

RESULTS REGARDING THE GENETIC CONTROL OF TOLERANCE TO ALUMINIUM ION TOXICITY IN WHEAT

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ABSTRACT

To study the genetic control of aluminium tolerance in winter wheat, a series of crosses between six Romanian genotypes were carried out. All genetic populations (P₁, P₂, F₁, F₂, B₁ and B₂) were obtained in the field in the same year (1995), and then tested in a four ppm Al solution, taking into account the maximum root length. Genetic effects and variances were estimated applying the statistical model proposed by Gamble in 1962. The genes with additive actions as well as those with dominant interactions are involved in controlling the aluminium tolerance but the epistatic interactions are very significant in many combinations, with positive and negative effects on tolerance. Separation of total variance in genetic and environmental variance suggests that the inheritance of aluminium tolerance in wheat is high, but the genotypes have a various capacity of hereditary transmission. Presence of additive genetic actions, interactions of dominance, and all types of epistatic interactions (AA, DD, AD), with positive and negative effects, demonstrates the complexity of genetic control of tolerance to aluminium ion toxicity in wheat.

Key words: aluminium, tolerance, diallel cross, root length, wheat

INTRODUCTION

The increasing needs for wheat, determined by the population increase all over the world, and the increase of the general standard of living have caused the spreading of wheat growing area even in regions with less suitable soils, as in the cases of areas with arid soils, salty or acid soils etc.

Acid soils covering 2.5 billion ha (Bona et al., 1994) all over the world have some unsuitable physico-chemical and mechanical properties, among which the high content of Al ions with toxic effect on plants, wheat included.

Kerridge and Kronstad (1968) emphasized the differentiated response of wheat genotypes to aluminium ion toxicity and, therefore, the existence of genetic variability for tolerance. The following years, the problem of elaboration of methods to test the response of genotypes to aluminium ion toxicity has been raised, meth-

ods able to permit a good characterization and differentiation of genotypes. So, a multitude of methods, criteria and indices to evaluate the level of aluminium tolerance have been proposed, without imposing an unitary system. For this reason, Macnair (1990) recommended, especially for genetic studies, to choose those estimation methods and aluminium concentrations allowing the differentiation of the analysed genotypes.

In the initial stages of research on inheritance of aluminium tolerance in wheat, the concluding idea was that the exteriorization of genotype tolerance is controlled by a dominant gene (Kerridge and Kronstad, 1968; Elliot and Morris, 1985; Lagos et al., 1986; Little, 1988). These authors operated only with cultivars characterized by a contrastive differentiation as tolerance concerned. Other authors detected two genes for tolerance, with dominant action or partially dominant (Campbell and Lafever, 1981). The same authors demonstrated that the effects of dominant genes are more obvious than the additive ones, and the epistatic effects are negligible.

After 1990, the conviction has been outlined that the aluminium tolerance is a complex trait, being controlled by some major genes and minor modification genes and the existence of some suppressor genes for tolerance have been also presumed (Aniol and Gustafson, 1990; Aniol, 1996).

The present investigations had in view to study the action type of genes present in some Romanian wheat genotypes, used frequently in crossings, so that the results could be applied in the breeding process.

MATERIALS AND METHODS

The biological material used in these investigations included six parental genotypes with different tolerant levels, from the very tolerant

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to susceptible. The parental genotypes belong to different varieties, those tolerant presenting a series of deficiencies determined by the plant height and resistance to lodging, wintering and some diseases.

The parental genotypes used for diallel crossing of p(p-1) type included two tolerant lines obtained at Oradea, one tolerant line developed at Fundulea, the medium tolerant Arie^oan cultivar and the sensitive cultivars Fundulea 4 and Fundulea 29 (Table 1). The tolerance sources existing in the genealogies of tolerant parental genotypes come from the Brazilian cultivars Colonias and S8 as well as from the Mengavi cultivar present in the genealogy of Fundulea 133 cultivar. These genotypes have been crossed between them, each one with each other, without reciprocal crosses, so that finally the used genetic populations consisted of those six parental genotypes (P₁, P₂), 15 F₁ hybrids, 15 F₂ hybrids and 30 backcross hybrids (B₁ and B₂). To obtain the 30 backcross populations, the respective F₁ hybrids were used as maternal genotypes.

Table 1. Parental genotypes used in diallel crosses of p(p-1) type

Genotype	Genealogy	Provenance
Oradea 30	Colonias/ F133 D 4 -23	Oradea
Oradea 33	S8/F9D49-31	Oradea
Fundulea 472	Colonias/ F 135 D// Flamura 80	Fundulea
Arie ^o an	Rubin/Bezostaia 1// Fiorello	Turda
Fundulea 4	Fundulea 29/ Lovrin 32	Fundulea
Fundulea 29	Aurora/ Riley	Fundulea

Testing the genetic populations concerning the aluminium tolerance was carried out under laboratory conditions, in a hydroponic solution with 4 ppm Al concentration. After 10 days from seed germination the maximum length of the roots was measured. The obtained values were used as a criterion to evaluate the level of aluminium tolerance. This testing method was presented in a previous paper (Bunta, 1996).

