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Diallel cross among inbred lines of maize differing in aluminum tolerance

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ABSTRACT

Diallel crosses among eight maize (*Zea mays* L.) inbred lines were evaluated under laboratory conditions for aluminum (Al) tolerance. Al tolerance was estimated by radicle length of plants grown in nutrient solution with 4.5 mg Al/liter. The diallel crosses were also evaluated for yield, plant height, and ear height under field conditions. Both laboratory and field evaluations were conducted in a randomized complete block design with three replications. The eight inbred lines included five Al-tolerant and three Al-sensitive lines.

The treatment effects in the diallel analysis were partitioned into general (GCA) and specific combining ability (SCA). In the analysis of variance, both GCA and SCA were statistically significant, although the GCA mean squares were greater in magnitude than SCA for all traits except yield, suggesting greater expression of additive genetic affects in the crosses. For grain yield, the SCA mean square was larger than the GCA mean square. For radicle length (RL) the diallel analysis was also partitioned to test for line and heterosis effects. Significant effects were detected for all sources, but the greater mean squares were for the effects of lines *per se* and for average heterosis. The high heterosis for RL was probably due to nonallelic interactions caused by deleterious genes with large effects, rather than to allelic interaction (dominance).

INTRODUCTION

A great portion of Brazilian soil is characterized by toxic levels of aluminium (Al). Al toxicity is one of the main causes of low maize yields (Olmos and Camargo, 1976; Lopes *et al.*, 1987). Al affects the development of the root system in sensitive plants, which leads to a lower absortion of water and nutrients. These effects are enhanced in soils with higher acidity levels in the sub-superficial layers (Foy *et al.*, 1978). The correction of soil acidity through lime application and the use of Al-tolerant cultivars seem to be reliable solutions from both technical and economic viewpoints (Bahia Filho *et al.*, 1976).

Genetic variability for tolerance to excess Al in maize has been reported (Lutz *et al.*, 1971; Clark and Brown, 1974; Rhue and Grogan, 1977; Bahia Filho *et al.*, 1976; Magnavaca, 1982; Furlani *et al.*, 1986; Prioli, 1987; Lima *et al.*, 1992). The pattern of inheritance of Al-tolerance has not been consistent. Rhue *et al.* (1978) and Garcia Jr. and Silva (1979) concluded that Al-tolerance in maize is controlled by a single dominant gene. Miranda *et al.* (1984) indicated that Al-tolerance was due to two complementary dominant genes. The dominant pattern for Al-tolerance was also reported by Prioli (1987). Magnavaca (1982) and Sawazaki and Furlani (1987) reported on the quantitative pattern of inheritance of Al-tolerance. Lima *et al.* (1992) clearly showed that Al-tolerance is quantitatively inherited in the analysis of F_1, F_2 and backcross generations between two subpopulations obtained by divergent selection for radicle length in Al-stressed nutrient

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solution. Lima *et al.* (1992) showed that the pattern of inheritance is essentially additive, as indicated by both estimated and realized heritabilities.

In diallel crosses with inbred lines, Magnavaca (1982) and Prioli (1987) found that the general combining ability effects were more expressive than specific combining ability effects, suggesting lesser importance of nonadditive genetic effects.

MATERIAL AND METHODS

Twenty eight single cross hybrids among eight inbred lines were produced by the diallel mating scheme. Three inbreds were dent types and Al-sensitive: **Ip 701.1.1**, derived from Tuxpan; **SLP 103.3.2**, from the collection SLP 103.3 (San Luis de Potosí, México); and **Col.2 (22)**, a yellow version of an originally white corn from Colombia. The inbreds **Ip 48.5.3** and **Ip 365.4.1** were derived from Cateto and are highly Al-tolerant (Miranda *et al.*, 1978; Miranda *et al.*, 1984; Furlani *et al.*, 1986). The inbreds **IAC 13.8**, **IAC 3.2** and **IAC 96.4** are Al-tolerant dent types, and derived from IAC-Taiuba (Lima *et al.*, 1988).

