Genetic analysis of aluminum tolerance and grain quality in wheat (*Triticum aestivum* L.)

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ABSTRACT

Grain quality has a major importance in the Brazilian wheat market and industry. However, one of the major limiting factor in quality wheat production is the presence of Aluminum (Al) toxicity in the soil. Twenty-five, 50 and 52 percent of soils in the world, Brazil and Paraná state respectively, contain acidity. The present study had the objective of estimating genetic parameters to identify gene action and heritability of traits in segregating populations of wheat. The Al screening in hydroponic solution and MS-SDS sedimentation analysis for quality were used in a generation mean analysis. Predominantly additive gene effects were present controlling the traits under evaluation, indicating possibilities of selection progress. The relatively high values of narrow sense heritability for sedimentation volume in the crosses IPR 85/OR 1, Iapar 78/Minnpro, Grandin/Iapar 46 and Iapar 53/Trigo BR 23, and Al tolerance in IPR 85/OR 1 and Grandin/Iapar 46 suggests that successful selection can be accomplished in the early segregating generations.

KEY WORDS: Wheat, aluminum, quality, gene action, heritability, selection

INTRODUCTION

One of the major wheat production limiting factors is the toxicity caused by Aluminum (Al) and Manganese (Mn) in the soil. It is estimated that 25% of the world arable land could contain acid soils, limiting the root development of several plant species, especially when the soil pH is below 5.5 (Van Wambeke, 1976). Approximately 50% of the soils in Brazil (Silva, 1976) and 52% of the soils in the state of Paraná (Igue et al., 1976) contain acidity with the presence of Al toxicity.

Genetic variability in Al tolerance has been observed between and within plant species. Many species have varieties with great differences towards their tolerance to the toxicity. These differences are genetically controlled, suggesting a promising alternative to the liming of the underground soil with calcium in order to grow certain crops (Foy, 1976).

Kerridge and Kronstad (1968) observed that the F_2 segregation of tolerant and sensitive wheat plants showed a 3:1 ratio, concluding that a dominant gene controls the tolerance. Due to the intermediate reaction of one of the progenitors in higher concentrations of Al, the authors admitted the possibility of other modifier genes be involved in the inheritance of the character.

In experiments of short duration, a criterion used to identify Al tolerance was the increment of the seedlings primary roots; in hydroponic solutions containing Al levels that identify tolerant plants (Foy et al., 1967; Camargo, 1983).

The technological quality of the grain has become an important issue in wheat trading for industrial uses in Brazil. Besides the genetic control, grain quality depends on the crop interactions with the field (effects of soils, climate, insects, diseases, crop management, etc.), as well as on operations of drying and cleaning grains for storage before milling and, later, for industrialization (Guarienti, 1993).

Matuz (1998), in a study carried out with four wheat populations, concluded that a single gene controlled the sedimentation volume. The Zeleny test estimates the bread-making potential (gluten strength) of a genotype. The method is based on the water soaking capacity of the gluten forming proteins, when submitted to partial denaturation by diluted solution of lactic acid (Zeleny, 1947). The micro-sedimentation test with sodium dodecyl sulfate (MS-SDS) is used mainly in the evaluation of the bread-making potential (gluten strength) in programs of genetic improvement (Axford et al., 1979). It is a fast and cost effective test, which requires a sample with a small amount of flour (1 g), facilitating the analysis of segregating generations by research programs.

Practical difficulty exists in obtaining simultaneously

Al tolerant and good quality genotypes. This is particularly true in Southern Brazil where the rainfall pattern during crop maturation is high and soil acidity predominates (Riede and Campos, 1988).

It is possible to use statistical techniques to determine the genetic components obtained from the means and variances of a population (Mather and Jinks, 1982). This work was carried out to identify genetic variability, to estimate genetic parameters and heritability of tolerance to Al and grain quality in a set of genotypes, with the purpose of obtaining essential information for the wheat breeding programs (Riede et al., 2001).