A number of 45 plants in each genetic population was analysed. The seed used for testing was obtained in the same year (1995) for all generations and combinations, aiming at the

elimination of influences of various environmental conditions on grain quality. The following procedures were used for processing the statistical data:

- computation of arithmetical mean, variance (s^2) and coefficient of variation (s%) to characterize the genetic populations;
- analysis of variance, F test and the least significant difference (LSD) in the case of the bifactorial experiment : aluminium concentration x parental genotypes;
- Duncan's multiple range test to establish the most adequate aluminium concentrations;
- decomposition of the total variance (TV) into environmental variance (EV) and genotypical variance (after Brewbaker, 1964);
- computation of heritability coefficient in a large sense (HL) (after Mahmud and Kramer, 1964), and in narrow sense (HN) as a ratio between additive and total variance (after Căbulea, 1975);
- estimation of effects and genetic variances (GV) according to the model proposed by Gamble (1962), model which permits also to point out the epistatic effects.

RESULTS AND DISCUSSIONS

To characterize the parental genotypes concerning the aluminium tolerance, the averages of maximum roots length at different Al concentrations (0, 2, 4 and 6 ppm) were taken into account. The analysis of variances in the bifactorial experiment (concentrations of aluminium x genotypes) emphasized a strong action of aluminium concentrations, distinctly significant, but also the distinct significant differences between genotypes and genotype x Al concentrations, respectively (Table 2).

Table 2. ANOVA for parental genotypes. Al rates and interactions

Source of variance	SS	DF	MS	F test
Large plots	115,686.9	11		
Replications	5.1	2		
Al rates	115,582.9	3	38,527.6	2,335.0**
Error (a)	99.0	6	16.5	
Small plots	156,656.6	71		
Parental genotypes	22,588.0	5	4,517.6	327.4**
Interactions of rates x parental genotypes	17,830.4	15	1,188.7	86.1**

Error (b) 551,1 40 13.8 The Duncan test permitted to separate the geno-

Table 3. The effect of Al concentrations on root length of parental genotypes

Parental geno- types	Averages and variances of root length							
	0 ppm Al		2 ppm Al		4 ppm Al		6 ppm Al	
	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2
Fundulea 29	123.9	181.1	40.2	87.1	32.2	107.4	12.9	4.6
Fundulea 4	120.4	174.1	42.3	89.4	40.4	62.0	12.4	6.3
Arie ^o an	124.1	235.0	115.9	122.1	76.0	17.7	18.1	25.4
Fundulea 472	126.8	212.8	117.8	185.5	79.4	172.1	18.8	31.1
Oradea 33	121.8	144.1	116.0	142.0	93.4	158.1	16.2	12.4
Oradea 30	137.7	133.8	133.7	165.1	110.1	192.9	17.7	18.6
Averages of parental geno- types	125.8	38.8	94.3	1734.6	72.0	914.1	16.0	7.6

Table 4. Root length of parental genotypes at 4 ppm Al concentration

Parental genotypes	Root length (mm)	Relative length (%)	Differences	Significance
Fundulea 29	32.2	44.7	- 39.8	000
Fundulea 4	40.4	56.1	- 31.6	000
Averages of parental genotypes	72.0	100.0	0.0	-
Arie ^o an	76.0	105.6	+ 4.0	
Fundulea 472	79.9	111.0	+ 7.9	*
Oradea 33	93.4	129.7	+ 21.4	***
Oradea 30	110.1	152.9	+ 38.1	***

LSD 5% = 6.1 mm; LSD 1% = 8.2 mm; LSD 0.1% = 10,8 mm

The length of roots, under conditions without aluminium, is clearly higher in the case of the Oradea 30 line, an additional quality of this genotype which provides the advantage of exploring a larger volume of poor soil characterized by a deficit of nutrients, as albic luvisols (Table 3). In addition, this genotype has the lowest variance of the root length, being, therefore, the most uniform from this point of view.

In the case of 2 ppm Al concentration, only Fundulea 4 and Fundulea 29 cultivars have severely reduced root length, all the genotypes being more or less affected. In the case of 6 ppm Al concentration, the root length of all genotypes are severely reduced, being less than 20 mm, and the variance of the root length averages of parental genotypes is very reduced. Taking into account the variances of genotype averages (variances between genotypes considered as a single population), it can be estimated that the 2 and 4 Al concentrations are the most appropriate to separate the genotypes (Table 4).

types into 3 classes in the case of 2 ppm Al and 5 classes in the case of 4 ppm Al (Table 5).

According to the results, 4 ppm Al concentration of testing solution is the most appropriate for obtaining the best genotype discrimination. The genetic populations of the 15 combinations could be characterized by the average maximum length (mm) and coefficient of variation (%) resulted after their testing in a solution containing 4 ppm Al (Table 6). The root length of parental genotypes (P_1 and P_2) varies from 32.2 mm (Fundulea 29) to 110.1 mm (Oradea 30), depending on the tolerance level, and the values of variation coefficient show a good uniformity. The root length of F_1 genetic populations range generally between the root length of parents, close to their average. There are also some exceptions: the combinations of Oradea 30/Fundulea 4 and Fundulea 472 /Fundulea 4 with lengths close to the best parent and even higher (Arie^oan /Fundulea 4). These situations

suggest the dominance genetic effects of genes which control the tolerance. values of the parental genotypes, close to the average of the two parents or closer to the best

Table 5. Appreciation of parental genotypes by root length (Duncan's test)

