0.65	21.5 ± 0.83	1180.9 ± 45.8

[a] P_1 and P_2 = parents; $BC_{(F_1 \times P_1)}$ = backcross to P_1; $BC_{(F_1 \times P_2)}$ = backcross to P_2.

Table 2 Chi-squared goodness-of-fit test and probability of fit to eight genetic models for flag-leaf angle (FLAngle), flag-leaf area (FLArea) and flag-leaf area duration (FLADuration) for four wheat crosses

Model[a]	FLAngle		FLArea		FLADuration	
	χ^2	P	χ^2	P	χ^2	P
Pucará × Chasicó						
m[d]	17.14	< 0.005	19.31	< 0.005	23.73	< 0.005
m[d][h]	14.64	< 0.005	1.86	0.75–0.50	10.41	0.025–0.01
m[d][h][i]	6.30	0.05–0.025	1.86	0.5–0.25	8.47	0.025–0.01
m[d][h][j]	12.52	< 0.005	0.43	0.9–0.75	9.58	0.01–0.005
m[d][h][l]	5.21	0.10–0.05	1.76	0.5–0.25	383.99	< 0.005
m[d][h][i][j]	3.45	0.10–0.05	0.43	0.75–0.5	7.64	0.01–0.005
m[d][h][i][l]	7.57	0.01–0.005	1.43	0.25–0.1	0.62	0.5–0.25
m[d][h][j][l]	63.71	< 0.005	0.34	0.75–0.5	3.17	0.1–0.05
Ciano × Parula						
m[d]	9.21	0.10–0.05	86.03	< 0.005	143.76	< 0.005
m[d][h]	5.77	0.25–0.1	83.47	< 0.005	138.89	< 0.005
m[d][h][i]	5.55	0.1–0.05	35.24	< 0.005	71.95	< 0.005
m[d][h][j]	5.06	0.1–0.05	66.87	< 0.005	137.94	< 0.005
m[d][h][l]	5.40	0.1–0.05	43.67	< 0.005	125.90	< 0.005
m[d][h][i][j]	4.83	0.05–0.025	23.49	< 0.005	71.26	< 0.005
m[d][h][i][l]	0.52	0.5–0.25	2.59	0.25–0.1	0.89	0.5–0.25
m[d][h][j][l]	11.99	< 0.005	46.64	< 0.005	125.91	< 0.005
Star × Ciano						
m[d]	21.83	< 0.005	14.14	0.01–0.005	13.86	0.01–0.005
m[d][h]	14.28	< 0.005	12.37	0.01–0.005	13.66	< 0.005
m[d][h][i]	11.61	< 0.005	193.12	< 0.005	3.13	0.25–0.10
m[d][h][j]	5.83	0.1–0.05	169.38	< 0.005	10.38	0.01–0.005
m[d][h][l]	15.56	< 0.005	3.76	0.25–0.1	1.38	0.75–0.5
m[d][h][i][j]	1.88	0.25–0.1	387.97	< 0.005	0.90	0.5–0.25
m[d][h][i][l]	15.67	< 0.005	1107.83	< 0.005	1.33	0.25–0.1
m[d][h][j][l]	25.50	0.05–0.025	164.08	< 0.005	0.21	0.75–0.5
Star × Parula						
m[d]	20.75	< 0.005	9.47	0.1–0.05	19.41	< 0.005
m[d][h]	18.97	< 0.005	6.60	0.1–0.05	18.45	< 0.005
m[d][h][i]	9.17	0.025–0.01	5.87	0.1–0.05	4.70	0.1–0.05
m[d][h][j]	11.33	< 0.005	3.70	0.25–0.1	18.15	< 0.005
m[d][h][l]	5.84	0.1–0.05	6.51	0.05–0.025	12.79	< 0.005
m[d][h][i][j]	3.43	0.1–0.05	0.21	0.75–0.5	1.91	0.25–0.1
m[d][h][i][l]	5.84	0.025–0.01	4.84	0.05–0.025	1.54	0.25–0.1
m[d][h][j][l]	0.03	0.90–0.75	1.07	0.5–0.25	10.43	< 0.005

[a] m = Estimated mean of all homozygous individuals, [d] = additive variance, [h] = dominance variance, [i] = additive × additive variance, [j] = additive × dominance variance, [l] = dominance × dominance variance

some interallelic interactions best fit the data. Although the fit of the six-parameter model could not be tested because of the lack of degrees of freedom, individual genetic components were. A maximum of five components were significant in any one model. This confirmed that other models with five or less components fit best.

For FLAngle, additive effects were highly significant and distinct in each of the four crosses, although dominance and epistatic effects were also significant. Similar results for this trait were found by Nigam and Srivastava (1976) and Borojevic and Kraljevic-Balalic (1984). The sign of dominance and epistatic effects were genotype-specific. This indicates that they operated in some cases by increasing the FLAngle and in others by reducing it but that their effects were compensated for in such a way that the F_1 always showed a higher angle (more horizontal) respect to the mid-parent (Table 1). Borojevic and Kraljevic-Balalic (1984) found similar results in many crosses. These results indicate that improvement for this character can not be obtained in hybrid combinations.

For FLArea, there were significant additive effects in all but one of the crosses. Dominance and epistasis also played an important role in some of the crosses. With one exception, significant dominance and epistatic effects were positive, indicating an increase in the FLArea in hybrid combinations with respect to the mid parent. This result is consistent with that of Hsu and Walton (1970) who found additive genetic effects for flag-leaf length and flag-leaf breadth.