The lines were numbered as follows:

1 - Col.2 (22)
2 - IAC 13.8
3 - IAC 3.2
4 - IAC 96.4
5 - Ip 48.5.3
6 - Ip 365.4.1
7 - Ip 701.1.1
8 - SLP 103.3.2

Al-tolerance was evaluated in the greenhouse in nutrient solution with 4.5 mg Al per liter, following the procedure described by Furlani *et al.* (1986). Data refer to radicle length (RL) 15 days after germination. A randomized complete block experiment was used, including 36 entries (eight parental lines and 28 single crosses), with three replications and six plants per plot.

A field experiment with 30 entries (28 single crosses and two checks) was conducted in the Experimental Station of *Instituto Agronômico de Campinas* (IAC) at Campinas (SP), within an area corrected for soil acidity. The design was in randomized complete blocks, with three replications in plots 10 meters long and spaced 1.0 m apart, with 50 plants per plot (25 hills with two plants per hill). In the field experiment the following traits were measured: GY - grain yield (t/ha), PH - plant height (m), and EH - ear height (m). Yield data were adjusted for stand variation (correction to 50 plants per plot) and grain moisture (correction to 15.5%).

After the preliminary analysis of variance the variation due to single crosses was partitioned into general combining ability (**GCA**) and specific combining ability (**SCA**), according to Method-4 of Griffing (1956) for diallel crosses, following the model:

$$Y_{ii'} = m + g_i + g_{i'} + s_{ii'} + e_{ii'}$$

where, for each trait, Y_{ii} is the mean over r replications of the single cross (i x i'); g_i and $s_{ii'}$ stand for GCA and SCA effects, respectively; and $e_{ii'}$ is the error associated with the single cross mean.

For radicle length the diallel analysis was also performed according to the model of Gardner and Eberhart (1966), including the parent lines:

$$Y_{ii'} = \mu + \frac{1}{2}(v_i + v_{i'}) + \theta(\bar{h} + h_i + s_{ii'}) + \bar{e}_{ii'}$$

where μ is the mean of the parent lines; v_i is the line effects; $\theta = 0$ for lines and $\theta = 1$ for hybrids; $\bar{h}$ is the average heterosis; h_i is the line heterosis; and $s_{ii'}$ is the specific heterosis. The diallel analyses were performed with means over three replications.

RESULTS AND DISCUSSION

The trait of primary interest was radicle length, as an indicator of the level of Al-tolerance. For this reason, three sensitive (S) lines were included for evaluation in crosses with tolerant (T) lines; crosses of the SxS and TxT type were also obtained, thus completing an 8x8 diallel cross. Among the eight parental lines, five (**1, 5, 6, 7** and **8**; see Table I) are used commercially and three (**1, 7** and **8**) are Al-sensitive. The remaining lines are experimental lines.

From Table I it is clear that sensitivity to Al is well differentiated by the radicle length of the two groups of lines: sensitive lines (11.9 cm) and tolerant lines (29.3 cm). Similarly, SxS crosses had shorter radicles, averaging 17.0 cm. The SxT or TxT crosses generally followed the tendency of the additive effects of genes controlling the trait, with averages of 28.1 cm (SxT) and 37.8 cm (TxT). The additive nature of the genetic system for RL in maize was also reported by Lima *et al.* (1992) in studying generations following the cross between two sub-populations divergently selected for RL; the response to selection after two cycles was 26.1% on average for both directions.

Table I also includes the heterosis expressed for RL in all crosses. The estimates varied from nearly

Table I - Means of eight inbred lines[#] and 28 diallel crosses evaluated for Al-tolerance and for yield and plant and ear height.