Genotypes	0 ppm Al		2 ppm Al		4 ppm Al		6 ppm Al		Appreciation
	length	sign.	length	sign.	length	sign.	length	sign.	
Fundulea 29	123.9	b	40.2	c	32.2	e	12.9	a	Very susceptible
Fundulea 4	120.4	b	42.3	c	40.4	d	12.4	a	Susceptible
Arie ^o an	124.1	b	115.9	b	76.0	c	18.1	a	Moderately tolerant
Fundulea 472	126.8	b	117.8	b	79.9	c	18.8	a	Moderately tolerant
Oradea 33	121.8	b	116.0	b	93.4	b	16.2	a	Tolerant
Oradea 30	137.7	a	133.7	a	110.1	a	17.7	a	Very tolerant

LSD 5% = 6.1; 6.5; 6.6; 6.8; 6.9 mm

Table 6. Values of statistical indices regarding tolerance to aluminium toxicity for the set of combinations

Combinations	Statistical indices	Genetic populations					
		P ₁	P ₂	F ₁	F ₂	B ₁	B ₂
Oradea 30/Oradea 33	\bar{x}	110.1	93.4	103.8	96.3	107.2	91.4
	S%	12.61	13.46	6.43	21.40	19.74	15.36
Oradea 30/Fundulea 472	\bar{x}	110.1	79.9	62.5	66.7	69.2	71.6
	S%	12.61	16.42	16.44	34.41	33.25	16.55
Oradea 30/Arie ^o an	\bar{x}	110.1	76.0	96.0	89.9	104.4	80.2
	S%	12.61	16.52	13.27	28.46	15.84	17.30
Oradea 30/Fundulea 4	\bar{x}	110.1	40.4	73.4	78.4	78.5	53.5
	S%	12.61	19.49	18.71	35.17	18.72	27.78
Oradea 30/Fundulea 29	\bar{x}	110.1	32.2	63.7	74.8	79.0	49.5
	S%	12.61	32.18	19.96	43.71	19.26	20.75
Oradea 33/Fundulea 472	\bar{x}	93.4	79.9	81.8	93.7	88.7	81.9
	S%	13.46	16.42	11.58	22.83	14.02	23.60
Oradea 33/Arie ^o an	\bar{x}	93.4	76.0	83.5	88.0	89.0	71.0
	S%	13.46	16.52	8.48	23.02	8.18	22.08
Oradea 33/Fundulea 4	\bar{x}	93.4	40.4	92.0	77.6	93.1	70.4
	S%	13.46	19.49	10.55	34.19	15.32	19.17
Oradea 33/Fundulea 29	\bar{x}	93.4	32.2	93.6	49.4	83.1	54.5
	S%	13.46	32.18	10.44	56.01	16.15	36.91
Fundulea 472/Arie ^o an	\bar{x}	79.9	76.0	79.5	76.7	84.4	78.3
	S%	16.42	16.52	13.03	36.88	12.93	14.68
Fundulea 472/Fundulea 4	\bar{x}	79.9	40.4	72.5	65.9	81.4	45.2
	S%	16.42	19.49	14.70	37.50	19.54	30.68
Fundulea 472/ Fundulea 29	\bar{x}	79.9	32.2	65.1	66.0	77.4	37.9
	S%	16.42	32.19	17.89	45.85	16.65	32.97
Arie ^o an/ Fundulea 4	\bar{x}	76.0	40.4	78.5	58.0	74.8	44.3
	S%	16.52	19.49	18.76	38.88	19.48	31.57
Arie ^o an/ Fundulea 29	\bar{x}	76.0	32.2	66.0	52.7	69.4	47.2
	S%	16.52	32.19	17.17	40.44	13.84	33.64
Fundulea 4/ Fundulea 29	\bar{x}	40.4	32.2	33.8	32.9	44.5	32.4
	S%	19.49	32.19	29.16	50.78	42.73	49.25

In the case of F₁ populations, the variation coefficient values are even less than in the case of parental genotypes, being below 20%, with one exception, demonstrating the uniform response of F₁ populations (genetically uniform) to aluminium ion toxicity.

The averages of F₂ hybrid populations, in most cases, are situated between the average

parent, confirming the presence of dominance effects. There are also cases where the averages of F₁ populations are closer to the parent with lower value or even below it, suggesting the intraallelic interactions as in the case of the following combinations: Oradea 30/ Fundulea 472, Oradea 33/Fundulea 29, Fundulea 4/ Fundulea 29. In a single case (combination Oradea

33/Fundulea 472), the average length of the F_2 population exceeds the best parent, probably, as a consequence of the complementary role of tolerance genes present in the two parents. Favourable transgressions are also possible.

In all cases, the variation coefficient of F_2 population has high values, between 21.40 and 96.01, suggesting a large gene recombination.

In the case of backcrosses (B_1) between F_1 hybrids and the more tolerant parent, the average values are situated between F_1 value and the best parent (P_1), suggesting the presence of the additive genic effects, easily to fix by selection in the breeding process. Three cases are to be mentioned when the average values of B_1 populations exceed the best parent, suggesting the presence of dominance and of valuable transgressive forms: combinations of Fundulea 472/Arie^oan, Fundulea 472/Fundulea 4 and Fundulea 4/Fundulea 29. There are also cases where the average values of B_1 population are smaller than the average values of F_1 population, situation which could be explained by the presence of the epistatic effects and probably by some suppressive genes (Oradea 33/Fundulea 29 and Arie^oan/Fundulea 4).

