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Genetics of lodging-resistance in wheat

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ABSTRACT - *Knowledge on the inheritance of lodging-resistance is of great value for the development of new wheat varieties (*Triticum aestivum *L.). Crosses among four different bread wheat genotypes were evaluated in the field. The analysis was based on three fixed (P_1, P_2 and F_1) and three segregant (F_2, BC_1F_1 and BC_2F_1) generations. Means and variances were computed for each generation in all crosses and the gene effects estimated. The lodging-resistance factor method (cLr) was measured. Partial or complete dominance of the lodging-susceptible over the lodging-resistant parent in each cross was evident. Results showed a large genetic variability among the genotypes.*

Key words: lodging-resistance factor index, heritability, quantitative genetics, gene action, *Triticum aestivum* L.

INTRODUCTION

Lodging caused by severe storms, high soil fertility or delayed harvest frequently leads to serious losses of small grain. It has been a longstanding major problem in agriculture and a challenging subject for agronomists (Watanabe 1997).

The incidence of lodging in wheat has decreased in southern Brazil due to the development of cultivars with improved lodging-resistance. Despite this progress, major yield losses caused by lodging still occur because of intensive agricultural practices that allow high plant population densities and fertilization rates (Cruz et al. 2001). Thus, selection for lodging-resistance remains of primary importance to breeders. However, very little attention has been given to the inheritance of lodging-resistance in wheat.

Direct selection for lodging-resistance in wheat has been ineffective due to a genotype x environment interaction that does not allow a differentiation among genotypes (Cruz et al. 2001). Several methods of evaluating the lodging-resistance in small grain varieties have been

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proposed. The most common method used to determine lodging-resistance is the lodging percentage observed and scored as visual scales. However, it is difficult to establish a uniform condition of evaluation, mainly in highly heterozygous populations. To solve this problem, many methods to measure lodging-resistance have been proposed, among them the cLr method, internationally recognized as the most efficient for indirect selection in segregant populations. The second most efficient method is known as 'pulling-down resistance' and the third as 'pushing-down resistance'. These methods do not require field evaluations but frequently measure lodging-resistance under laboratory conditions (Watanabe 1977). The lodging-resistance factor index (cLr) measures the traction or weight that a unit length of a grass stem can support (Murphy et al. 1958). The cLr index has high heritability and is controlled primarily by additive gene action, and has been proposed as an indirect mean of selection because it is correlated with lodging-resistance (Watanabe 1997).

The present study aimed to determine the mode of inheritance and heritability of lodging-resistance in wheat as measured by the cLr index.

MATERIAL AND METHODS

Four wheat genotypes were used as described in Table 1 and their F_1, F_2, BC_1F_1, and BC_2F_1 were evaluated.

The fixed and segregant populations were established individually, distributed in random blocks at a distance of 0.30 m between rows. The rows were 3 m long and the plants spaced 0.30 m apart within the row, keeping the plant density up to 10 plants per row. The experimental area was prepared by tilling and harrowing, and the fertilizers used were urea [$CO(NH_2)_2$] and potassium chloride (KCl). Initially 1/3 of the urea doses were applied at sowing and 2/3 at the time of the first weeding, 40 days after crop emergence. The soil pH was corrected using approximately 3 t ha^{-1} of dolomite limestone, based on the recommendations of the Southern Brazil Wheat Research Committee (1999).

The genotypes were evaluated approximately 25 days after anthesis, evaluating the three most advanced tillers in each plant, where cLr = F/b, being F = the weight (g) of the part that was suspended by a chain weighing 0.5 g per ring and with two rings per cm, fixed to the ear base, and b = the stem length (cm), measured from the soil surface to the ear base.

The cLr value is the chain weight divided by the stem length. The chain weight is the product of the weight of a chain unit times the number of units attached to the ear base of the wheat plant. The measurement is made when the chain weight balances with the bending strength of the stem. If any evaluating method is used, it is important to measure it at the same growth stage. In Japanese environments, the appropriate measurement stage is estimated to be between 30 to 40 days after heading time, because lodging-resistance is relatively less variable at this stage (Watanabe 1997).

