

GENETICS AND MONOSOMIC ANALYSIS OF ALUMINUM TOLERANCE IN WHEAT (*Triticum aestivum* L.)

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ABSTRACT

Experiments were conducted in order to investigate the genetics of tolerance to aluminum (Al^{+++}) in wheat and to determine the chromosome location of major genes involved, by monosomic analysis. The responses to Al^{+++} were assessed by measuring the root regrowth, as described by C.E. de O. Camargo (Ph.D. Thesis, Oregon State University, 1978).

The level of Al^{+++} that best discriminated between sensitive and tolerant plants was found to be 4 ppm. Genetic analysis of crosses with the variety BH 1146 demonstrated one or two different genes. Monosomic analysis revealed that the gene for tolerance to Al^{+++} present in BH 1146 was located on chromosome 4D.

INTRODUCTION

Aluminum toxicity has been one of the more striking environmental stresses that affect crop plants in the sub-tropical soils of Brazil. The injurious effects of aluminum (Al^{+++}) have been described for several crop species and considerable genetic variation has been reported among and within species (Foy *et al.*, 1965). Differences in tolerance to Al^{+++} were recognized in the early years of wheat (*Triticum aestivum* L.) breeding in

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southern Brazil (Beckman, 1926; Paiva, 1942). However, definite recognition that Al^{+++} was the cause of the poor plant development was made by Araujo (1948).

Wheat varieties developed under acid soil conditions in Brazil usually present a greater tolerance to Al^{+++} than varieties developed abroad, emphasizing the importance and efficiency of natural selection for this trait (Araujo, 1951; Foy *et al.*, 1965; Mesdag and Sloomaker, 1969). The Al/Ca ratio has an important influence on expression of the sensitive phenotype (Andrade, 1976).

Preliminary studies on the genetics of Al^{+++} tolerance were made by Beckman (1954) without any conclusive results. Kerridge and Kronstad (1968) showed that Al^{+++} tolerance in the wheat variety Atlas 66 was due to a single gene. Iorczeski (1977) used a laboratory technique for screening for Al^{+++} tolerance in several crosses involving Brazilian, Mexican and U.S.A. wheat varieties. However, the results were inconclusive.

A complete genetic analysis of Al^{+++} tolerance was done by (Camargo, 1978) using a laboratory technique. He demonstrated that the Brazilian variety BH 1146 carried a major gene for Al^{+++} tolerance. Using the same technique Aniol (1984) observed that BH 1146 was not homozygous for Al^{+++} tolerance. He also obtained two different patterns of segregating populations with one and two genes. A different approach was taken by Nodari *et al.* (1982), who identified two major genes determining tolerance to Al^{+++} in the field.

Sloomaker (1974) suggested that the A genome is important for tolerance to low levels of Al^{+++} , and that for hexaploid wheat the D genome was of more importance. The major gene present in Atlas 66 was located on chromosome 5D by Prestes *et al.* (1975).

Brazilian wheat varieties are used extensively as sources of Al^{+++} tolerance in breeding programs throughout the world. It is therefore, of importance to investigate the genetics of tolerance to Al^{+++} and to determine through monosomic analysis the chromosome location of the major genes involved.

MATERIAL AND METHODS

The technique used in this study was described by (Camargo, 1978, 1981) who measured root regrowth. After 48 hr of growth in a pure nutritive solution, seedlings were grown for 48 hr in a nutritive solution with varying concentrations of Al^{+++} . The seedlings were then returned to a nutritive solution without Al^{+++} and the length of the primary root regrowth measured after 72 hr.

Experiment 1. Varieties utilized in this experiment are described in Table I. This experiment was conducted to determine the Al^{+++} concentration that best separated tolerant and susceptible varieties. The concentrations tested were 0, 2, 4, 6, 8 and 10 ppm

of Al^{+++} . Forty seeds were used per replication, with four replicates per variety and Al^{+++} concentration.

Table I - Genealogy and origin of the cultivars subjected to 0, 2, 4, 6, 8 and 10 ppm of Al^{+++} .

Cultivar	Genealogy	Origin
BH 1146	PG1//Fronteira/Mentana	Brazil
CI 14124	Chancellor ⁸ /Yuma	U.S.A.
Atlas 66	Fronoso/Redhart 3/Noll 28	U.S.A.
Siete Cerros	Penjamo "S"/3/Timstein/Kenya//Gabo	Mexico
Chinese Spring	-	China

Experiment 2. Parents, F_1 and F_2 of three crosses were grown as described by Camargo (1978). The number of crosses and plants per generation varied as described in Table II.