The values of variation coefficients of B_1 populations are, in all cases, much smaller than in the case of F_2 hybrid populations, an evidence of some more reduced gene recombination.

In the case of the backcrosses between F_1 and the more sensitive parent (B_2), the average values are generally situated between the average values of F_1 population and the average values of the more sensitive parent (P_2), suggesting the preponderant presence of additive effects. Two exceptions are represented by the combinations Oradea 30/Oradea 33 and Oradea 33/Arie^oan, with average even smaller than the more susceptible parent, probably due to the epistatic interactions. The values of the variation coefficients in the B_2 populations are smaller than those in the F_2 populations and generally higher than in the case of B_1 populations, an evidence of a more reduced gene recombination. The values of B_2 populations of the Oradea 30/ Oradea 33 and Oradea 30/ Fundulea 472 combinations, having a variation coefficient in B_2 smaller than in B_1 , deviate from the tendency.

A particular situation presents the average values of the populations of Oradea 30/Fundulea 472 combination: the average value of F_1 smaller than F_2 , F_2 bigger than F_1 , B_2 bigger than F_1 and B_1 . A plausible and possible explanation for this situation is argued in another work, that is the tolerance of the Fundulea 472 line is given, at least partially, by the action of some cytoplasmic genes (plasmagenes).

The mathematical model proposed by Gamble (1962) and used to process these data permits the separation of the additive genetic effects, of dominance and epistatic, considering the maternal and reciprocal effects as inexistent. The effects and variances of the genetic mechanisms corresponding to the 15 hybrid combinations are presented in Table 7.

In Oradea 30/Oradea 33 combination, the additive gene actions of the homozygous loci are preponderant, but also the interallelic interactions of additive x dominant type between the homozygous and heterozygous loci contribute to tolerance increasing. In the case of the following combination, a significant weight is due to the genic interactions of dominance and interallelic interactions with epistatic effects of the additive x dominant type, but with negative sense of reducing the tolerance level. The Oradea 30/Arie^oan combinations with the Fundulea 4 and Fundulea 29 intolerant cultivars manifest a complex inheritance with all types of genic actions and interactions, with both positive and negative sense. In all combinations of the Oradea 33 line, the interallelic interactions of genes in heterozygous loci have dominant genic effects, having positive action only in combination with intolerant genotypes. Among the interactions, the interallelic interactions between the heterozygous loci (epistases of dominant x dominant type) have a higher importance.

In the combinations of Fundulea 472 line, the additive effects have a positive sense due to the favourable action of homozygous loci and interallelic interactions between homozygous and heterozygous loci (of additive x dominant type), while the other genic effects can have positive but also negative sense. The combinations of Arie^oan cultivar with the two susceptible cultivars present only positive effects, this

cultivar having a breeding value for them. In the situation when both parental genotypes were susceptible (Fundulea 4/ Fundulea 29), the inheritance of tolerance is complex, all the genetic effects had a positive sense, except for the interallelic epistatic interactions (of dominant x dominant type) between the heterozygous loci.

Analysing the values of the combinations set, the important weight of additive genic actions of homozygous loci is evident, having in all cases a favourable effect on tolerance increasing. No combination presented only additive genic actions.

The genic interactions of dominance are significant in 12 out of 15 combinations, hence

Table 7. Effects and variances of genetic control for tolerance to aluminium toxicity

