

INHERITANCE OF FLAG LEAF ANGLE IN WHEAT (*Triticum aestivum* L.)*

Rosa Maria Oviedo de Cristaldo, Fernando Irajá Felix de Carvalho,
José F. Barbosa-Neto and Luiz Carlos Federizzi

ABSTRACT

Inheritance of leaf angle was determined for four wheat (*Triticum aestivum* L.) genotypes with different leaf angles. Data were obtained at heading, anthesis, and milk stages of crop growth, in six generations from six different crosses. The six generations included the two parents (P_1 and P_2), F_1 and F_2 , and backcrosses with each parent (BC_1F_1 and BC_2F_1). Genetic differences were detected among parental genotypes with erect leaves (PF 855520 and Parula 's'), intermediate leaves (PF 85372) and pendent leaves (PF 83144). Heading and milk stage data were the most adequate for analysis of genetic parameters. Segregant data showed the existence of one gene with at least three distinct alleles controlling the expression of leaf angle, although the existence of two independent genes could not be ignored. Estimates of additive and dominance effects and heritability were significant. Data suggest that efficient selection for erect leaf in wheat is possible and that considerable genetic improvement can be expected for leaf angle.

INTRODUCTION

The major objective of cereal programs is to develop genotypes with a high potential for grain yield. Higher grain yield has been attained through use of hybrid varieties, by developing varieties resistant to pests and disease, reducing plant height, and increasing harvest index. Changes in plant architecture that might permit more effective utilization of available resources appears to be an appropriate breeding strategy.

* Part of a thesis submitted by R.M.O.C. to Universidade Federal do Rio Grande do Sul in partial fulfillment of the requirements for the Master's degree.

In areas of advanced agriculture, maximum yield rarely reaches half the total biomass production, indicating that the photosynthesis potential of cultivars is not being fully exploited (Army and Greer, 1969; Mackey, 1979; Good and Bell, 1980). Grain yield is a function of photosynthesis products, and an optimum distribution and arrangement of leaves may increase the efficiency of biomass production in crop cultures. A greater penetration of light into the structure of a crop plant, combined with morphophysiological traits that contribute to increase productivity appears to be an appropriate goal. Modifications of leaf angle and flag leaf angle have been emphasized by investigators as a means of obtaining better light utilization, with more upright leaves permitting the penetration of solar energy into the lower levels of the aerial structure of plants (Jennings, 1964; Tanner *et al.*, 1966; Mackey, 1966; Pearce *et al.*, 1967; Donald, 1968).

The study of variability and of the genetic basis of morphophysiological traits associated with grain yield is a high priority in breeding programs. Borojevic and Dencic (1986) studied a collection of hexaploid wheats and recognized the existence of variability in flag leaf position. Carvalho and Qualset (1978) indicated two loci were responsible for flag leaf angle in wheat, with a high heritability and a high level of dominance for the widest angle. Nigam and Srivastava (1976) and Wu *et al.* (1984) reported that leaf angle was a quantitative trait in wheat, with highly significant variance components, and with the narrower angle partially dominant over the wider angle.

Determination of the inheritance and of the gene action of the flag leaf angle trait permits appropriate management in hybrid programs and in genotype identification in segregant populations. Because the erect leaf trait represents an alternative for increasing grain yield in cereal crops, the present study was undertaken with the objective of estimating the number of genes and the gene action involved in the control of flag leaf angle in wheat (*Triticum aestivum* L.) genotypes, and to determine appropriate selection strategies for incorporating angle characters in breeding programs.

MATERIAL AND METHODS

The trial was conducted in the field, in a screened area, and in the greenhouse in 1988 and 1989. The field trial was conducted at the Experimental Agronomy Station of the Federal University of Rio Grande do Sul, using the following wheat genotypes: PF 85520 and Parula 's' (erect leaves), PF 83144 (pendent leaves) and PF 85372 (intermediate angle leaves). PF 85520, PF 83144, and PF 85372 are of Brazilian origin and Parula 's' is of Mexican origin.

Generations P₁, P₂, F₁, F₂, BC₁F₁ and BC₂F₁ of each cross were obtained in 1988 and sown in the experimental field in July 1989, using a randomized complete block design with two replications. The experimental units for the parental and backcross generations included two 3 m long rows spaced 0,30 m. Generations F₁ and F₂ were sown

in plots in which the number of rows depended on the amount of seed available, with 0,30 m spacing between plants for all generations.