Distribution of frequencies for cLr data were applied to each generation of all crosses obtained by a seven gram interval, with the purpose of estimating gene action and number of genes involved in the control of the trait using biometrical methods. The adjustment of the obtained distributions was verified by χ^2 test applications. Means and variances were calculated for each generation based on the observed value frequencies. Some genetic parameters were estimated: phenotypic (σ^2_P), environment (σ^2_E), genetic (σ^2_G), dominance (σ^2_D) and additive (σ^2_A) variances, as well as broad-sense (h^2_a) and narrow-sense (h^2_r) heritabilities, according to Carvalho (1982).

Genetic effects were tested in all crosses by the technique described by Mather and Jinks (1982), known as the joint scaling test. By this method, the parameter mean [m], additivity [a] and dominance [d], as well as the interactions aa, ad and dd, from the means of all studied crosses were estimated, followed by chi-square test (χ^2).

RESULTS AND DISCUSSION

The evaluation of three fixed generations (P_1, P_2 and F_1) and three segregant generations (F_2, BC_1F_1 and BC_2F_1) in six different crosses among genotypes EMB40, TB429, TB951 and TB961 allowed a complete analysis of the trait lodging-resistance factor index (cLr) (Table 1). The genotypes used in the crosses showed different responses to induced lodging as measured by cLr index, revealing two important aspects for breeders. First, trait segregation was observed in F_2, BC_1F_1 and BC_2F_1 generations. Second, there were some evidences of complete dominance among plants of the fixed F_1 generation. Therefore, there is indication of genetic variability for this trait.

All crosses involving genotype EMB 40, which showed the greatest lodging susceptibility, allowed the

Table 1. Genealogy of evaluated wheat genotypes

Genotype	Genealogy
TB 951	TB 108 // BR 23 * 2/PF 869114
TB 966	D-1TB // 1TB
TB 429	B-1TB // 1TB
EMB 40	PF 7650/NS18-78//CNT 8/PF7577

SOURCE: CPACT/EMBRAPA

application of a cut off point between classes 28 g m^{-1} and 35 g m^{-1}. Therefore, it was possible to establish frequencies of individuals with high susceptibility to the trait (< 35g m^{-1}) in comparison to individuals of high resistance (> 35g m^{-1}), resulting in around 75% lodging-susceptible and 25% lodging-resistant plants in the F_2 generation, revealing a 3:1 ratio. (Table 2). Moreover, 1:1, and 1:0 ratios were observed in the backcross generations BC_1F_1 and BC_2F_1, respectively. Thus, the one-gene-two-alleles hypothesis for the control of the trait lodging is acceptable in these three crosses (TB 429 x EM 40; TB 951 x EMB 40; TB 961 x EMB 40), supported by χ^2 values ranging from 0.48 to 1.00 (Table 3).

Crosses that did not involve genotype EMB 40 also showed genetic variability regarding means and variances estimated for segregant generations (F_2, BC_1F_1 and BC_2F_1) in comparison to values obtained for fixed generations (P_1, P_2 and F_1), except in the cross TB951 x TB961 (Table 2). These two genotypes do probably not differ regarding the trait lodging, suggesting that both have the same resistance genes. Consequently, these two genotypes cannot express segregation in the generations F_2, BC_1F_1 and BC_2F_1. There is evidence that in the crosses TB961 x TB429 and TB951 x TB429 the dominance is strongly expressed in the sense of susceptibility. Applying the cut off point between classes 49 and 56 g m^{-1}, it was possible to establish susceptible and resistant plant groups in the crosses involving TB951 and TB961 with TB429. According to this criterion it was possible to determine the frequency of plants with the highest (> 56 g m^{-1}) and those with the lowest (< 56 g m^{-1}) degree of lodging-resistance, allowing the establishment of a ratio of 3:1 of lodging-susceptible to lodging-resistant plants in generation F_2 (Table 2). Backcross populations BC_1F_1 and BC_2F_1 showed 1:1 or 1:0 ratios, respectively (Table 2). Consequently, the hypothesis of one gene with two alleles can also be attributed to differences in the expression of the lodging trait for these two crosses (TB951 x TB429 and TB961 x TB429) considering the support evidenced by the χ^2 test, which ranged from 0.53 to 1.00 (Table 3).