Combinations	Elements	Action type of genes					
		M(F ₂)	A	D	AA	AD	DD
Oradea 30/ Oradea 33	\bar{x}	96.3	15.8**	14.1	12.0	7.4**	1.9
	v	424.6	645.1	9.506.3	9.374.0	732.8	17.644.6
	t		3.53	1.89	0.94	3.04	0.19
Oradea 30/ Fundulea 472	\bar{x}	66.7	-2.4	-17.1*	14.8	-17.5***	18.6
	v	526.8	669.8	11.304.7	11.108.0	760.9	19.932.3
	t		0.61	2.21	1.12	7.34	1.75
Oradea 30/ Arie ^o an	\bar{x}	89.9	24.2***	12.55	22.15	7.15***	-0.7
	v	654.6	465.9	12.587.1	12,337.2	553.5	18,927.8
	t		8.16	1.59	1.86	3.64	0.07
Oradea 30/ Fundulea 4	\bar{x}	78.4	25.0***	-51.45***	-49.6***	-9.85***	82.9***
	v	760.1	436.8	14,161.0	13,908.8	500.5	20,159.3
	t		8.11	5.91	3.55	5.17	7.98
Oradea 30/ Fundulea 29	\bar{x}	74.8	29.5***	-49.65***	-42.2**	-9.45***	54.9***
	v	1,069.0	337.0	18,688.8	18,452.0	412.1	23,119.7
	t		11.92	5.08	2.78	5.61	5.06
Oradea 33/ Fundulea 472	\bar{x}	93.7	6.8	-38.45***	-33.6**	0.05	29.3**
	v	457.5	528.1	9,604.7	9,432.4	610.6	16,459.0
	t		1.75	5.23	2.79	0.02	3.05
Oradea 33/ Arie ^o an	\bar{x}	88.0	18.0***	-33.2***	-32.0	9.3***	48.4***
	v	410.3	298.8	7,889.0	7,760.0	377.7	11,861.8
	t		7.36	5.22	3.25	5.66	6.22
Oradea 33/ Fundulea 4	\bar{x}	77.6	22.7***	41.7***	16.6	-3.8	-25.8**
	v	704.1	385.6	12,957.2	12,808.0	440.6	18,032.1
	t		7.75	5.09	1.25	2.10	2.67
Oradea 33/ Fundulea 29	\bar{x}	49.4	28.6***	108.4***	77.6***	-2.0	-40.0***
	v	765.6	584.7	14,750.3	14,588.4	651.1	22,252.3
	t		6.14	11.81	4.76	0.84	3.55
Fundulea 472/ Arie ^o an	\bar{x}	76.7	6.1**	20.15*	18.6	4.15**	-29.1**
	v	800.3	251.3	13,999.8	13,810.1	333.8	17,584.9
	t		3.01	2.43	1.45	2.79	3.13
Fundulea 472/ Fu n- dulea 4	\bar{x}	65.9	36.2***	1.95	-10.4	16.45***	22.5*
	v	610.8	445.2	10,966.4	11,553.0	503.7	17,583.4
	t		11.12	0.26	0.81	8.42	2.33
Fundulea 472/ Fu n- dulea	\bar{x}	66.0	39.5***	-24.35**	-33.4*	15.65***	45.1***
	v	915.7	322.2	16,141.1	15,940.6	392.1	20,629.3
	t		16.02	2.66	2.31	9.45	4.36
Arie ^o an / Fundulea 4	\bar{x}	58.0	30.5***	26.5***	6.2	12.7***	29.0**
	v	508.6	408.0	10,041.3	9,769.6	462.9	15,752.5
	t		10.68	3.65	0.54	6.99	3.18
Arie ^o an / Fundulea 29	\bar{x}	52.7	22.2***	34.3***	22.4	0.3	-15.4
	v	454.2	344.4	8,840.7	8,644.8	410.7	13,556.3
	t		7.84	4.88	1.96	0.17	1.77
Fundulea 4/ Fundulea 29	\bar{x}	32.9	12.1**	19.7**	22.2*	8.0***	-35.8***
	v	279.1	616.1	7,069.6	6,930.2	658.4	14,881.2
	t		3.41	3.25	2.34	3.68	4.08

the importance of the intraallelic interactions of genes from the heterozygous loci in inheritance of aluminium tolerance. The interactions of dominance type have positive sign only in combinations between Oradea 33 and the more susceptible genotypes, as well as in the case of combinations between the Arie^oan and medium tolerant or susceptible genotypes.

The epistatic interactions of additive x additive type of genes situated on homozygous loci are significant only in 7 cases, their sense being positive only in two combinations, both belonging to the Fundulea 29 genotype.

The epistases of the additive x dominant type, as a result of the interactions between homozygous and heterozygous loci, have a higher frequency, 11 cases out of 15, respectively, having a negative sense only in three combinations, all of them belonging to the Oradea 30 genotype. The epistatic interactions of the dominant x dominant type between the heterozygous loci are present and significant in 11 cases of which only in 4 cases have a negative sense of reducing the tolerance level.

All types of genic interactions are present in the combinations : Oradea 30/ Fundulea 4, Oradea 30/Fundulea 29, Oradea 33/Arie^oan, Fundulea 472/Fundulea 29 and Fundulea 4/ Fundulea 29. These data demonstrate that the aluminium tolerance is a complex quantitative trait, polygenically controlled, where all the types of genetic effects can be involved. Only in some recent researches (Aniol, 1990; McKendry et al., 1996), it has been demonstrated that the winter wheat tolerance to aluminium ion toxicity has a complex heredity, with the implication of at least two genes fa-

vourable for tolerance and of some suppressor and even modifying genes. Our researches led to the conclusion that, at least at the reduced toxicity levels, the aluminium tolerance has a complex heredity.

These results have important implications in the breeding process. In combinations where the additive genic effects are positive and preponderant (Oradea 30/Oradea 33, Oradea 30/Arie^oan etc.), the genealogical selection will have a good efficiency. In combinations where non-additive (dominance and epistases) genic effects also occur, as a result of the genic interactions, it is expected that the recurrent or recurrent-reciprocal selection possess a higher efficiency, especially if they are followed also, in more advanced generations, by genealogical selection, to fix the genes with minor action, too.

In order to appreciate the contribution of genotype in expressing the aluminium tolerance, the environmental variance was separated from the total (phenotypical) variance. The total variance (variance of F_2 population) is high, with an average of 622.8, between the limits of 279.1 and 1,069. Generally, the total variance value is proportional to the difference between the parental genotypes (Table 8).

