

C. R. Spehar · N. W. Galwey

## Diallel analysis for aluminium tolerance in tropical soybeans [*Glycine max* (L.) Merrill]

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**Abstract** The soybean is a major crop in the agricultural systems of the Brazilian Cerrados (Savannahs), whose soils are acidic, devoid of nutrients and need to be amended before they are cultivated. However, below the ploughed layer there is a scarcity of nutrients and toxic aluminium (Al). These limit root growth, subsequently causing nutritional imbalance and drought stress. Our aim in the investigation described here was to identify genetic differences in the aluminium tolerance of soybeans by a 9 × 9 diallel cross among contrasting varieties grown in high-Al areas and in hydroponics. Combining ability analysis indicated predominantly additive gene effects, and the additive-dominance model explained most of the genetic differences in this germ plasm for mineral element absorption and root growth under aluminium stress. The relationship between the two factors suggest that conjugation hydroponics and field evaluations in breeding programmes would further improve soybeans with respect to yield stability under tropical cultivation conditions.

**Key words** Cerrado · Savannah · Acid soils · Hydroponics · Nutrient · Variety · Genetics · Inheritance

### Introduction

The Brazilian Cerrados (a savannah-like environment) have poor and acidic soils that need to be amended with lime and fertilizer before cultivation. Technological advancements with respect to soil improvement have in-

tensified its settlement in recent years, and low-input production systems have evolved into modern agricultural ones in which the soybean plays a major role (Spehar 1995 a). The ploughed layer benefits mostly from any amendments, and only in the long run do nutrients leach down into the subsoil, given that there is no physical impediment, mostly caused by vicious tillage. Cultivated plants fully adapted to these environments should possess a tolerance to toxic aluminium (Al) and be efficient in nutrient utilization, mainly calcium, for deep root growth (Spehar 1995b). This results in a tolerance to dry spells during the growing season that cause grain yield reduction.

Major concerns in the field selection of Al-tolerant varieties are the Al × nutrient interaction and the confounding effects of uncontrolled environmental factors, even though natural selection has played a role in crop adaptation (Foy et al. 1992; Hecht-Buchholz and Schuster 1987; Spehar 1994 c). It is necessary to identify the genetic mechanism that regulates aluminium tolerance, which can be measured in the plant by mineral element absorption and by root growth in hydroponics, to further enhance soybeans to acid soil cultivation (Spehar 1994 c, 1995 b).

Genetic analysis can be performed using the diallel-cross procedure (Jinks and Hayman 1953; Dickinson and Jinks 1956; Griffing 1956). The procedure tests combining ability and adequacy of the additive-dominance model for estimating genetic parameters; these are important guides to breeders.

The inferences to be made on gene action depends on the diversity among the genotypes and their number in the diallel. If a small number is used, the genetic estimates are related only to the parents and crosses and not to a larger population (Spehar 1995 b). The model for diallel analysis implies diploid segregation, no reciprocal differences, independent action of non-allelic genes, no multiple allelism, homozygous parents and the independent distribution of genes. Thus, the linear regression of covariance ( $W_p$ ) on variance ( $V_p$ ) has a slope that is not significantly different from 1 (Mather and Jinks 1982).

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C. R. Spehar (✉)  
Centro de Pesquisa Agropecuária dos Cerrados, EMBRAPA-CPAC,  
Caixa Postal 08223, Planaltina, DF, Brazil (CEP 73301-970)

N. W. Galwey  
Faculty of Agriculture, University of Western Australia, Nedlands,  
WA 6709, Australia

In diallel-cross field experiments with maize (Gorsline et al. 1968), sorghum (Gorz et al. 1987) and soybeans (Spehar 1995 b), differential absorption of nutrients by the plant has shown quantitative inheritance as measured by the additive-dominance model. Boye-Goni and Marcarian (1985) utilized a half-diallel cross of sorghum among six contrasting varieties for genetic studies in hydroponics. Analysis of the  $F_1$ s indicated that general combining ability was predominant, suggesting that inheritance to aluminium is controlled largely by additive effects, with different genotypic contributions.

In hydroponics experiments, aluminium availability is dependant on the speciation of monomers, which is a direct function of pH. The proportion of hydroxy-aluminium increases at a pH above 4.0, thus reducing Al phytotoxicity to root seedlings (Kinraide 1991).