This hypothesis that one gene with two alleles controls lodging only finds support when the analysis is done for each cross individually, since a group of plants with intermediate phenotypes for lodging was observed, mainly in the crosses TB951 x EMB40 and TB961 x EMB40 in the generations F_2, BC_1F_1, and BC_2F_1. Moreover, segregant generations F_2, BC_1F_1, and BC_2F_1 of the crosses TB951 x TB429 and TB951 x TB429 showed plant groups with lodging susceptibility such as EMB40. For this reason, the hypothesis of one gene with two alleles does not fit for complete analysis of all crosses. Consequently, a new hypothesis needs to be formulated, assuming two independent genes with two alleles each that would control the lodging trait in wheat. This hypothesis can fit to the intermediate plant groups of the crosses TB951 x EMB40 and TB961 x EMB40 and to those involving TB429 as parent. In the first two crosses two cutting points were needed between the classes 28 and 35, and 49 and 56 m^{-1} (Table 2). This fact allows the proposal of 12:3:1 in the F_2 generation, 2:1:1 in BC_1F_1 and 1:0:0 in BC_2F_1. This proposal had to be adjusted to the chi-square test, ranging from 0.70 to 1.00 probability for BC_1F_1 and BC_2F_1, respectively. Thus, the phenotypic ratios of expected classes in F_2, BC_1F_1 and BC_2F_1, as well as the respective probabilities of adjustment by the chi-square test (Tables 2 and 3) agree with the hypothesis that genotype EMB40 has two independent genes with dominant alleles for lodging susceptibility (genetic constitution *AABB*). On the other hand, genotypes TB951 and TB961 must have two independent genes with recessive alleles (genetic constitution *aabb*) for stem lodging-resistance in wheat. The intermediate response expressed by genitor TB429 may be due to the presence of two genes with two alleles, of which one locus is recessive and the other dominant (genetic constitution *aaBB*).

The analysis of frequency distribution of fixed and segregant generations from each cross (Table 2) led to the establishment of a hypothesis about the number of genes by which genotypes differ in relation to cLr. This is very important for breeders since it establishes the size of the initial population and the best time to use the maximum of artificial selection pressure.

Phenotypic ratios of cLr classes expected from generations F_2, BC_1F_1 and BC_2F_1 as well as respective probabilities of adjustment by the chi-square test are presented in Table 3.

The cross TB951 x TB961 does not evidence any discontinuity or transgressive segregation in F_2. The distribution of F_2 was also consistent with that verified for respective backcrosses (P=1.00). This observation suggests that the genetic constitution of parents is *AABB*, in agreement with results obtained in the crosses above.

Table 2. Frequency distribution, number of individuals (**N**), means (**X**) and variances (s^2) for the lodging-resistance factor method (cLr) in three non-segregating (P_1, P_2 and F_1) and three segregating generations (F_2, BC_1F_1 and BC_2F_1), in six crosses, involving four wheat genotypes