MATERIAL AND METHODS

A set of diverse Brazilian and USA wheat genotypes, chosen from the Wheat Breeding Program at IAPAR were characterized for its desirable traits reaction to Al tolerance and grain quality, through a hydroponic solution system and alveograph methodologies as presented in Table 1.

Population Development

Four populations whose genitors carried one or both of the mentioned traits were developed by the following single crosses: C1 (IPR 85/OR1), C2 (Iapar 78/Minnpro), C3 (Grandin/Iapar 46) and C4 (Iapar 53/Trigo BR 23). Seed material per generation used in the study was obtained as illustrated in Figure 1.

Crosses were made using the Crossing Block facilities to obtain F_1 seeds to be tested and to be selfed to generate F_2 seeds. From the F_1 rows, F_2 seeds were obtained to proceed with the work. Each F_2 population was sowed in two plots of six times 10 m length rows, with 20 cm spacing between them. In this system, seeds of random $F_{2:3}$ families were obtained for testing.

Field Experiment

The experiment was carried out in the field as hill-plots with plants individually randomized, in a complete randomized design, in the 1999 season. Each population contained 30 individuals of each genitor (P_1 and P_2), 20 F_1 individuals, 200 F_2 individuals and 30 $F_{2:3}$ families with 10 individuals per family, adding up to 580 treatments. The sowing was done on May 8, 1999, with spacing of 20 cm among hill-plots. Each of 580 hill-plots per population was sown with two to three seeds. After the emergence, extra-germinated seedlings were thinned, just leaving a single plant per hill-plot. This was done to avoid problems with stand failure of the experiment.

Agronomic field characters such as heading date (d), maturation (d)), plant height (cm), number of heads(nº) and grain yield (g/plot), were obtained for each treatment by population. The ripe plants had their ears harvested and threshed in an individual plant thresher. Those seeds were used in the laboratory, to evaluate sedimentation volume (cm) and tolerance to the Al (mm). The methodology of hill-plots presents some advantages in relation to the conventional plots such as: the use of smaller field area, the simultaneous testing of larger number of genotypes; the reduced soil variability due to the limitations of the area involved and the use of a small amount of seeds.

Laboratory Experiments

a) Quality Evaluation

The SDS (Sodium Dodecyl Sulphate) sedimentation volume test was used to access the bread making quality of treatments according to the methodology proposed by Axford et al. (1979), substituting however the ethyl alcohol for lactic acid as in Zeleny (1947).

b) Tolerance to Aluminum Evaluation

The hydroponic evaluation methodology for tolerance to Al was the same used by Camargo and Oliveira (1981), complemented by the hematoxylin root demarcation technique used by Lopez-Cesati et al.

Table 1. Characterization of parental genotypes used in the study.

	'IPR 85'	'OR 1'	'Iapar 53'	'Iapar 78'	'Iapar 46'	'Trigo BR 23'	'Grandin[a/]'	'Minnpro[a/]'
Quality[b/]	374	227	256	196	113	154	190	384
Aluminum[c/]	MT	MS	MS	MT	T	T	S	MT

[a/] Genotypes introduced from North Dakota and Minnesota (USA) known for their good to excellent quality; [b/]Alveograph (W) Quality Rating: Excelent - (strong gluten) W > 300 x 10^{-4}J; Good - (bread type) W> 180 x 10^{-4}J; Soft - (weak gluten) W> 50 x 10^{-4}J; [c/] Reaction to Al - T: Tolerant, MT: Moderately Tolerant, MS: Moderately Sensitive, S: Sensitive.

(1988), to evaluate segregating wheat populations from the CIMMYT breeding program. Each population was evaluated as a separate batch at the same date, using large plastic trays holding styrofoam support for 100 seedlings each.