Diallel analyses for aluminium tolerance of maize plants under field and hydroponics conditions indicated quantitative inheritance, with the additive effects being more important than dominance in both cases (Lopes et al. 1987; Pandey et al. 1994). In a field experiment with soybeans, the predominant additive effects for mineral composition suggested the use of modified pedigree and recurrent selection schemes for crop improvement. Little, however, has been reported on genetic differences in soybean for aluminium tolerance and its interference with the genetics of nutrient absorption (Spehar 1994 c, 1995 b).

A diallel-cross experiment was planned among selected soybean varieties, previously tested in high- and low-aluminium environments and in hydroponics (Spehar 1994 a, 1994 b). The investigation had the following objectives: (1) to assess the genetics of aluminium tolerance in soybean by Al-rich field and hydroponics experiments, and (2) to verify the effect of aluminum on genetic differences for mineral element accumulation in soybean.

## Materials and methods

The assessment of soybean varietal response to aluminium stress in field experiments was carried out in order to plan hybridization for genetic studies. The following varieties were used in a diallel-cross scheme: 'IAC-2', 'IAC-5', 'UFV-1', 'Vx5-281.5', 'IAC-8', 'IAC-7', 'IAC-9', 'Biloxi' and 'Cristalina'. These varieties represent a range of variability for Al tolerance and, with the exception of 'Biloxi', have been adapted to Central Brazil (Spehar 1994 a). A description of their genealogy has been presented by Spehar (1995 b).

Hybridizations were produced in a glasshouse among all the parental varieties. Genetic markers were used in the  $F_1$  generation to distinguish between crossed and selfed seeds (Spehar 1995 b). The hybrid seeds were advanced to the  $F_2$  generation in the glasshouse to generate a larger bulk of seeds for the diallel experiments. Randomly chosen  $F_2$  plants were chosen to generate the  $F_3$  generation. The experiments were conducted in field and in hydroponics Al-rich environments with all of the hybrids and parents.

The experimental area was fertilized with 500 kg/ha dolomitic limestone with 100% neutralizing power, or its  $\text{CaCO}_3$  equivalent, 150 kg/ha P, 75 kg/ha K and 40 kg/ha of a slow-release source of micronutrients, FTEBR-12. The calcium carbonate equivalent is the acid-neutralizing capacity of lime expressed as a weight percentage of

calcium carbonate (Tisdale et al. 1985). All amendments were applied broadcast and incorporated into the soil to a depth of approximately 20 cm by a rotavator. Chemical analyses of soil samples collected after the experiment indicated a pH ( $\text{H}_2\text{O}$  1:1) of 5.1; 0.97 cmol/kg Al; 1.65 cmol/kg Ca + Mg; 3.1 mg/kg P 51 mg/kg K.

To enable the testing of all of the hybrids, we used the hill plot scheme. Ten  $F_2$  plants per hill were grown, and these constituted one plot. Three replications were used. The hills were 0.70 m apart in one direction and 1.00 m apart in the other, which has been shown to be sufficient to avoid interplot competition (Spehar 1995 b).

The seventh and the eighth fully expanded leaf from the bottom of each plant were harvested for mineral element evaluation (Spehar 1995 b). One composite sample of 20 leaves was collected per replicate. These were washed and rinsed in deionized water, dried, milled, digested with concentrated  $\text{H}_2\text{SO}_4$  and analysed for mineral composition in the Inductively Coupled Plasma Emission Spectrometer (ICPES).

The  $F_2$ s were tested in 2 mg/l (three replications) and 4 mg/l (two replications) Al, respectively, and the  $F_3$ s were tested in 2 mg/l Al (four replications), in randomized complete blocks. The hydroponic solution had a one-fourth salt concentration, and aluminium was added to in the form of  $\text{Al}_2(\text{SO}_4)_3 \cdot 16\text{H}_2\text{O}$  (Spehar 1994 b); the pH was adjusted to 4.0 by 1 N  $\text{H}_2\text{SO}_4$ . Phosphorus was omitted from the treatment solution to avoid any precipitation of aluminium. Daily pH adjustments were made to maintain a high availability of  $\text{Al}^{3+}$  monomers to the plants (Kinraide 1991). Ten seedlings per replication were used.