Table II - Number of plants tolerant (T) and sensitive (S) to 4 ppm of Al^{+++} in the F_1 and F_2 generations and χ^2 for goodness of fit for several wheat crosses with the variety BH 1146.

Crosses	F ₁ number of plants	F ₂ number of plants		Ratio	P
	T/S	T	S	T/S	
BH 1146/CI 14124	28/0	121	22	13:3	.25
BH 1146/Atlas 66	22/0	143	10	15:1	.50
Favorit/BH 1146	22/0	75	31	3:1	.25

Experiment 3. This experiment included 20 seedlings of the F_2 population of the cross BH 1146 x Chinese Spring that were tested in 0, 2, 4, 6, 8 and 10 ppm of Al^{+++} . A test for a genetic model was made for each Al^{+++} level.

Experiment 4. Monosomic lines ($2n = 41$) of Al^{+++} - sensitive Chinese Spring, kindly supplied by Dr. E.R. Sears, were used as female parents in crosses with a pure line, cv. BH 1146, tolerant to Al^{+++} . Monosomic F_1 plants were left to self pollinate. The resulting F_2 populations and the F_2 of a cross of Chinese Spring ($2n = 42$) and BH 1146 were grown in a nutritive solution containing 4 ppm of Al^{+++} . The identification of

tolerant and sensitive plants was made by measuring root regrowth as described by Camargo (1978). A test for goodness of fit to the 3 tolerant: 1 sensitive ratio was made for all monosomic families. All cytological checks were conducted as described by UNRAU (1950).

RESULTS

Results of the different Al^{+++} concentrations for all the parental varieties are presented in Figure 1. The roots of sensitive varieties were severely damaged by Al^{+++} and regrowth was completely inhibited. The Brazilian wheat BH 1146 showed a tolerant reaction over the range of Al^{+++} concentrations. The varieties Atlas 66 and CI 14124 showed good tolerance to 2 and 4 ppm of Al^{+++} and a sensitive reaction to 8 and 10 ppm. The other varieties (Chinese Spring, Siete Cerros) showed sensitivity to very low concentrations of Al^{+++} . Based on these results, a level of 4 ppm was chosen as the screening standard for the remaining tests (Figure 1).

The relation of tolerant and sensitive plants in the F_1 and F_2 populations of several crosses is described in Table II. Crosses of BH 1146 with the sensitive varieties, CI 14124, and Favorit, gave results suggestive of segregation for two and one gene, respectively (Table II). The cross BH 1146 x Atlas 66 fit a two gene model, with a 1S:15T ratio. The frequency distribution for the parental, F_1 and F_2 populations for this cross are shown in Table III. It was clear that the regrowth conferred by the gene present in Atlas 66 was less than that determined by the gene present in BH 1146. This suggests there are different levels of expression of genes for Al^{+++} tolerance. These results demonstrated that BH 1146 carried a major gene for Al^{+++} tolerance and that another gene for tolerance was present in Atlas 66.

Segregations for disomic F_2 populations from the cross BH 1146 x Chinese Spring, tested with various levels of Al^{+++} , are listed in Table IV. One major gene difference was observed for four Al^{+++} concentrations; however, the dominance was reversed at 6 ppm and 8 ppm and no tolerance was observed at 10 ppm.

The results for the 21 monosomic crosses involving BH 1146 are given in Table V. For the A and B genomes only chromosome 3B did not fit the 3T:1S ratio, and a higher percentage (37%) of sensitive plants was observed. The major gene for tolerance to Al^{+++} present in BH 1146 was clearly carried by chromosome 4D. Results for most of the chromosomes of the D genome, however, did not fit a 3T:1S ratio. An increase in the proportion of sensitive plants was observed in relation to the ratio expected for these families. In addition, results for chromosome 5D showed a reversion of dominance. These results indicate that most of the chromosomes of the D genome carry modifiers that are