The genotypical variance has lower values, its weight in phenotypical variance ranging from 17.3 to 71.9 per cent, and also being proportional to the difference of tolerance between the genotypes present in the combination. The average value of the genotypical variance weight in the total variance is 54.5 per cent. That means that the genetic variance has a significant role in phenotypical expression of alu-

Table 8. Genotype and environment weight in phenotypical expression of tolerance to aluminium toxicity

Combinations	T.V.		G.V.		E.V.		H.L.	H.S.
	value	% of T.V.	value	% of T.V.	value	% of T.V.		
Oradea 30/ Oradea 33	426.6	73.6	17.3	351.0	82.7	0.59	0.43	
Oradea 30/ Fundulea 472	526.8	161.8	30.7	365.0	69.3	0.96	0.42	
Oradea 30/ Arie ^o an	654.6	304.0	46.4	350.6	53.6	0.73	0.28	
Oradea 30/ Fu ndulea 4	760.1	505.2	66.5	254.9	33.5	0.86	0.35	
Oradea 30/ Fundulea 29	106.9	768.7	71.9	300.3	28.1	0.87	0.19	
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Oradea 33/ Arie ^o an	410.3	94.5	23.0	315.8	77.0	0.62	0.34	
Oradea 33/ Fu ndulea 4	704.1	484.0	68.7	220.1	31.3	0.86	0.43	
Oradea 33/ Fundulea 29	765.6	500.1	65.3	265.5	34.7	0.83	0.27	
Fundulea 472/ Arie ^o an	800.3	470.5	58.8	329.8	41.2	0.79	0.16	
Fundulea 472/ Fundulea 4	610.8	376.6	61.7	234.1	38.3	0.83	0.37	
Fundulea 472/ Fundulea 29	915.7	636.1	69.5	279.6	30.5	0.85	0.27	
Arie ^o an/ Fu ndulea 4	508.6	288.9	56.8	219.7	43.2	0.81	0.35	
Arie ^o an/ Fu ndulea 29	454.2	189.1	41.6	265.1	58.4	0.71	0.29	
Fundulea 4/ Fundulea 29	279.1	109.7	39.3	169.4	60.7	0.71	0.47	
Averages	622.8	339.3	54.5	283.5	45.5	0.78	0.34	

minium tolerance, in 8 out of 15 cases exceeding the weight of the environmental variance. It is obvious that the expression of aluminium tolerance by means of the root length depends firstly on the genotype, therefore the trait has a good hereditary transmission. The differences concerning the weight of genotypical variance demonstrates the genotype differentiated contribution in the hereditary transmission of aluminium tolerance.

The genotype priority in hereditary tolerance transmission is confirmed by high values of hereditary coefficient in a large sense (HL), with limits between 0.59 and 0.90. The values of this coefficient reflect also the differentiated role of genotypes in the trait heredity. The values of hereditary coefficient in a narrow sense (HN) are much lower, between 0.16 and 0.47. This fact suggests the important role of non-additive genic effects (of dominance and epistasis) in the hereditary transmission of tolerance. As an exception, the Oradea 30/Oradea 33 combination could be mentioned.

CONCLUSIONS

The Oradea 30 line, besides the fact that it has a very good aluminium tolerance, has a vigorous root system, with a rapid development rhythm, that explains the productive performance obtained on an acid soil, poor in nutrients and with an aluminium excess. The most appropriate aluminium concentration to appreciate the tolerance proved to be 4 ppm, this permitting the separation of genotypes into 5 groups.

The genotypes used as parental forms presented a good capacity of the hereditary transmission, but with a different contribution in phenotypical expression of the aluminium tolerance. In genetic control of aluminium tolerance, the additive effects have a positive action as a result of the favourable action of the homozygous loci. The dominant genic interactions have also an important weight, but their sense was both positive, to increase the tolerance, and especially negative, to reduce it, depending on the

genes in the heterozygous loci involved in intrallelic interactions.

A particular important role for breeding is played by the interallelic interactions of epistasis type of genes located on heterozygous loci, whose action is generally strong and positive. The presence of all types of genic actions, with both positive and negative sense, demonstrates the genetic complex control of tolerance to aluminium ion toxicity in winter wheat.

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Table 1. Parental genotypes used in diallel crosses of p(p-1) type

Genotype	Genealogy	Provenance
Oradea 30	Colonias/ F133 D 4 -23	Oradea
Oradea 33	S8/F9D49-31	Oradea
Fundulea 472	Colonias/ F 135 D// Flamura 80	Fundulea
Arie ^o an	Rubin/Bezostaia 1// Fiorello	Turda
Fundulea 4	Fundulea 29/ Lovrin 32	Fundulea
Fundulea 29	Aurora/ Riley	Fundulea

Table 2. ANOVA for parental genotypes. Al rates and interactions

Source of variance	SS	DF	MS	F test
Large plots	115.686.9	11		
Replications	5.1	2		
Al rates	115.582.9	3	38.527.6	2.335.0**
Error (a)	99.0	6	16.5	
Small plots	156.656.6	71		
Parental genotypes	22.588.0	5	4.517.6	327.4**
Interactions of rates x parental genotypes	17.830.4	15	1.188.7	86.1**
Error (b)	551.1	40	13.8	

Table 3. The effect of Al concentrations on root length of parental genotypes

Parental genotypes	Averages and variances of root length							
	0 ppm Al		2 ppm Al		4 ppm Al		6 ppm Al	
	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2	\bar{x}	s^2
Fundulea 29	123.9	181.1	40.2	87.1	32.2	107.4	12.9	4.6
Fundulea 4	120.4	174.1	42.3	89.4	40.4	62.0	12.4	6.3
Arie ^o an	124.1	235.0	115.9	122.1	76.0	17.7	18.1	25.4
Fundulea 472	126.8	212.8	117.8	185.5	79.4	172.1	18.8	31.1
Oradea 33	121.8	144.1	116.0	142.0	93.4	158.1	16.2	12.4
Oradea 30	137.7	133.8	133.7	165.1	110.1	192.9	17.7	18.6
Averages of parental genotypes	125.8	38.8	94.3	1734.6	72.0	914.1	16.0	7.6