The hydroponics experiments were conducted in a growth cabinet kept at 25 °C and  $\pm 1^\circ\text{C}$  16-h light. Seedlings previously germinated were grown in the treatment solutions for 5 days. At harvest the longest secondary root in the solution that was entirely formed was measured (Spehar 1994 c).

No maternal effect for mineral composition was detected, and the data was treated as half diallel, with another set of replications provided by the reciprocal crosses. The field and  $F_2$ s and  $F_3$ s hydroponics experimental data were statistically analysed (Griffing 1956; Mather and Jinks 1982). Combining abilities,  $V_r$  and  $W_r$  were calculated. A *t*-test was used on the regression of  $W_r - V_r$  values to verify if the additive-dominance model explained the genetic pattern of segregation for the observed characters.

## Results and discussion

The analysis for mineral composition of plants grown in the field experiment showed that general combining ability (GCA) was larger than specific combining ability (SCA) for all of the elements. The ratio GCA/SCA was high for calcium and magnesium, followed by copper and potassium. Aluminium, iron and the other elements had a relatively low ratio (Table 1).

The present results differ in magnitude from those previously reported using the same crosses grown in the absence of aluminium (Spehar 1995 b), and indicate that the presence of abundant aluminium in the soil affected mineral element absorption, making the genotypic differences more evident. However, the specificity detected confirms that dominant genes are present in the parental lines at different frequencies. It may be confounded with additive and mask the real magnitude of dominant gene effects (Spehar 1995 b). The results for calcium and magnesium confirm their association with aluminium, and selection for tolerance may be carried out by assessing their level in the plant (Hecht-Buchholz and Schuster 1987; Kinraide 1991; Foy et al. 1992; Spehar 1995 b).

**Table 1** General, specific and reciprocal combining abilities (GCA, SCA, RCA) for mineral composition and root growth of the 9 × 9 soybean diallel cross

	Source of variation	df	M.S.	F	P	GCA/SCA
Potassium	Blocks	5	1.314	45.31	< 0.001	3.3
	GCA	8	0.152	5.24	0.007	
	SCA	36	0.046	1.59	0.060	
	Error	220	0.029			
Calcium	Blocks	5	0.413	27.53	< 0.001	5.7
	GCA	8	0.109	7.27	0.003	
	SCA	36	0.046	1.59	0.060	
	Error	220	0.015			
Magnesium	Blocks	5	0.0244	18.46	< 0.001	18.8
	GCA	8	0.0210	18.77	< 0.001	
	SCA	36	0.0013	1.00	n.s.	
	Error	220	0.0013			
Iron	Blocks	5	132035	10.55	< 0.001	2.5
	GCA	8	51797	4.14	0.015	
	SCA	36	20758	1.66	0.025	
	Error	220	12215			
Aluminium	Blocks	5	380122	10.63	< 0.001	2.1
	GCA	8	121235	3.39	0.030	
	SCA	36	57374	1.60	0.025	
	Error	220	35760			
Zinc	Blocks	5	1954	10.34	< 0.001	1.3
	GCA	8	416	2.20	0.010	
	SCA	36	316	1.67	0.025	
	Error	220	189			
Copper	Blocks	5	4.53	3.30	0.090	3.5
	GCA	8	7.42	5.41	0.006	
	SCA	36	2.14	1.56	0.006	
	Error	220	1.37			
Manganese	Blocks	5	878	1.76	0.030	2.2
	GCA	8	1230	2.46	0.090	
	SCA	36	557	1.12	0.300	
	Error	220	499			
F <sub>2</sub> , 2 mg/l	Blocks	2	0.119	3.96	0.250	11.7
	GCA	8	2.954	98.47	< 0.001	
	SCA	36	0.254	8.47	0.001	
	Error	88	0.030			
F <sub>3</sub> , 4 mg/l	Blocks	1	0.183	9.63	0.250	16.4
	GCA	8	0.736	38.74	< 0.001	
	SCA	36	0.045	2.36	0.100	
	RCA	36	0.065	3.42	0.030	
	Error	44	0.019			
F <sub>3</sub> , 2 mg/l	Blocks	3	2.625	25.48	0.020	9.3
	GCA	8	4.603	44.69	< 0.001	
	SCA	36	0.496	4.82	0.001	
	Error	132	0.103			

Secondary root growth in Al-stress hydroponics showed a high GCA/SCA ratio, which also indicates more additive than dominance gene effects; this ratio was detected in both the F<sub>2</sub> and F<sub>3</sub> experiments (Table 1). When the level of aluminium was increased in the treatment solution, there was an expected decrease in the magnitude of the variances. The significant reciprocal combining ability (RCA) at  $P = 0.03$  indicated reciprocal differences in the diallel test at 4 mg/l. However, the observations on the available reciprocals for 2 mg/l Al treatment indicated no evidence of maternal effect. It is possible that differences in seed vigour for some of the reciprocals contributed to enlarging the magnitude of its effects.