The flag leaf angle from the vertical plane was measured on the main stalk of each plant with a protractor. The measurements were made at three different developmental stages proposed by Zadocks *et al.* (1974): i.e., when 50% of the ear was outside of the sheath (heading, stage 54), during anthesis (stage 64), and during the milk stage (stage 75).

Statistical analyses included the frequency distributions, means of each generation and variance component estimates within the different generations. Frequency distributions were constructed from data for each generation of each cross by grouping individuals into classes at 15° intervals. Expected and obtained frequencies were tested with chi-square, considering only the measurements made at the heading and the milk stages. The measurements made at anthesis were not considered because the population distribution could not be characterized adequately.

Phenotypic (VP), genetic (VG), additive (VA), dominance (VD) and environmental (VE) variances were calculated by the method of Allard (1960) and Falconer (1960) as follows:

$$VP = VF_2$$

$$VG = VF_2 - VE$$

$$VA = 2VF_2 - (VBC_1F_1 + VBC_2F_1)^{1/3}$$

$$VE = (VP_1 \cdot VP_2 \cdot VF_1)$$

and, in the absence of epistasis,

$$VD = VF_1 - VA - VE$$

where VP_1 , VP_2 , VF_1 , VF_2 , VBC_1F_1 and VBC_2F_1 , represented the variation within generations P_1 , P_2 , F_1 , F_2 , BC_1F_1 , and BC_2F_1 respectively.

For each cross, gene action was estimated by use of the model proposed by Mather and Jinks (1971). The method involves the estimate of the mean (m), additivity (a), and dominance (d) effects from the means of all generations available for each cross, followed by chi-square adjustment between observed and estimated means. Thus:

$$P_1 = m + a$$

$$P_2 = m - a$$

$$F_1 = m + d$$

$$F_2 = m + 1/2 d$$

$$BC_1F_1 = m + 1/2 a + 1/2 d$$

$$BC_2F_1 = m - 1/2 a + 1/2 d$$

where m is the mean (mean parental value), a the additivity effect, and d the dominance effect. Heritability of the erect leaf trait was estimated using the model described by Allard (1960).

RESULTS

The parental lines differed in the mean values at leaf angle (Table I). Three groups were formed: PF 85520 and Parula's' (erect leaf), PF 85372 (intermediate leaf) and PF 83144 (pendent leaf). Erect leaves were observed in PF 85520 and Parula's' at both measuring times, and pendent leaves were observed in PF 83144 at all measuring times. In contrast, PF 85372 presented erect leaves at the heading stage and pendent leaves at the milk stage, showing the existence of variability due to genotype x time of evaluation interaction (Table I).

Table I - Parental mean and t-test value for the erect leaf trait determined at heading and milk stages of development in six wheat crosses. Eldorado do Sul, 1989.

Cross	Angle (°)		t-test value
	\bar{P}_1	\bar{P}_2	
Heading stage			
PF 85520 x PF 83144	34.38	141.66	27.71**
PF 85520 x Parula's'	32.67	30.00	1.50
PF 85372 x PF 85520	47.64	30.88	3.73**
PF 85372 x PF 83144	51.09	135.88	18.92**
PF 85372 x Parula's'	37.50	32.50	1.18
PF 83144 x Parula's'	137.30	34.82	28.62**
Milk stage			
PF 85520 x PF 83144	40.63	157.00	22.47**
PF 85520 x Parula's'	38.57	55.00	3.02
PF 85372 x PF 85520	153.52	44.18	24.09**
PF 85372 x PF 83144	152.81	158.82	1.43
PF 85372 x Parula's'	155.62	45.83	15.20**
PF 83144 x Parula's'	160.38	48.75	19.75**

** Significant at the 1% level of probability.

To estimate the nature of genetic control of the erect leaf trait on the basis of the major gene model, the differences between the parents of each cross and the variability observed were taken as reference points. A sharp difference in mean leaf angle values was obtained between erect leaf and pendent leaf genotypes, F_2 populations had wide distributions. The frequency distributions observed in the parental generations may be represented by a normal curve in which the variances of these generations were reduced when compared with the variances of other generations. In contrast, the segregant generations presented discontinuities which led us to formulate the hypothesis of segregation of a small number of genes in the expression of the trait. On this basis, the F_2 generation of each cross had a 3:1 segregation at the heading stage when the crosses were between erect leaf and pendent leaf genotypes (Table II), indicating that the difference between the parents was at one locus, with dominance for the narrower leaf angle. Similarly, the F_2 generations of the crosses between genotypes with different leaf angles indicated the occurrence of a 1:3 proportion during the milk stage, i.e., an inversion of the proportion observed during the heading stage, indicating dominance of the wider leaf angle (Table II). The F_2 generations of the crosses between genotypes with similar leaf angles presented continuous variation at both evaluation times, demonstrating the absence of variability. PF 85372, however, had a different distribution; i.e., crosses involving PF 85372 had continuous variation at the heading stage and 1:3 segregation at the milk stage, indicating that the allele responsible for the manifestation of the trait in this genotype was different from the others.