Crosses and Generations	Classes (interval: 7.00cm)													N	$\bar{X}$	σ^2
TB429 X EMB40	7	14	21	28	35	42	49	56	63	70	77	84	91			
P_1				4	19	20	1							44	37.9	23.5
P_2	5	10	26	10										51	19.6	37.3
F_1	3	14	41	29										87	21.7	30.8
F_2	1	85	78	20	30	28	1							243	23.3	95.2
BC_1F_1	1	4	10	10	12	15								52	30.8	94.6
BC_2F_1	6	7	7	8	2									30	19.4	76.7
TB961 X TB429	7	14	21	28	35	42	49	56	63	70	77	84	91	N	$\bar{X}$	σ^2
P_1								6	18	26	14			64	68.3	40.4
P_2				8	24	27	11							70	39.1	39
F_1				9	45	51	10							115	38.8	28.6
F_2				2	60	136	59	5	41	29	4			336	47.5	127.6
BC_1F_1					3	4	13	4	9	7				40	54.8	115.0
BC_2F_1				15	8	9	14							46	38.3	75.7
TB951 X EMB40	7	14	21	28	35	42	49	56	63	70	77	84	91	N	$\bar{X}$	σ^2
P_1								3	10	31	29	2	1	76	71.8	41.0
P_2	10	58	64	11										143	17.7	26.8
F_1	5	11	35	15	7									73	21.8	49.8
F_2	33	100	92	80	20	32	25	1	4	7	8	4	5	411	27.4	308.4
BC_1F_1	1	18	19	1	5	9	5	4	10	9				81	36.6	429.1
BC_2F_1	4	4	10	9										27	20.2	54.0
TB951 X TB961	7	14	21	28	35	42	49	56	63	70	77	84	91	N	$\bar{X}$	σ^2
P_1								5	14	29	11	1		60	68.7	39.0
P_2								3	7	15	11	2		38	70.4	50.2
F_1								4	14	16	6	1		41	67.6	43.1
F_2								21	72	105	51	12		261	69.0	47.0
BC_1F_1								4	13	11	11			39	68.2	48.3
BC_2F_1								6	15	9	5			35	65.6	43.5
TB951 X TB429	7	14	21	28	35	42	49	56	63	70	77	84	91	N	$\bar{X}$	σ^2
P_1								2	10	12	8			32	68.7	39.3
P_2				3	14	12	4							33	38.6	34.1
F_1				3	23	24	4							54	38.8	25.4
F_2				2	28	70	28	6	19	14	2			169	47.4	125.8
BC_1F_1					3	1	6	2	6	3				21	54.3	131.8
BC_2F_1				6	5	5	6							22	38.5	68.8
TB961 X EMB40	7	14	21	28	35	42	49	56	63	70	77	84	91	N	$\bar{X}$	σ^2
P_1								3	4	17	14	0	1	39	71.3	48.7
P_2	6	28	33	5										72	17.6	27.6
F_1	2	10	40	18	10									80	23.1	42.7
F_2	10	47	51	39	10	14	13	2	1	3	5	3	2	200	28.4	314.1
BC_1F_1	2	8	11	2	4	5	6	1	6	6				51	37.5	419.1
BC_2F_1	4	3	4	7										18	19.4	72.4

Table 3. Adjustment test of chi-square (χ^2) applied to scores observed in segregating generations (F_2, BC_1F_1 and BC_2F_1)

Crosses and Generations	Observed frequency		Total	Expected frequency	χ^2	Probability (0.05)
	< 35	≥ 35				
TB429 x EMB40						
F_2	184	59	243	3:1	0.07	0.80
BC_1F_1	25	27	52	1:1	0.08	0.78
BC_2F_1	28	2	30	1:0	0.13	0.54
TB961 x TB429						
F_2	257	79	336	3:1	0.40	0.53
BC_1F_1	20	20	40	1:1	0.00	1.00
BC_2F_1	32	0	32	1:0	0.00	1.00
TB951 x EMB40						
F_2	305	106	411	3:1	0.14	0.71
BC_1F_1	39	42	81	1:1	0.11	0.74
BC_2F_1	27	0	27	1:0	0.00	1.00
TB951 x TB961						
F_2	0	261	261	0:1	0.00	1.00
BC_1F_1	0	39	39	0:1	0.00	1.00
BC_2F_1	0	35	35	0:1	0.00	1.00
TB951 x TB429						
F_2	128	41	169	3:1	0.05	0.82
BC_1F_1	10	11	21	1:1	0.05	0.83
BC_2F_1	16	0	16	1:0	0.00	1.00
TB961 x EMB40						
F_2	147	53	200	3:1	0.24	0.62
BC_1F_1	23	28	51	1:1	0.49	0.48
BC_2F_1	18	0	18	1:0	0.00	1.00

The highest values of phenotypic variances were observed in crosses between the resistant genotypes TB951 and TB961 with the susceptible EMB40 (Table 4). The lowest value was verified in the cross between resistant genotypes TB951 and TB961, possibly with the same genetic constitution.