The means over arrays for leaf mineral composition and root growth from the diallel are presented in Table 2.

In general, crosses whose common parents were Al-tolerant 'Biloxi' and 'IAC-9' had the higher values for calcium, magnesium, aluminium, iron and zinc in leaves than crosses involving the Al-susceptible genotypes 'UFV-1' and 'Vx5-281.5'. The differences for potassium and copper were not so clear. The absorption of calcium and magnesium is negatively affected by aluminium; their scarcity in the soil, when in association with available aluminium, was more evident than when they are abundant in Al-free, fully-limed soils (Kinraide 1991; Foy et al. 1992; Spehar 1995 b).

Most of the aluminium absorbed by the plants remains in the root, where it causes damage, and only part of it is transferred to leaves, of which a reduced amount will accumulate in the grain (Spehar 1994 b). However, the higher levels of aluminium in leaves of tolerant × tolerant hybrids than in the intolerant ones can be

**Table 2** Array means for mineral elements in leaves and root growth of the 9 × 9 soybean diallel

	Array								
	Biloxi	Cristal	IAC-2	IAC-5	IAC-7	IAC-8	IAC-9	UFV-1	Vx5-281
Leaf composition, high-Al, field experiment									
Potassium (g/100 g)	3.34	3.79	3.54	3.39	3.43	3.39	3.42	3.32	3.44
Calcium (g/100 g)	0.95	0.87	0.93	0.86	0.91	0.93	0.96	0.88	0.89
Magnesium (g/100 g)	0.42	0.38	0.40	0.38	0.38	0.36	0.39	0.36	0.37
Iron (mg/kg)	550	561	503	511	527	557	539	492	473
Aluminium (mg/kg)	866	899	804	808	838	846	861	801	749
Manganese (mg/kg)	114	106	112	114	117	118	113	112	110
Zinc (mg/kg)	64	63	61	65	70	66	67	62	63
Copper (mg/kg)	10	10	10	10	10	10	10	9	10
Root growth (cm), hydroponics experiment									
F <sub>2</sub>									
2 mg/1 Al	2.85	2.84	2.55	2.80	2.62	1.98	2.80	2.35	2.23
4 mg/1 Al	1.14	1.05	1.31	1.47	1.34	1.33	1.38	1.20	1.09
F <sub>3</sub>									
2 mg/1 Al	3.11	2.83	2.57	3.05	2.75	2.27	3.08	2.66	2.36

explained by root growth in high-Al zones in the soil (Spehar 1995 b).

The varieties 'UFV-1', 'IAC-8' and 'Vx5-281.5' and some of their crosses produced shorter secondary roots than the crosses among 'Biloxi', 'IAC 7', 'IAC-5', 'IAC-9' and 'Cristalina'. This result is not unexpected since these groups of varieties had a contrasting response to aluminium in field and hydroponics screening experiments (Spehar 1994a,c). The crosses tended to respond differently at 4 mg/l than at 2 mg/l Al, and this is possibly explained by some of the tolerant hybrids losing their reaction at high aluminium levels.

The results for the variance ( $V_r$ )-covariance ( $W_r$ ) regression analysis are presented in Table 3. The  $t$ -test indicated that the additive-dominance model explained the genetic effects for magnesium, aluminium, iron and copper. Calcium absorption appeared to have a more complex inheritance, even though genetic differences were mostly additive (Spehar 1995 b). The additive-dominance model also explained the genetic differences for secondary root growth in the hydroponics experiment. Similar results have been obtained for maize in field and hydroponics investigations (Lopes et al. 1987; Pandey et al. 1994).