The crosses of similar genotypes presented reduced total phenotypic variance at the heading stage, whereas F_2 variance was considerable in crosses of phenotypically distinct genotypes (Table III). Partition of the total phenotypic variance revealed that additivity variance was predominant in the expression of the trait, with dominance deviation also being of significant importance in some crosses. Data at the milk stage showed elevated phenotypic variances for all crosses (Table III), whereas environmental variances were reduced. Partitioning of phenotypic variance demonstrated that additive and dominance effects were important in the determination of leaf angle (Table III).

Estimates of the additive (a) and dominance (d) effects estimated from the generations means showed that both were important in the expression of erect and pendent leaves (Table IV). At the heading stage, dominance was negative, indicating that the alleles that decreased the aperture of the flag leaf angle were dominant over the alleles that increased the angle. In contrast, dominance was positive at the milk stage, indicating that the alleles which increased the leaf angle were dominant at this time (Table IV).

Broad-sense heritability (h^2b) was high for crosses of genotypes with erect and pendent leaves and lower for crosses of similar genotypes (Table V). Narrow-sense heritability (h^2n) could be calculated only for those crosses for which backcrossed populations were available. Estimates of h^2n were lower than h^2b estimates, in agreement with the marked dominance deviations observed (Table V).

Table II - Chi-square test for the proportions of observed and expected number of F₂ plants with the erect leaf trait, as determined at heading (1st) and milk (3rd) stages of plant development. Eldorado do sul, 1989.

Cross	Evaluation	Nº of plants observed			Expected proportion	X ²	P
		Erect leaf	Pendent leaf	Total			
PF 85520 x PF 83144	1st 3rd	108 45	33 96	141 141	3:1 1:3	0.18 3.58	0.75-0.50 0.10-0.05
PF 85520 x Parula's'	1st 3rd	329 252	0 77	329 329	1:0 1:0	0.00 18.02	1.00 1.00
PF 85372 x PF 85520	1st 3rd	357 103	0 254	357 357	1:0 1:3	0.00 1.13	1.00 0.50-0.25
PF 85372 x PF 83144	1st 3rd	158 15	59 202	217 217	3:1 0:1	0.55 1.03	0.50 0.50-0.25
PF 85372 x Parula's'	1st 3rd	135 40	0 95	135 135	1:0 1:3	0.00 3.48	1.00 0.10-0.05
PF 83144 x Parula's'	1st 3rd	121 45	33 109	154 154	3:1 1:3	0.87 1.70	0.25-0.50 0.25-0.50

Table III - Estimates of phenotypic (VF₂), genetic (VG), environmental (VE), additive (VA), and dominance (VD) variances of the erect leaf trait at heading (1st) and milk (3rd) stages of plant development. Eldorado do Sul, 1989.

Cross	Evaluation	VF ₂	VG	VE	VA	VD
PF 85520 x PF 83144	1st	1,303.79	1,083.26	220.53	939.97	143.29
	3rd	3,251.76	2,913.31	338.45	1,255.24	1,658.07
PF 85520 x Parula's'	1st	108.07	56.91	51.16	--	--
	3rd	2,218.43	1,656.12	562.31	--	--
PF 85372 x PF 85520	1st	449.67	216.85	232.82	542.51	-325.82
	3rd	2,928.48	2,595.10	333.38	1,550.81	1,044.29
PF 85372 x PF 83144	1st	1,343.61	1,051.01	292.60	632.07	418.94
	3rd	1,083.91	938.67	145.24	1,673.38	-734.71
PF 85372 x Parula's'	1st	338.05	213.56	124.49	--	--
	3rd	2,860.74	2,548.98	311.76	--	--
PF 83144 x Parula's'	1st	1,319.97	1,148.64	171.33	--	--
	3rd	2,993.17	2,773.56	219.61	--	--

Table IV - Mean (m), additive (a) and dominance (d) effects estimates according to Mather and Jinks (1971) at heading (1st) and milk (3rd) stages of development. Eldorado do Sul, 1989.