Analysis of the Data

The genetic components of the generation means were estimated by the group scale test of Cavalli (1952), using the Fortran language program for PC-XT microcomputers or compatible (Toledo, 1991). This procedure allows an evaluation of the quality of the adjustment of the obtained genetic model, through a x^2 test that uses a number of degrees of freedom equal to the number of generations minus the number of studied parameters. A simpler genetic model, with all the parameters significantly different from zero, given by the t test at 5% level of probability, was adopted as correct in the adjustment procedure . This model was appropriate to explain the present variability in the generations used x^2 of the adjustment quality of the model non significant at the 5% level). Considering the absence of non-alelic interaction, linkage and genotype x environment interaction, a simple genetic model involving effects of **D**, **H** and **E,** was used first to estimate the genetic and environment components of the variance of the evaluated generations. In the model, **D** represents the additive component of the variation, **H** the dominance component and **E** the environmental component, using the estimation methodology described by Hayman (1960). $F_{2:3}$ families were used to represent the F_3 generation, but due to the design of the experiment, these families were not considered in the analysis. Broad sense h_b^2 and narrow sense heritabilities h_s^2 were calculated for agronomic characters such as heading date, maturation, plant height, number of heads and grain yield additionally to the sedimentation volume and aluminum tolerance as in Mahmud and Kramer (1951) and Warner (1952).

RESULTS AND DISCUSSION

Analysis of the Genetic Components

Means, variances and the degrees of freedom for generations P_1, P_2, F_1, F_2 and F_3, used to obtain the genetic parameters of the traits sedimentation volume and Al tolerance are presented in Table 2. All the adjusted genetic models that had degrees of freedom available for the adjustment test were x^2 non significant (P>5%), indicating that the models were satisfactory to explain the variability. However, for some crosses the mean models were not adjusted using the mean and the variance models for all generations. In this case the withdrawal of the F_3 generation was done during the model adjustment.

Mean genetic components

Initially the mean components were estimated for the main generations by a model involving additive and dominance effects. Due to the fact that a simple model was not enough to explain the genetic mechanisms, another model, including non-allelic interactions was adjusted. The genetic models for mean and variance adjusted for the sedimentation volume and aluminum tolerance traits are shown in Table 3.

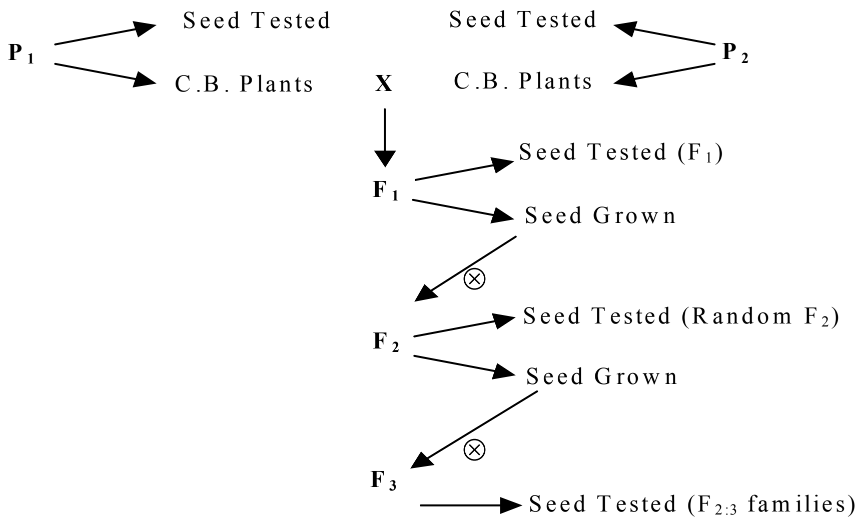

Figure 1. Population development and seed generation cycle used in the genetic study (CB: Crossing Block).

Table 2. Degrees of freedom, mean and variance of parents, F_1, F_2 and F_3 generations for different traits of the four crosses under evaluation.