Table 4. Root length of parental genotypes at 4 ppm Al concentration

Parental genotypes	Root length (mm)	Relative length (%)	Differences	Significance
Fundulea 29	32.2	44.7	- 39.8	000
Fundulea 4	40.4	56.1	- 31.6	000
Averages of parental genotypes	72.0	100.0	0.0	-
Arie ^o an	76.0	105.6	+ 4.0	
Fundulea 472	79.9	111.0	+ 7.9	*
Oradea 33	93.4	129.7	+ 21.4	***
Oradea 30	110.1	152.9	+ 38.1	***

LSD_{5%} = 6.1 mm; LSD_{1%} = 8.2 mm; LSD_{0.1%} = 10,8 mm

Table 5. Appreciation of parental genotypes by root length (Duncan's test)

Genotypes	0 ppm Al		2 ppm Al		4 ppm Al		6 ppm Al		Appreciation
	Length	Sign.	Length	Sign.	Length	Sign.	Length	Sign.	
Fundulea 29	123.9	b	40.2	c	32.2	e	12.9	a	Very susceptible
Fundulea 4	120.4	b	42.3	c	40.4	d	12.4	a	Very susceptible
Arie°an	124.1	b	115.9	b	76.0	c	18.1	a	Susceptible
Fundulea 472	126.8	b	117.8	b	79.9	c	18.8	a	Moderately tolerant
Oradea 33	121.8	b	116.0	b	93.4	b	16.2	a	Moderately tolerant
Oradea 30	137.7	a	133.7	a	110.1	a	17.7	a	Tolerant
LSD _{5%} = 6.1; 6.5; 6.6; 6.8; 6.9 mm									

Table 6. Values of statistical indices regarding tolerance to aluminium toxicity for the set of combinations

Combinations	Statistical indices	Genetic populations					
		P ₁	P ₂	F ₁	F ₂	B ₁	B ₂
Oradea 30/Oradea 33	\bar{x}	110.1	93.4	103.8	96.3	107.2	91.4
	S%	12.61	13.46	6.43	21.40	19.74	15.36
Oradea 30/Fundulea 472	\bar{x}	110.1	79.9	62.5	66.7	69.2	71.6
	S%	12.61	16.42	16.44	34.41	33.25	16.55
Oradea 30/Arie°an	\bar{x}	110.1	76.0	96.0	89.9	104.4	80.2
	S%	12.61	16.52	13.27	28.46	15.84	17.30
Oradea 30/Fundulea 4	\bar{x}	110.1	40.4	73.4	78.4	78.5	53.5
	S%	12.61	19.49	18.71	35.17	18.72	27.78
Oradea 30/Fundulea 29	\bar{x}	110.1	32.2	63.7	74.8	79.0	49.5
	S%	12.61	32.18	19.96	43.71	19.26	20.75
Oradea 33/Fundulea 472	\bar{x}	93.4	79.9	81.8	93.7	88.7	81.9
	S%	13.46	16.42	11.58	22.83	14.02	23.60
Oradea 33/Arie°an	\bar{x}	93.4	76.0	83.5	88.0	89.0	71.0
	S%	13.46	16.52	8.48	23.02	8.18	22.08
Oradea 33/Fundulea 4	\bar{x}	93.4	40.4	92.0	77.6	93.1	70.4
	S%	13.46	19.49	10.55	34.19	15.32	19.17
Oradea 33/Fundulea 29	\bar{x}	93.4	32.2	93.6	49.4	83.1	54.5
	S%	13.46	32.18	10.44	56.01	16.15	36.91
Fundulea 472/Arie°an	\bar{x}	79.9	76.0	79.5	76.7	84.4	78.3
	S%	16.42	16.52	13.03	36.88	12.93	14.68
Fundulea 472/Fundulea 4	\bar{x}	79.9	40.4	72.5	65.9	81.4	45.2
	S%	16.42	19.49	14.70	37.50	19.54	30.68
Fundulea 472/Fundulea 29	\bar{x}	79.9	32.2	65.1	66.0	77.4	37.9
	S%	16.42	32.19	17.89	45.85	16.65	32.97
Arie°an/Fundulea 4	\bar{x}	76.0	40.4	78.5	58.0	74.8	44.3
	S%	16.52	19.49	18.76	38.88	19.48	31.57
Arie°an/Fundulea 29	\bar{x}	76.0	32.2	66.0	52.7	69.4	47.2
	S%	16.52	32.19	17.17	40.44	13.84	33.64
Fundulea 4/Fundulea 29	\bar{x}	40.4	32.2	33.8	32.9	44.5	32.4
	S%	19.49	32.19	29.16	50.78	42.73	49.25

Table 7. Effects and variances of genetic control for tolerance to aluminium toxicity