Cross	Evaluation	m	a	d	X2	P
PF 85520	1st	87.58	-52.56	-45.28	0.4168	0.90-0.95
x						
PF 83144	3rd	99.22	-57.79	41.89	0.1836	> 0.95
PF 85520	1st	31.33	2.39	0.82	0.1144	0.90-0.95
x						
Parula's'	3rd	47.78	-7.62	19.35	0.5012	0.70-0.80
PF 85372	1st	39.35	5.70	5.78	0.4553	0.90-0.95
x						
PF 85520	3rd	98.59	54.59	39.59	0.0366	> 0.95
PF 85372	1st	92.82	-42.05	-26.66	0.1699	> 0.95
x						
PF 83144	3rd	153.29	-3.99	3.57	0.6318	0.75-0.90
PF 85372	1st	35.86	3.18	9.28	0.1940	0.90-0.95
x						
Parula's'	3rd	100.23	54.74	20.82	0.1940	> 0.95
PF 83144	1st	85.10	50.46	-35.39	0.4760	0.90-0.95
x						
Parula's'	3rd	104.13	55.76	45.19	0.1749	> 0.95

Table V - Broad-sense (h^2_b) and narrow-sense (h^2_n) heritability estimates for the erect leaf trait at heading and milk stages of development. Eldorado do Sul, 1989.

Cross	Heading stage		Milk stage	
	h^2_b	h^2_n	h^2_b	h^2_n
PF 85520 x PF 83144	0.83	0.72	0.89	0.37
PF 85520 x Parula's'	0.52	--	0.74	--
PF 85372 x PF 85520	0.48	1.20	0.88	0.53
PF 85372 x PF 83144	0.78	0.47	0.86	1.54
PF 85372 x Parula's'	0.63	--	0.89	--
PF 83144 x Parula's'	0.87	--	0.92	--

DISCUSSION

Changes in architecture that permit plants to better intercept light have been suggested as an appropriate means of improving grain yield in cereal crops.

Studies have reported that flag leaf angle is a trait with quantitative behavior in wheat (Borojevic and Kraljevic-Balalic, 1984; Wu *et al.*, 1984; Borojevic and Dencic, 1986). Carvalho and Qualset (1978) suggested that the flag leaf angle may be explained by the presence of two loci. Frequency distributions of the crosses suggest a major gene differentiates the parents in the control of leaf angle, with considerable differences between the most erect and the most pendent parent (Table II). Other investigators have also indicated that continuous variance traits, which are normally considered to be under the control of a large number of genes with small effects, may present Mendelian type variations, controlled by one or a few genes (Weber, 1959; Qualset, 1979).

We studied flag leaf angle variability by testing the plants at three growth stages. Genotypes may maintain erect or pendent leaves throughout the growth stages or may modify their leaf angle over time, a behavior also reported by others (Borojevic and Kraljevic-Balalic, 1984; Borojevic and Dencic, 1986). PF 85520 and Parula's' maintained erect leaves throughout plant development, with only small changes in flag leaf angle due to natural senescence. PF 83144 (pendent leaf) also maintained the trait unchanged until full plant maturation. In contrast, PF 85372, which had erect leaves at heading stage, underwent a continuous change in leaf angle, with leaves being pendent at the milk stage. This agrees with one of the erect leaf types described by Borojevic and Dencic (1986), which presented erect leaves at ear formation, horizontal leaves at the kernel filling stage, and pendent leaves at the end of the final stage. Frequency distribu-

tions showed a consistent monohybrid proportion in segregant populations, indicating that the alleles involved in the expression of the erect trait are probably members of the same allele series with different levels of dominance. PF 83144 probably is the carrier of the dominant allele (AA), PF 85520 and Parula's' have the recessive allele (aa), and PF 85372 has an allele that has an intermediate behavior (A'A'). The gradation of dominance may be $A > A' > a$, with the full expression of the trait occurring at the milk stage, demonstrating dominance for pendent leaves. However, the data do not permit us to discard the hypothesis of multiple gene action, with the possible presence of two independent genes acting at different times. According to this hypothesis, the genotypes would be as follows: PF 85520 and Parula's' (AA bb). PF 85372 (AA BB) and PF 83144 (aa BB). On this basis, genotype (AA bb) would present erect leaves at the heading stage with dominant gene action for this type of leaf; genotype (aa BB) would present pendent leaves and dominant gene action for pendent leaves at milk stage, and genotype (AABB) would present both leaf types, i.e., erect leaf at heading stage and pendent leaf at milk stage.