Parameters	IPR 85/OR 1 (C1)			Iapar 78/Minnpro (C2)			Grandin/Iapar 46 (C3)			Iapar 53/Trigo BR 23 (C4)		
Sedimentation Volume (cm)	Df	Mean	Variance	Df	Mean	Variance	Df	Mean	Variance	Df	Mean	Variance
P1	22	18.31	6.93	20	11.13	0.89	22	14.61	0.86	21	10.71	1.34
P2	19	13.16	3.76	23	19.96	2.88	22	14.23	4.74	24	11.87	4.16
F1	12	15.94	2.15	13	14.86	3.40	18	15.28	1.77	11	11.06	1.20
F2	126	15.56	5.06	116	14.87	5.60	140	15.49	5.20	138	11.19	2.30
F3	216	15.64	5.21	189	14.80	5.78	224	15.49	7.15	109	11.76	3.69
Aluminum Tol. (mm)												
P1	19	2.42	38.25	21	1.93	15.34	25	0.06	0.11	24	0.34	1.31
P2	15	0.84	11.39	25	3.98	23.61	23	7.16	24.86	25	17.99	140.21
F1	12	3.21	17.95	15	3.34	20.51	19	3.76	18.49	10	22.94	85.14
F2	99	2.41	27.43	130	3.76	31.26	148	3.04	28.32	147	13.34	142.13
F3	184	3.71	50.62	196	0.67	07.01	242	1.82	15.51	145	9.35	142.12

Sedimentation Volume

Additive effects [d] were observed in the C1, C2 and C4 crosses, and dominance effects in C2, C3 and C4. The non-detection of the parameter [d] in C3 does not indicate that additive effect inexists, but that dispersion of genes in the parents might be occurring. This can be proven by the analysis of the additive variance component that is not affected by the dispersion of the genes in the parents. In the C3 cross, [h] was positive, with a negative epistatic component [l], indicating epistatic effects of duplicated genes. The strong correlation between [h] and [l] makes it difficult to interpret the sign of [h] in a model where both are present.

Aluminum Tolerance

Additive effects were observed in crosses C1, C3 and C4 and positive [h] effects in C3 and C4. The positive sign of [h] indicates dominance in the sense of increasing the Al tolerance in C3 and C4. It was observed also, epistatic effects [i] among homozygous loci in C3. The small value of [d], in relation to [h], in C4, indicates that there is dispersion of the genes in the parents, or what is more likely, the presence of an overdominance effect.

Variance genetic components

Genetic and environment components of variance for generations P_1, P_2, F_1, F_2 and F_3 were estimated for the four crosses (Table 3). The variance model was adjusted involving interaction genotype x microenvironment. The term interaction genotype x microenvironment is related to the differentiated interaction of each genotype with the environment to which it was submitted (Mather and Jinks, 1982). The models with significant probabilities were not satisfactory to explain the existent variability. However, the additive variances of these models were used for calculation of the heritability in the narrow sense (h_s^2).

Sedimentation Volume

Variance models were adjusted and statistically accepted for all the crosses. The presence of additive variance in all the models indicates possibility of a selection with genetic gains for these traits in improvement programs, confirmed by the mean models. The variance due to the dominance effects **H** was absent in the four crosses. The effects of the genotype x microenvironment (**E1** and **E2**) interaction did not have a wide magnitude, indicating that differentiated interaction among parents does not exist in the microenvironment in which they were evaluated.

Aluminum Tolerance

Only for the C4 cross the variance model was adjusted, presenting additive variance and absence of dominance variance. The presence of the dominance effects in the mean models and the dominance variance, absent in the adjusted variance models, indicates occurrence of gene dispersion in the parents. Effects of genotype x microenvironment (**E1** and **E2**) interaction were present, indicating existence of differentiated interaction among the parents and the microenvironment in which they were evaluated.

Table 3. Genetic parameters adjusted to the means and variances of two traits in four wheat crosses.