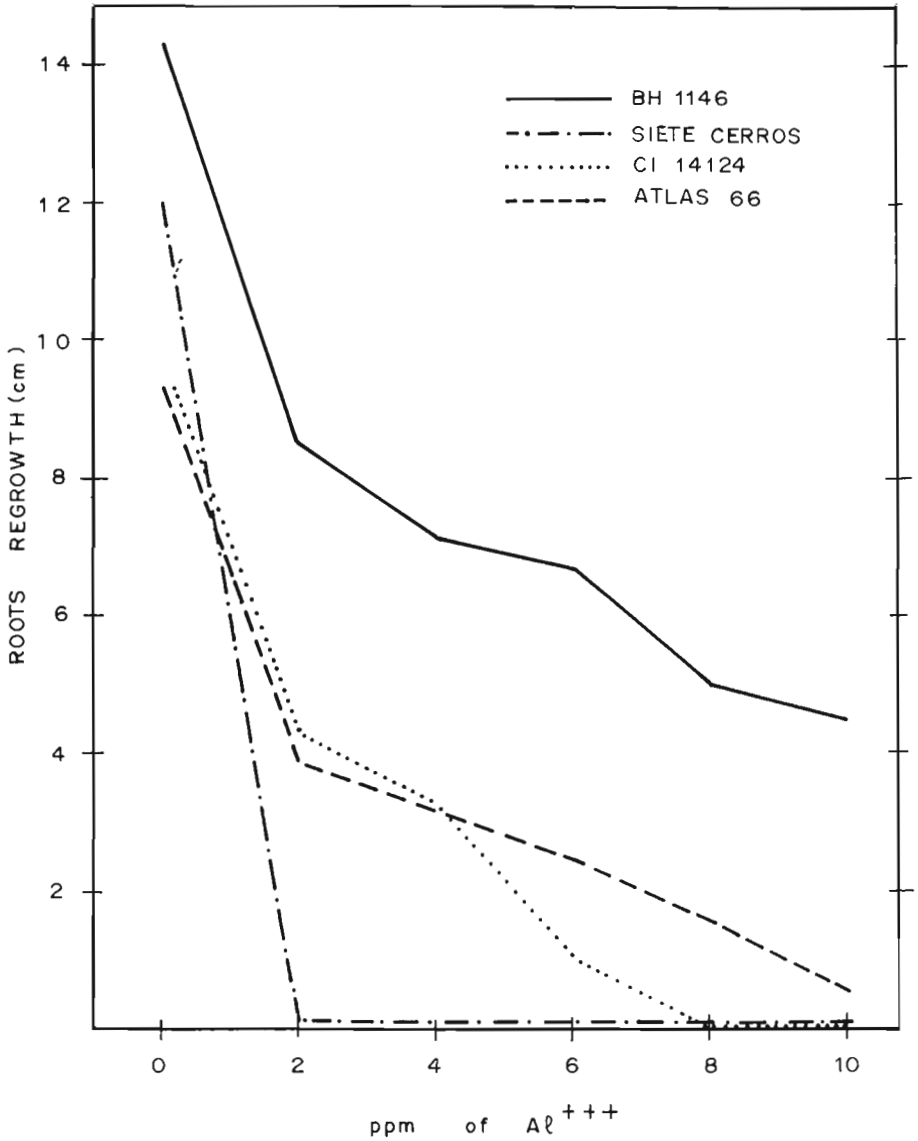


Figure 1 - Root regrowth of four wheat varieties at different levels of aluminum.

important for the complete expression of the gene for Al⁺⁺⁺ tolerance present in chromosome 4D.

Table III - Frequency distribution for root regrowth of the F₂ population of the cross BH 1146 x Atlas 66 submitted to 4 ppm of Al⁺⁺⁺.

Length of regrowth (mm)	BH	Atlas 66	F ₁	F ₂	Proportion	P
0	0			10	1/16	
0.1 - 5						
6 - 10		2	3	8		
11 - 15		4	1	12		
16 - 20		2		4		
21 - 25		6	3	8		
26 - 30			3	10		
31 - 35			6	12	15/16	
36 - 40	1		3	30		
41 - 45	1		1	30		
46 - 50	1		2	16		
51 - 55	3			11		
56 - 60	3			1		
61 - 65	1					
66 - 70	6			1		
71 - 75	3					
Total	19	14	19	153	16/16	.50

Table IV - Number of tolerant and sensitive plants from the F₂ population of the cross Chinese Spring x BH 1146 submitted to various levels of Al⁺⁺⁺.

Al ⁺⁺⁺ (ppm)	Number of plants		ratio T:S	χ^2	P
	T	S			
0	20	0	1:0		1.0
2	18	6	3:1		1.0
4	13	4	3:1	0.02	.80
6	6	19	1:3	0.01	.90
8	7	19	1:3	0.05	.80
10	0	23	0:1		1.0

Table V - Segregation of Al⁺⁺⁺ tolerance in F₂ progenies from crosses of Chinese Spring monosomic lines with cv. BH 1146.