Entry	##	Radicle length		Yield	Plant	Ear
		mean (cm)	h%	(t/ha)	height (m)	height (m)
1	S	10.97	--	--	--	--
2	T	31.86	--	--	--	--
3	T	28.28	--	--	--	--
4	T	34.30	--	--	--	--
5	T	29.49	--	--	--	--
6	T	22.77	--	--	--	--
7	S	10.38	--	--	--	--
8	S	14.41	--	--	--	--
1x2	ST	20.83	-2.7	8.75	2.42	1.45
1x3	ST	23.52	19.8	9.29	2.22	1.30
1x4	ST	40.84	80.4	7.40	2.11	1.21
1x5	ST	30.36	50.1	8.72	2.39	1.42
1x6	ST	32.52	92.8	8.30	2.42	1.56
1x7	SS	16.33	53.0	8.45	2.39	1.30
1x8	SS	19.13	50.7	8.30	2.44	1.50
2x3	TT	30.38	1.0	9.98	2.17	1.12
2x4	TT	45.66	38.0	9.64	2.34	1.41
2x5	TT	44.64	45.5	8.92	2.33	1.47
2x6	TT	38.47	40.7	7.70	2.36	1.53
2x7	ST	20.11	-4.8	7.24	2.22	1.31
2x8	ST	22.61	-2.3	7.80	2.51	1.65
3x4	TT	34.67	10.8	2.39	1.66	0.70
3x5	TT	37.71	30.5	9.70	2.17	1.13
3x6	TT	35.99	41.0	10.03	2.31	1.21
3x7	ST	33.61	73.9	6.56	2.07	0.99
3x8	ST	25.86	21.1	8.07	2.47	1.32
4x5	TT	42.34	32.8	9.87	2.34	1.28
4x6	TT	33.52	17.5	8.77	2.24	1.24
4x7	ST	24.68	10.5	7.84	2.11	1.05
4x8	ST	26.77	9.9	8.71	2.44	1.34
5x6	TT	34.81	33.2	5.21	2.37	1.49
5x7	ST	33.21	66.5	7.55	2.37	1.38
5x8	ST	30.51	39.0	8.00	2.54	1.59
6x7	ST	30.43	83.5	6.47	2.33	1.45
6x8	ST	25.31	36.1	5.65	2.45	1.60
7x8	SS	15.58	25.7	5.20	2.35	1.43
C-511	--	--	--	9.53	2.16	1.20
Ag-401	--	--	--	6.48	2.23	1.36

[#]: 1- Col.2 (22); 2- IAC 13.8; 3- IAC 3.2; 4- IAC 96.4; 5- Ip 48.5.3; 6- Ip 365.4.1; 7- Ip 701.1.1; 8- SLP 103.3.2.
##: S- Al-sensitive; T- Al-tolerant; ST- sensitive x tolerant. h% - mid-parent heterosis.

zero to 92.8%, and about 67% of the crosses showed heterosis above 30%. Heterosis is an expression of non-additive gene effects and, particularly for RL, it seems to be a consequence of recovery of vigor that was lost in the inbred lines through the action of deleterious genes with epistatic effects. Deleterious genes affecting the development of the whole plant would also preclude the full development of the radicle. Nevertheless, the additive effects seem more important in controlling RL in crosses of inbred lines (Table I).

The mean squares for RL were highly significant ($P < 0.01$) for variation among lines, among

Table II - Analysis of variance of four traits for eight maize inbred lines and their 28 diallel crosses.

Source		Radicle length		Mean squares		
	df	MS	df	Yield[3]	P. height[4]	E. height[4]
Replications	2	7.17	2	1.2	548.8**	318.9**
Entries	35	245.03**	29	8767.1**	892.1**	1248.1**
Diallel (D)	35	245.03**	27	8895.1**	930.3**	1318.7**
Lines (L)	7	280.20**	--	--	--	--
Crosses (C)	27	205.47**	27	8895.1**	930.3**	1318.7**
L vs C		1	1066.93**	--	--	--
Checks (C)	--	--	1	13981.2**	73.5	384.0**
D vs C		--	--	1	97.4	677.6**
Error	70	5.060	58	829.4	55.2	42.6
Means: lines		22.81		--	--	--
crosses		30.37		7.88	2.31	1.34
checks		--		8.00	2.20	1.28
		(cm)		(t/ha)	(m)	(m)
C.V.%		7.84		11.55	3.23	4.89

[3,4] Mean squares multiplied by 10^3 and 10^4, respectively.

crosses, and for the contrast lines vs crosses (average heterosis) (Table II and III). Although there was significance for all sources of variation, the largest mean squares were for lines and average heterosis; i.e., the line heterosis and specific heterosis, although significant, were less important as a source of variation for RL in the crosses. The highly significant average heterosis indicates that the presence of deleterious genes is probably the main cause for inbreeding effects in the parental lines.