Parameters	IPR 85/OR 1 (C1)	Iapar 78/Minnpro (C2)	Grandin/Iapar 46 (C3)	Iapar 53/Trigo BR 23 (C4)
Sedimentation Volume				
m	15.64 ± 0.11	15.29 ± 0.16	14.62 ± 0.17	11.55 ± 0.17
[d]	2.55 ± 0.34	4.29 ± 0.19	-	0.70 ± 0.23
[h]	-	-0.89 ± 0.44	3.51 ± 0.91	-0.53 ± 0.36
[i]	-	-	-	-
[l]	-	-	-2.91 ± 0.94	-
X^2 / G.l. / PROB.	0.77 / 3 / 0.8556	4.83 / 2 / 0.0890	2.41 / 2 / 0.3002	5.24 / 3 / 0.0725
D	1.84 ± 0.74	4.29 ± 1.09	4.28 ± 1.22	1.13 ± 0.42
H	-	-	-	-
E1	4.98 ± 0.99	0.98 ± 0.30	0.85 ± 0.26	2.71 ± 0.51
E2	4.23 ± 0.24	4.60 ± 0.83	4.72 ± 0.86	1.08 ± 0.32
X^2 / G.l. / PROB.	8.03 / 4 / 0.09	4.11/ 3 / 0.25	2.20 / 3 / 0.53	6.07 / 3 / 0.11
Aluminum Tolerance				
m	2.90 ± 0.32	3.40 ± 0.37	1.09 ± 0.45	7.66 ± 0.94
[d]	1.37 ± 0.73	-	3.55 ± 0.51	7.35 ± 0.95
[h]	-	-	3.22 ± 1.17	11.80 ± 2.40
[i]	-	-	2.51 ± 0.69	-
[l]	-	-	-	-
X^2 / G.l. / PROB.	6.77 / 3 /0.08	4.02 / [2/]3 / 0.26	1.03 / 1 / 0.31	4.90 / 2 / 0.09
D	14.86 ± 4.64		16.66 ± 4.25	18.84 ± 13.94
H	-		-	-
E1	23.11 ± 4.50		0.11 ± 0.03	240.68 ± 24.42
E2	8.18 ± 3.07		22.66 ± 3.21	1.31 ± 0.38
X^2 / G.l. / PROB.	13.00 / 3 / [1/]		30.71 / 3 / [1/]	3.38 / 3 / 0.34

[1/] Probability lower than 5%. [2/] Models with the generations P_1, P_2, F_1 e F_2.

Heritability

The high values of broad sense heritability h_b^2, mean and genetic variability of he crosses C3, C1 and C2 crosses suggests that the selection for aluminum tolerance and quality traits can be done in the early segregating generations. The coefficient of variation (data not presented) of the different crosses for the traits grain yield, sedimentation volume and tolerance to Al, attests that the dispersion of the treatments in relation to the mean was relatively equal for all the crosses within each trait.

Broad Sense

The h_b^2 for seven traits were calculated by the genetic and F_2 variances (Table 4). For heading date, days for maturation and plant height, the was high, confirming the information that those traits are controlled by few genes (Camargo et al., 1984; Felício et al., 1998). Number of heads and grain yield present low for three of the four crosses. For the C4 cross, the values for these two traits were 0.51 and 0.44, contradicting the expected results. C2 and C3 presented relatively high values of for the sedimentation volume and tolerance to Al traits. However, for C1, the values were smaller than in the previous crosses. C4 presented low for sedimentation volume and relatively high for tolerance to Al. Matuz (1998), in a study with four populations, observed very similar results for sedimentation volume. For Al tolerance, similar results were obtained by Camargo (1987). Negative values of heritability indicated high variability in the parents and F_1 in relation to F_2 generation.

Narrow Sense

The narrow sense heritability h_s^2 was estimated based on the additive and F2 variances for three important traits (Table 5). For grain yield, cross C1 overcame the other crosses. The h_s^2 for sedimentation volume of all the crosses had similar behavior as the h_b^2, showing however always higher values. For Al tolerance, C1 and C3, presented relatively high h_s^2, and low for C4.