Monosomic	Resistant		Sensitive		χ^2 3T:1S	P
	No.	%	No.	%		
1A	67	73.6	24	26.4	0.09	.75
2A	11	78.6	3	21.4	0.09	.75
3A	128	72.3	49	27.7	0.68	.25
4A	154	75.5	50	24.5	0.03	.75
5A	29	70.7	12	29.3	0.40	.50
6A	114	74.5	39	25.5	0.02	.75
7A	6	54.5	5	45.5	2.42	.10
Total (A)	509	73.7	182	26.3	0.66	.25
1B	50	76.9	15	23.1	0.13	.25
2B	63	74.1	22	25.9	0.03	.75
3B	88	62.9	52	37.1	11.01	.01
4B	163	76.5	50	23.5	0.29	.50
5B	48	77.4	14	22.6	0.19	.75
6B	96	76.2	30	23.8	0.09	.75
7B	79	76.7	24	23.3	0.16	.50
Total (B)	587	73.9	207	26.1	0.48	.25
1D	110	70.1	47	29.9	2.02	.10
2D	130	54.2	110	45.8	45.88	.01
3D	112	60.2	74	39.8	22.50	.01
4D***	196	95.6	9	4.4	45.48	.01
5D	15	27.8	39	72.2	63.34	.01
6D	157	65.1	84	34.9	9.59	.01
7D	150	67.0	74	33.0	7.72	.01
Total (D)	870	66.6	437	33.4	49.60	.01

DISCUSSION

This study demonstrated a technique useful for the separation of Al⁺⁺⁺ sensitive and tolerant plants. Additionally, the range of Al⁺⁺⁺ concentrations permitted the identification of critical sensitivity levels.

Considerable genetic variation for Al^{+++} tolerance were identified in the parental lines BH 1146 and Atlas 66 as previously reported by Kerridge and Kronstad (1968), Camargo (1981) and Aniol (1984). The major gene present in BH 1146 was more dominant for tolerance to Al^{+++} than the gene present in Atlas 66.

Most chromosomes in the D genome did not fit the 3T:1S ratio, and an increase in the number of sensitive plants was evident, with the exception of chromosome 4D where the resistant gene present in BH 1146 is located. These results showed that the complete substitution of one genome with another from a different variety may have a significant effect on the Al^{+++} response. These results may also explain why several studies on Al^{+++} tolerance have given inconclusive results.

The finding that the efficiency of the tolerance is lost with an increase in Al^{+++} concentrations agrees with previous studies by Camargo (1981). It appears that the major gene works in a threshold-like system; when a certain concentration is reached the level of tolerance decreases rapidly.

The location of the major gene for Al^{+++} tolerance in BH 1146 was chromosome 4D, which is different from that reported for Atlas 66 (Prestes *et al.*, 1975). This finding agrees with the genetic studies reported here that two varieties have different genes with different expressions of Al^{+++} tolerance.

The location of the major gene for Al^{+++} tolerance on chromosome 4D increases the importance of chromosome 4D, which also carries gene Rht2, for reduced plant height. It also increases the importance of homologous group 4, since in barley (*Hordeum vulgare*), the gene for tolerance to Al^{+++} is also located on the group 4 chromosome (Stolen and Andersens, 1978).

The results observed with the monosomic analysis show that the D genome is important for tolerance to Al^{+++} as previously suggested by Sloomaker (1974). Despite the involvement of several chromosomes with large effects on the expression of the tolerance to Al^{+++} , selection of wheat varieties with high levels of tolerance to Al^{+++} has been easily obtained in Brazilian breeding programs (Lagos, 1983).

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RESUMO

Foram realizados diferentes experimentos para investigar as bases genéticas da tolerância ao Al^{+++} em trigo e determinar a localização cromossômica de genes maiores envolvidos através da análise monossômica. A técnica usada foi descrita por Camargo (1978) onde as respostas ao Al^{+++} foram determinadas pela medida do recrescimento das raízes.

O nível de 4 ppm de Al^{+++} foi o que melhor discriminou entre plantas sensíveis e tolerantes. A análise genética revelou que a variedade BH 1146 tem um gene para tolerância ao Al^{+++} . A análise monossômica revelou que o gene para tolerância ao Al^{+++} no genótipo BH 1146 está localizado no cromossoma 4D.

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