The estimates of the line effects (v_i) were more negative for the sensitive lines (**1, 7** and **8**, Table III); line **4** (IAC 96.4) had the highest positive effects (11.49) for increasing RL. The line heterosis (h_i) showed the highest positive effects in lines **5** (Ip 48.5.3) and **6** (Ip 365.4.1); both lines derived from Cateto.

The mean squares for general combining ability (GCA) and specific combining ability (SCA, or specific heterosis) showed that the former was much greater than the SCA mean square (Table III), suggesting that non-additive effects were less important as a source of variation for RL. Magnavaca (1982) studied crosses involving eight Al-sensitive and Al-tolerant inbred lines and concluded that the greater portion of variation in six variables related to Al-tolerance was due to GCA, although significance for SCA was found in some instances. Similar conclusions were reported by Prioli (1987) for several traits in crosses involving Al-sensitive and tolerant lines.

Table III - Analysis of radicle length for eight maize inbred lines and their 28 diallel crosses, according to the model of Gardner and Eberhart (1966).

Source	d.f.	MS
Entries	35	81.68**
Lines	7	268.82**
Heterosis	28	34.89**
Avg. heterosis	1	355.64**
Line heterosis	7	15.62**
Specific heterosis	20	25.60**
Error	70	1.66
GCA[a]	7	191.04
SCA[a]	20	25.60

Estimates of effects

$\hat{v}_1 = -11.84$ $\hat{h}_1 = 1.08$
$\hat{v}_2 = 9.05$ $\hat{h}_2 = -2.85$
$\hat{v}_3 = 5.47$ $\hat{h}_3 = -1.21$
$\hat{v}_4 = 11.49$ $\hat{h}_4 = 0.24$
$\hat{v}_5 = 6.68$ $\hat{h}_5 = 3.49$
$\hat{v}_6 = -0.04$ $\hat{h}_6 = 3.09$
$\hat{v}_7 = -12.43$ $\hat{h}_7 = -0.23$
$\hat{v}_8 = -8.40$ $\hat{h}_8 = -3.61$

$\hat{\mu} = 22.81$ $\bar{h} = 7.56$
$\bar{h}\% = 33.2\%$

[a] - According to Method 4 of Griffing (1956).

The means of crosses for grain yield (GY), plant height (PH) and ear height (EH) are also shown in Table I. The means for GY varied from 2.38 t/ha to 10.03 t/ha, or 29.8% and 125.3% of the check means, respectively. More than 50% of the crosses had yields above the average of checks and five outyielded the best check (C-511). Three of the superior yielding crosses (**IAC 13.8** x **IAC 3.2**, **IAC 3.2** x **Ip 48.5.3**, and **IAC 3.2** x **Ip 365.4.1**) also had lower ear heights than the average of checks. The lowest yielding cross was **3x4** (**IAC 3.2** x **IAC 96.4**).

The analysis of variance for GY, PH, and EH also indicated significant variation among crosses (Table II). The contrast that measures the difference between checks was nonsignificant only for EH. The contrast for comparing the diallel mean with the check mean was nonsignificant only for yield, indicating that the average yield of the crosses did not differ from check hybrids.

The analysis of variance of the diallel crosses indicated significance for GCA and SCA for all traits (Table IV). The PH and EH mean squares for SCA were much smaller than for GCA, indicating that nonadditive genetic effects are less important. For yield the SCA mean square was larger than the GCA mean square. It is known that nonadditive effects are generally more important for yield than for plant and ear height, as indicated by data summarized by Hallauer and Miranda Filho (1988). The greater expression of nonadditive effects for yield must be partially due to the differentiation among lines, related to the presence of deleterious genes that cause inbreeding depression.

The estimates of GCA effects for RL show that the Al-sensitive lines had greater negative g_i estimates (Table V). Because g_i estimates are based on line performance in crosses, the g_i effects suggest the prevalence of additive effects for RL; because $g_i = 1/2v_i + h_i$, the correspondence between g_i and v_i (Table III) is indicative of the lower effects of h_i, that is a function of nonadditive effects. Line 5 (**Ip 48.5.3**) had the largest GCA estimate (g_5 = 6.83 cm), indicating that it can contribute to increased RL and Al-tolerance in crosses.