CONCLUSIONS

Although grain quality is always thought of as a genetically complex character, the parameter sedimentation volume used to represent the trait was controlled predominately by additive effects which facilitate genetic gain due to selection in a breeding program. Epistasis and dominance effects were of lower magnitude and they are likely not to pose a serious threat to selection efficiency. Additive effects for aluminum tolerance were present in three out of four crosses, indicating a good possibility of selection in the early generations. Dominance and epistatic effects were of lower magnitude in all but the Iapar 53/Trigo BR 23 cross indicating the presence of the overdominance effect or dispersion of the genes in the parents.

The relatively high values of the narrow and broad sense heritabilities for the traits tolerance to Al and sedimentation volume of the crosses IPR 85/OR 1, Iapar 78/Minnpro and Grandin/Iapar 46, confirmed that selection can be successful in the early segregating generations. The Iapar 53/Trigo BR 23 cross presented low heritability for sedimentation volume and relatively high for aluminum tolerance, indicating that the simultaneous selection would not be effective in this population.

The information obtained in this work will encourage the investment and research efforts towards the improvement of important quality and adaptative traits for the wheat crop sustainability.

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Table 4. Broad sense heritability (h_b^2) for seven traits of four wheat crosses.

CHARACTER	IPR 85/OR 1 (C1)	Iapar 78/Minnpro (C2)	Grandin/Iapar 46 (C3)	Iapar 53/Trigo BR 23 (C4)
Heading Date	0.42	0.94	0.72	0.75
Maturation	0.41	0.85	0.77	0.82
Plant Height	0.75	0.88	0.56	0.36
Number of Heads	0.06	-0.18	-0.16	0.51
Grain Yield	-0.40	0.07	-0.13	0.44
Sedimentation Volume	0.15	0.57	0.53	0.03
Aluminum Tolerance	0.18	0.37	0.49	0.47

Table 5. Narrow sense heritability (h_s^2) for three different traits of four wheat crosses.

CHARACTER	IPR 85/OR 1 (C1)	Iapar 78/Minnpro (C2)	Grandin/Iapar 46 (C3)	Iapar 53/Trigo BR 23 (C4)
Grain Yield	0.38	0.10	[1/]	0.20
Sedimentation Volume	0.36	0.77	0.81	0.49
Aluminum Tolerance	0.54	[1/]	0.59	0.13

[1/]Additive variance in the variance model was not obtained.

RESUMO

Análise genética da tolerância ao alumínio e qualidade de grãos em trigo (*Triticum aestivum* L.)

Um dos principais fatores limitantes da produtividade do trigo é o Alumínio (Al) tóxico dos solos. É estimado que no mundo, no Brasil e no estado do Paraná, as percentagens de solos agricultáveis contendo solos ácidos com alumínio são 25, 50 e 52 respectivamente. A Qualidade de grão tem uma importância cada vez maior no mercado de trigo brasileiro. O presente estudo teve como objetivos a estimativa de parâmetros genéticos, a determinação da ação gênica e herdabilidade de caracteres avaliados em populações segregantes de trigo. Análises de média de gerações usando os programas SGQ, Excel e Genfit foram realizadas. A avaliação de reação ao alumínio em solução hidropônica e a análise de sedimentação pelo método MS-SDS para qualidade foram utilizadas. Predominantemente efeitos genéticos aditivos estiveram presentes controlando as características em avaliação, indicando possibilidades de progresso na seleção. Os valores relativamente altos da herdabilidade em sentido restrito para a variável volume de sedimentação nos cruzamentos IPR 85/OR 1, Iapar 78/Minnpro, Grandin/Iapar 46 e Iapar 53/Trigo BR 23 e tolerância ao Al em IPR 85/OR 1 e Grandin/Iapar 46 sugerem que seleção pode ser realizada para estas populações em gerações segregantes precoces com sucesso.

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