Values observed for environmental variance were of low magnitude when compared with values of phenotypic variance in all crosses, except for the cross involving resistant genotypes where both the phenotypic and environmental variances were very low and similar. These data characterize a high correlation between phenotypic and genetic variances and, consequently, high values for heritability, except for the cross TB951 x TB961.

In relation to the genetic effects estimated by Mather and Jinks' (1971) method, Table 5 shows that the dominance was superior to the additive effect in the cross TB429 x EMB40. However, additivity revealed its contribution to the genetic variance in the other crosses, except for TB951 x TB961 where genetic variance was not observed due to the lack of genetic differences between parents for the cLr trait.

Table 4. Scores of phenotypic (σ^2_P), environment (σ^2_E), genetic (σ^2_G), additive (σ^2_A) and dominance (σ^2_D) variances and heritability coefficient in the broad (h^2_a) and narrow sense (h^2_r), for lodging-resistance factor index (cLr) in wheat plant

CROSSES	Lodging-resistance factor method (cLr)					%	
	σ^2_P	σ^2_E	σ^2_G	σ^2_A	σ^2_D	h^2a	h^2r
TB429 x EMB40	95.2	30.6	64.6	19.0	45.5	67.8	20.0
TB961 x TB429	127.7	34.2	93.4	64.3	29.2	73.2	50.4
TB951 x EMB40	308.4	41.8	266.6	133.7	132.9	86.4	43.3
TB951 x TB961	47.0	43.9	3.1	2.2	0.9	6.6	4.6
TB951 x TB429	125.8	31.0	94.8	51.0	43.8	75.3	40.5
TB961 x EMB40	314.1	40.4	273.7	136.7	137.7	87.1	43.5

The non-significant values of χ^2 statistics in all crosses (Table 5) suggest that an additive-dominant model is enough to explain these trait variances.

The presence of one or two major genes controlling the trait became evident in an analysis of frequency distribution across generations in each cross. Genotypic differences were not detected among resistant genotypes. However, a difference of only one gene with two alleles

was detected between the resistant and the intermediate genotypes, and between the intermediate and the susceptible genotype. A difference of two genes was detected between the resistant and susceptible genotypes. Therefore, the presence of only one dominant allele *A* would be enough to express lodging susceptibility, while for an intermediate response a lack of dominant allele *A* and the presence of dominant allele *B* would be necessary. In this sense, only the presence of dominant allele *A* would be necessary to express lodging susceptibility. Consequently, it was possible to suggest a hypothesis for the genetic constitution of parents in relation to the cLr trait from global data analysis, shown in Table 6. This hypothesis expresses the variability among the analyzed genotypes, corroborated by the significant difference of cLr mean values among parents as well as by the high values observed for genetic variance (Table 5).

The evaluation of the genetic potential of a genotype based on its phenotype is not very accurate in cases where the trait heritability is low. However, the accuracy of selection may be increased by using an average of several phenotypic scores, approaching the genotypic value and increasing the heritability. In this case, it is important to observe whether the variances refer to individuals or average scores. Actually, heritability is important to predict the gain from selection, therefore, the unit must be related to the common unit used in the selection.

The heritability obtained for trait cLr in the present work was relatively high despite having been obtained from the means of three replications within the same plant (cLr value for each plant was the mean of observations in the three most advanced tillers).