Table IV - Analysis of variance of 28 diallel crosses among eight maize inbred lines for yield (GY), plant height (PH) and ear height (EH), according to Method 4 of Griffing (1956).

Source	d.f.	Mean squares*		
		GY	PH	EH
Hybrids	27	2.9650	31.011	43.957
GCA	7	2.4786	83.499	151.11
SCA	20	3.1353	12.640	6.4524
Error	58	0.2765	1.8405	1.4189

*F tests were significant in all instances at $P < 0.01$.

Table V - Estimates of general combining ability and ranges for specific combining ability effects for all traits for eight maize inbred lines.

g_i		Radicle length	Yield	Plant height	Ear height
g_1		-4.84	0.681	0.044	0.066
g_2		1.68	0.816	0.035	0.097
g_3		1.53	0.148	-0.176	-0.266
g_4		5.98	-0.086	-0.150	-0.188
g_5		6.83	0.473	0.061	0.068
g_6		3.07	-0.497	0.057	0.120
g_7		-6.44	-0.970	-0.049	-0.076
g_8		-7.80	-0.566	0.178	0.179
$s_{ii'}$	←	-6.37	-5.550	-0.319	-0.187
	→	9.33	2.507	0.167	0.166

←, →: lower and upper limits of $s_{ii'}$, respectively.
For RL: $g_i = 1/2v_i + h_i$ (see Table II).

Lines **1** (**Col.2 (22)**) and **2** (**IAC 13.8**) had the highest values of GCA effects for yield. For PH and EH, lines **3** (**IAC 3.2**) and **4** (**IAC 96.4**) showed negative values for g_i and thus can contribute to a decrease in height in crosses.

The SCA effects for RL varied from -6.37 cm to 9.33 cm; the lower SCA estimate was for the cross **1x2** (sensitive x tolerant) and the higher SCA estimate was for the cross **1x4** (sensitive x tolerant). The range for SCA indicates that nonadditive effects may contribute to the expression of RL in crosses, even though the additive effects are more expressive. For GY, the most negative SCA effect was for the cross IAC 3.2 x IAC 96.4, probably because both lines have the same origin (IAC-Taiúba). A positive $s_{ii'}$ estimate was found in the cross **IAC 3.2 x Ip 365.4.1**. For plant and ear height the most negative effect was for the cross **3x4**, which was the lowest yielding cross.

Our results suggest the existence of high genetic variability for radicle length in Al-stressed nutrient solution. The greater portion of the variability is additive in nature, although nonadditive effects may contribute substantially to the expression of the trait in crosses. For the other traits, outstanding hybrids could be identified and, particularly for grain yield, nonadditive genetic effects may also be an important source of variation among crosses.

The effect of aluminum sensitivity, as expressed by the radicle length, on other traits would be better known if the experimental trials were conducted in Al-stressed acid soils without correction for acidity (Lima *et al.*, 1992).

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RESUMO

Cruzamentos dialélicos entre oito linhagens endogâmicas de milho (*Zea mays* L.) foram avaliados em laboratório para tolerância ao alumínio. A tolerância ao Al foi estimada pelo comprimento da radícula de plântulas em solução nutritiva com 4,5 mg Al/litro. Os cruzamentos também foram avaliados para produção de grãos, altura de planta e altura da espiga em condições de campo. Ambas as avaliações, de campo e de laboratório, foram segundo o delineamento em blocos casualizados com três repetições. As linhagens compreenderam cinco Al-tolerantes e três Al-sensíveis.

Os efeitos de tratamentos na análise dialélica foram desdobrados em capacidade geral (CGC) e capacidade específica de combinação (CEC). Na análise da variância, tanto CGC como CEC mostraram significância estatística, embora os quadrados médios para CGC tenham sido maiores do que para CEC, para todos os caracteres, exceto produção.

Para comprimento da radícula, a análise dialélica também foi desdobrada para testes dos efeitos de linhagens e de heterose. Efeitos significativos foram detectados para todas as fontes de variação, mas os quadrados médios foram maiores para os efeitos de linhagens *per se* e para a heterose média. A alta heterose para comprimento da radícula foi provavelmente devida a interações não alélicas causadas por genes deletérios de grande efeito, em vez de interações alélicas (dominância).

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