For FLADuration, additive effects were also significant in the four crosses. Dominance and epistatic effects also played an important role. The sign of

Table 3 Fit of the individual genetic components and standard errors to the models with the best chi-squared fit for the flag-leaf angle (FLAngle), flag-leaf area (FLArea) and flag-leaf area duration (FLADuration)

Cross	FLAngle	FLArea	FLADuration
Pucará × Chasicó	[m] 14.14 ± 3.26 [d] 2.94 ± 1.07** [h] 11.95 ± 4.99* [i] 7.16 ± 3.43* [j] – 3.47 ± 3.32	[m] 25.3 ± 0.53 [d] 0.80 ± 0.56 [h] 4.93 ± 1.18*** [j] – 3.79 ± 3.17	[m] 1402.04 ± 37.44 [d] 43.43 ± 20.49* [h] – 1004.53 ± 495* [i] – 381.19 ± 210.52† [l] 856.39 ± 305.42**
Ciano × Parula	[m] 31.86 ± 3.93 [d] 1.70 ± 0.35*** [h] – 18.25 ± 8.66* [i] – 8.63 ± 3.91* [l] 11.35 ± 5.06*	[m] 54.5 ± 4.66 [d] 4.99 ± 0.93*** [h] 62.16 ± 121.8 [i] – 33.6 ± 21.07 [l] 30.57 ± 44.79	[m] 3662.14 ± 10.05 [d] 331.65 ± 32.79*** [h] – 5269.83 ± 531.30*** [j] – 2677.29 ± 229.21*** [l] 2718.79 ± 315.32***
Star × Ciano	[m] 23.55 ± 1.36 [d] 1.71 ± 0.63** [h] 4.21 ± 1.91* [i] 3.02 ± 1.52† [j] – 8.7 ± 2.79***	[m] 26.27 ± 1.61 [d] 2.58 ± 1.03* [h] 12.29 ± 0.92*** [l] – 11.35 ± 0.78***	[m] 1240.68 ± 61.24 [d] 109.72 ± 61.24† [h] 901.06 ± 280.96** [j] – 275.89 ± 255.04 [l] – 874.40 ± 274.21**
Star × Parula	[m] 24.82 ± 4.98 [d] 3.16 ± 0.64*** [h] – 6.08 ± 2.60* [j] 5.55 ± 2.31* [l] 8.75 ± 2.60***	[m] 21.21 ± 1.85 [d] 3.53 ± 0.93*** [h] 0.15 ± 2.55 [i] – 2.74 ± 2.13 [j] 7.58 ± 3.20*	[m] 1665.85 ± 222.39 [d] 286.09 ± 41.17*** [h] – 1264.98 ± 535.83* [i] – 746.83 ± 219.71** [l] 590.21 ± 331.41†

†, *, **, *** Significant at 0.1, 0.05, 0.01 and 0.001 probability level (Student's *t*-test), respectively

dominance as well as additive × additive and additive × dominance interaction effects were also genotype- and trait-specific, but there was also a compensation among those effects. Thus, the F_1 had greater values than the mid-parent or even than the best parent. In the literature, information on the inheritance of FLADuration is lacking. Considering the importance of FLADuration in grain filling, the results agreed with a previous report by Mou and Kronstad (1994) who found a preponderance of additive genetic effects but also dominance effects controlling grain-filling duration.

Broad-sense heritability estimates are indicated in Table 4. Values were low to intermediate for flag-leaf angle (average 36.1%), moderately low for leaf area (average 25.1%), and low to intermediate for leaf-area duration (average 33.3%). This indicates that the environmental variance was important for all traits studied.

The findings of important additive effects indicates that improvement can be made by conventional breeding methods, especially for FLAngle in these crosses. The scope of influence of this paper could be extended to other genotypes and environments, considering that these results are consistent with those found by some other researchers. However, progress is likely to be slow due to the environmental effects. The additive × additive effects which were important in some crosses for the FLAngle and FLADuration are also fixable in pure inbred lines.

Dominance, dominance × dominance and additive × dominance effects may be exploited, but only if hybrid wheat is the objective of the breeding program and a feasible option. Nevertheless, the significance and sign of such effects depend on the cross and trait. Still, the presence of these effects must be considered. Because neither the simple nor the epistatic gene effects can be fixed in homozygous lines it may be necessary for selection pressure to be lenient in early generations and only be intensified when homozygosity is approached. The proportionally larger dominance component found for FLArea area and FLADuration compared to FLAngle indicates that improvement in those traits would be slower with conventional selection procedures.

Table 4 Broad-sense heritability values and standard errors for flag-leaf angle (FLAngle), flag-leaf area (FLArea) and flag-leaf area duration (FLADuration)

	Heritability ± SE		
	FLAngle	FLArea	FLADuration
Pucará × Chasicó	25.1 ± 20.4	24.8 ± 19.3	20.8 ± 20.3
Ciano × Parula	62.1 ± 7.34	26.5 ± 10.9	46.5 ± 18.5
Star × Ciano	39.8 ± 11.6	27.9 ± 17.1	52.7 ± 16.7
Star × Parula	17.5 ± 18.7	21.1 ± 18.5	13.2 ± 19.2

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