Combinations	Ele-ments	Actions type of genes					
		M(F ₂)	A	D	AA	AD	DD
Oradea 30/ Oradea 33	\bar{x}	96.3	15.8**	14.1	12.0	7.4**	1.9
	v	424.6	645.1	9.506.3	9.374.0	732.8	17.644.6
	t		3.53	1.89	0.94	3.04	0.19
Oradea 30/ Fundulea 472	\bar{x}	66.7	-2.4	-17.1*	14.8	-17.5***	18.6
	v	526.8	669.8	11.304.7	11.108.0	760.9	19.932.3
	t		0.61	2.21	1.12	7.34	1.75
Oradea 30/ Arie ^o an	\bar{x}	89.9	24.2***	12.55	22.15	7.15***	-0.7
	v	654.6	465.9	12.587.1	12,337.2	553.5	18,927.8
	t		8.16	1.59	1.86	3.64	0.07
Oradea 30/ Fundulea 4	\bar{x}	78.4	25.0***	-51.45***	-49.6***	-9.85***	82.9***
	v	760.1	436.8	14,161.0	13,908.8	500.5	20,159.3
	t		8.11	5.91	3.55	5.17	7.98
Oradea 30/ Fundulea 29	\bar{x}	74.8	29.5***	-49.65***	-42.2**	-9.45***	54.9***
	v	1,069.0	337.0	18,688.8	18,452.0	412.1	23,119.7
	t		11.92	5.08	2.78	5.61	5.06
Oradea 33/ Fundulea 472	\bar{x}	93.7	6.8	-38.45***	-33.6**	0.05	29.3**
	v	457.5	528.1	9,604.7	9,432.4	610.6	16,459.0
	t		1.75	5.23	2.79	0.02	3.05
Oradea 33/ Arie ^o an	\bar{x}	88.0	18.0***	-33.2***	-32.0	9.3***	48.4***
	v	410.3	298.8	7,889.0	7,760.0	377.7	11,861.8
	t		7.36	5.22	3.25	5.66	6.22
Oradea 33/ Fundulea 4	\bar{x}	77.6	22.7***	41.7***	16.6	-3.8	-25.8**
	v	704.1	385.6	12,957.2	12,808.0	440.6	18,032.1
	t		7.75	5.09	1.25	2.10	2.67
Oradea 33/ Fundulea 29	\bar{x}	49.4	28.6***	108.4***	77.6***	-2.0	-40.0***
	v	765.6	584.7	14,750.3	14,588.4	651.1	22,252.3
	t		6.14	11.81	4.76	0.84	3.55
Fundulea 472/ Arie ^o an	\bar{x}	76.7	6.1**	20.15*	18.6	4.15**	-29.1**
	v	800.3	251.3	13,999.8	13,810.1	333.8	17,584.9
	t		3.01	2.43	1.45	2.79	3.13
Fundulea 472/ Fu n- dulea 4	\bar{x}	65.9	36.2***	1.95	-10.4	16.45***	22.5*
	v	610.8	445.2	10,966.4	11,553.0	503.7	17,583.4
	t		11.12	0.26	0.81	8.42	2.33
Fundulea 472/ Fu n- dulea	\bar{x}	66.0	39.5***	-24.35**	-33.4*	15.65***	45.1***
	v	915.7	322.2	16,141.1	15,940.6	392.1	20,629.3
	t		16.02	2.66	2.31	9.45	4.36
Arie ^o an / Fundulea 4	\bar{x}	58.0	30.5***	26.5***	6.2	12.7***	29.0**
	v	508.6	408.0	10,041.3	9,769.6	462.9	15,752.5
	t		10.68	3.65	0.54	6.99	3.18
Arie ^o an / Fundulea 29	\bar{x}	52.7	22.2***	34.3***	22.4	0.3	-15.4
	v	454.2	344.4	8,840.7	8,644.8	410.7	13,556.3
	t		7.84	4.88	1.96	0.17	1.77
Fundulea 4/ Fundulea 29	\bar{x}	32.9	12.1**	19.7**	22.2*	8.0***	-35.8***
	v	279.1	616.1	7,069.6	6,930.2	658.4	14,881.2
	t		3.41	3.25	2.34	3.68	4.08

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Table 8. Genotype and environment weight in phenotypical expression of tolerance to aluminium toxicity

Combinations	T.V.	G.V.		E.V.		H.L.	H.S.
		value	% of T.V.	value	% of T.V.		
Oradea 30/ Oradea 33	426.6	73.6	17.3	351.0	82.7	0.59	0.43
Oradea 30/ Fundulea 472	526.8	161.8	30.7	365.0	69.3	0.96	0.42
Oradea 30/ Arie ^o an	654.6	304.0	46.4	350.6	53.6	0.73	0.28
Oradea 30/ Fundulea 4	760.1	505.2	66.5	254.9	33.5	0.86	0.35
Oradea 30/ Fundulea 29	1,069	768.7	71.9	300.3	28.1	0.87	0.19
Oradea 33/ Fundulea 472	457.5	127.3	27.8	330.2	72.2	0.64	0.41
Oradea 33/ Arie ^o an	410.3	94.5	23.0	315.8	77.0	0.62	0.34
Oradea 33/ Fundulea 4	704.1	484.0	68.7	220.1	31.3	0.86	0.43
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Fundulea 472/ Fundulea 29	915.7	636.1	69.5	279.6	30.5	0.85	0.27
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Fundulea 4/ Fundulea 29	279.1	109.7	39.3	169.4	60.7	0.71	0.47
Averages	622.8	339.3	54.5	283.5	45.5	0.78	0.34