Estimates of genetic variances were high in all crosses between distinct genotypes (Table III). Crosses of genotypes with very similar leaf angle genetic variance estimates were similar to those of environmental variation at heading stage. In contrast, at milk stage the genetic variances were very high for all crosses when compared with environmental variances, revealing that environmental effects on trait expression were not significant. Partition of the total F_2 phenotypic variance (Allard, 1960) and of the estimates of genetic effects obtained by the model of Mather and Jinks (1971) demonstrated that the components of additive and dominance variances (Table III) and additive and dominance effects (Table IV) were similar in most crosses. Similarly, the frequency distributions of F_1 generations revealed dominant gene action for the narrower flag leaf angle at heading stage, and dominant gene action for the wider flag angle at milk stage, both with partial dominance. Additive, nonadditive, and partial dominance effects have also been reported by other investigators of wheat (Carvalho and Quallsert, 1978; Borojevic and Kraljevic-Balalic, 1984; Nigam and Srivastava, 1976; Wu *et al.*, 1984).

Broad-sense heritability estimates were relatively high, suggesting small environmental effects on crosses of erect leaf and pendent leaf genotypes (Table V). Heritability estimates were lower in crosses of genotypes having similar leaf angles. Narrow-sense heritability values suggested dominance deviations in crosses of erect leaf and pendent leaf genotypes. High broad-sense and narrow-sense heritability values were also obtained by Carvalho and Qualset (1978) for flag leaf angle in wheat.

The utilization of the erect leaf trait in breeding programs is viable because the inheritance of the trait is relatively simple and is not correlated with other traits (Carvalho, 1974), and the incorporation of genes easily identifiable on the basis of phenotype permits selection during the first segregant generations. Erect leaf has high heritability, but

dominance deviation should be considered, especially in crosses of genotypes with quite distinct flag leaf angles, in which dominance for the narrower angle at heading stage and later segregation may make it difficult to identify the desired genotypes. Similarly, Rasmusson (1987) considered that the heritability estimates for erect leaves in barley (*Hordeum vulgare* L.) were sufficiently high to permit effective selection in the first segregant generations. When the difference between genotypes is very high, the influence of environment does not represent a problem in the identification of the desired individuals. For crosses of genotypes that have little variation, manifestation of the trait may be affected by the environment, particularly by air humidity, plant nutritional status and sowing density (Borojevic and Dencic, 1986). Selection, using crosses of parents having similar leaf angles makes it more difficult to identify genotypes having more erect leaves, especially when selection is performed at the heading stage. It is important to emphasize that changes in leaf angle during plant maturation, requires at least two measurements during the growth cycle in order to provide precise genotype identification of the individuals in the population.

CONCLUSIONS

Analysis of the results obtained for the characterization of the genetic basis of flag leaf angle inheritance in four wheat genotypes led us to formulate the hypothesis of a gene with at least three alleles encoding expression of the trait. However, the possibility of two independent genes acting at different times cannot be omitted. Additivity and dominance deviation effects were significant, with the direction of dominance being more erect leaves at heading stage to pendent leaves at milk stage.

The use of the erect leaf trait as a selection criterion is viable because of its high heritability. However, the monogenic inheritance found indicates little flexibility in trait manipulation, mainly due to the restricted possibility of obtaining variability through new recombinant types. The stage of plant development at which selection is made, however, is of fundamental importance since some genotypes present phenotypes changes up to the maturation phase.

RESUMO

Quatro genótipos de trigo (*Triticum aestivum* L.) com distintos ângulos de inserção da folha bandeira foram utilizados para estudar a herança deste caráter. Na caracterização das bases genéticas foram estudadas seis gerações (P₁, P₂, F₁, F₂, RC₁F₁ e RC₂F₁) provenientes de seis cruzamentos distintos, sendo efetuadas três observações nos estádios de espigamento, antese e grão leitoso. Os resultados obtidos indicaram a existência de diferenças genéticas entre os genótipos de folha ereta (PF 85520 e Parula's') intermediária (PF 85372) e pendente (PF 83144). Em todas as situações as observações no espigamento e em grão leitoso permitiram uma

análise mais adequadas dos parâmetros genéticos. Os dados das populações segregantes mostraram a presença de um gene e três alelos na expressão do caráter, entretanto, a possibilidade da existência de dois genes independentes controlando o caráter não pode ser descartada. As estimativas dos efeitos de aditividade, dos desvios da dominância e da herdabilidade foram elevadas, apontando que a seleção para obtenção de genótipos com folha ereta poderá ser realizada de maneira simples e eficiente, resultando em progresso genético rápido e expressivo.

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(Received January 28, 1991)