Many studies conducted in Japan with rice had reported high heritabilities for the cLr trait, even when

Table 5. Genetic effects for the model of three and six parameters for the study of the lodging-resistance factor index (cLr) in wheat plants

Generations and Parameters	Lodging-resistance factor method (cLr)		
	TB429 x EMB40	**TB961 x TB429**	**TB951 x EMB40**
P_1	37.9 ± 4.8	68.3 ± 6.4	71.8 ± 6.4
P_2	19.6 ± 6.1	39.1 ± 6.2	17.7 ± 5.2
F_1	21.7 ± 5.5	38.8 ± 5.3	21.8 ± 7.1
F_2	23.3 ± 9.8	47.5 ± 11.3	27.4 ± 17.6
BC_1F_1	30.8 ± 9.7	54.8 ± 10.7	36.6 ± 20.7
BC_2F_1	19.4 ± 8.8	38.3 ± 8.7	20.2 ± 7.3
M	28.2 ± 0.5	54.0 ± 0.5	44.1 ± 0.4
[a]	9.4 ± 0.5	14.7 ± 0.5	26.6 ± 0.4
[d]	-7.1 ± 0.8	-15.0 ± 0.7	-24.6 ± 0.9
c^2	0.2	0.1	2.6
G.L	3	3	3
P	1.0	1.0	0.8
Generations and Parameters	**TB951 x TB961**	**TB951 x TB429**	**TB961 x EMB40**
P_1	68.7 ± 6.2	68.7 ± 6.3	71.3 ± 7.0
P_2	70.3 ± 7.1	38.6 ± 5.8	17.6 ± 5.3
F_1	67.8 ± 6.6	38.8 ± 5.0	23.1 ± 6.5
F_2	69.0 ± 6.9	47.4 ± 11.2	28.4 ± 17.7
BC_1F_1	68.0 ± 6.9	54.3 ± 11.5	37.5 ± 20.5
BC_2F_1	66.0 ± 6.6	38.5 ± 8.3	19.4 ± 8.5
M	69.3 ± 0.6	54.0 ± 0.7	43.5 ± 0.6
[a]	-0.3 ± 0.6	15.1 ± 0.7	26.2 ± 0.6
[d]	-1.7 ± 1.2	-14.9 ± 1.0	-21.5 ± 1.0
c^2	0.1	0.0	2.2
G.L	3	3	3
P	1.0	1.0	0.8

heritability was estimated at individual levels. However, other authors found low values for cLr trait heritability in oats (Brown and Patterson 1992). Watanabe (1997) reported that although there are few genetic analyses to determine a mode of inheritance of lodging-resistance in rice plants, the results obtained so far have revealed that the number of genes controlling lodging-resistance is limited and that heritability for lodging-resistance is lower than that for heading time and stem length, but higher than that for number of panicles and yield; this implies that selection for lodging tends to be effective.

Table 6. Parents, putative genotypes, means and phenotypic groups for heading date and height

	Lodging-resistance factor index cLr		
Parent	**Putative genotypes**	[1]**means** g m^{-1}	[2]**phenotypic group**
TB 951	*aabb*	69.73 a	lodging-resistant
TB 961	*aabb*	70.00 a	lodging-resistant
TB 429	*aaBB*	38.53 b	intermediate
EMB 40	*AABB*	18.30 c	lodging susceptible

[1]Means followed by the same letter are not different according to Tukey at 5%
[2]Phenotypic groups based on data obtained in the current study

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Genética da resistência ao acamamento em trigo

RESUMO - *O conhecimento da herança de resistência ao acamamento é de grande valor para o desenvolvimento de novas variedades de trigo (*Triticum aestivum *L.). Cruzamentos entre quatro genótipos de trigo foram avaliados em condições de campo. A análise foi baseada em três gerações fixas (P_1, P_2 e F_1) e três gerações segregantes (F_2, BC_1F_1 e BC_2F_1). Médias e variâncias foram computadas para cada geração em todos os cruzamentos. A natureza e os efeitos dos genes envolvidos foram estimados. A resistência ao acamamento foi mensurada pelo método (cLr). Dominância parcial ou completa de suscetibilidade ao acamamento ou de resistência foi evidenciado em cada cruzamento. Resultados demonstraram grande variabilidade genética entre os genótipos estudados.*

Palavras-chave: coeficiente de resistência ao acamamento, herdabilidade, genética quantitativa, ação gênica, *Triticum aestivum* L.

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