The analysis of the components  $a$ ,  $b$ ,  $b_1$ ,  $b_2$  and  $b_3$ , confirms the predominance of additive genetic variance as detected by combining ability analysis. The estimates of genetic and environmental components for the leaf mineral composition of the F<sub>2</sub> diallel are presented in Tables 4 and 5.

The positive values of  $H_1 - H_2$  indicates that allele frequency over all loci was unequal, except for calcium,

**Table 3** Regression of covariance ( $W_r$ ) on Variance ( $V_r$ ) for mineral composition and root growth of 9 × 9 soybean diallel

	Regression equation	Test for b = 1	
		$t$	$P$
Mineral Composition			
Potassium	0.0029 + 0.078V <sub>r</sub>	2.49	0.034
Calcium	0.0013 + 0.297V <sub>r</sub>	3.14	0.018
Magnesium	0.0001 + 0.860V <sub>r</sub>	0.79	0.490
Iron	- 708.69 + 0.558V <sub>r</sub>	2.06	0.090
Aluminium	- 1978.6 + 0.555V <sub>r</sub>	1.66	0.150
Manganese	17.327 + 0.436V <sub>r</sub>	3.90	0.006
Zinc	- 2.136 + 0.168V <sub>r</sub>	2.89	0.025
Copper	- 0.0076 + 0.566V <sub>r</sub>	1.61	0.160
Root growth			
F <sub>2</sub> , 2 mg/1	0.0581 + 0.486V <sub>r</sub>	2.07	0.090
F <sub>2</sub> , 4 mg/1	0.0071 + 1.096V <sub>r</sub>	0.63	> 0.500
F <sub>3</sub> 2 mg/1	0.0606 + 0.831V <sub>r</sub>	0.91	0.390

manganese and 4 mg/l Al. This is confirmed by the  $H_2/4H_1$  ratio which was, in general, less than 0.25. The estimates of allele frequency, given by the ratio  $((4DH_1)^{1/2} + F)/((4DH_1)^{1/2} - F)$ , were higher than 1, with the exception of calcium, manganese and root growth. In one case, the genotypes contain more dominant and in the other more recessive alleles. The degree of dominance, as measured by  $(H_1/D)^{1/2}$ , was higher than 1, except for manganese and 4 mg/l Al in solution. This indicates an overdominance effect, but it is possible that the parental varieties, homozygous for morphological characteristics, were heterozygous for mineral element

**Table 4** Estimates of genetic and environmental components for mineral composition of soybean leaves in the 9 × 9 diallel

Character	Element							
	Potassium	Calcium	Magnesium	Iron	Aluminium	Manganese	Zinc	Copper
$V_p$	0.0210	0.0057	0.0099	3728	14965	56.28	27.45	0.759
$V_r$	0.0068	0.0031	0.0005	3262	9013	106.66	31.68	0.389
$V_e$	0.0015	0.0011	0.0003	817	1928	12.78	7.69	0.129
$\bar{W}_r$	0.0034	0.0022	0.0007	1113	3028	-0.41	3.19	0.213
E	0.0035	0.0024	0.0002	1206	3822	173.19	19.61	0.223
D	0.0175	0.0033	0.0016	2521	11143	-116.90	7.83	0.536
F	0.0427	-0.0044	0.0008	1181	20350	-464.32	5.82	0.444
H <sub>1</sub>	0.0999	0.0113	0.0019	35899	113160	-82.04	347.72	3.382
H <sub>2</sub>	0.0571	0.0134	0.0012	29473	82787	20.51	226.93	2.383
H <sub>1</sub> - H <sub>2</sub>	0.0428	-0.0021	0.0007	6426	30373	-61.53	120.79	0.999
H <sub>2</sub> /4 H <sub>1</sub>	0.143	0.297	0.167	0.205	0.183	-0.062	0.163	0.176
(H <sub>1</sub> /D) <sup>1/2</sup>	2.389	1.848	1.062	3.773	3.187	0.838	6.662	2.511
((4DH <sub>1</sub> ) <sup>1/2</sup> + F)/((4DH <sub>1</sub> ) <sup>1/2</sup> - F)	3.089	0.473	1.558	1.132	1.803	-0.407	1.118	1.394
Heritability								
Broad sense	66.70	68.08	79.22	74.96	71.21	21.02	61.68	68.88
Narrow sense	32.61	13.45	71.42	36.72	32.24	20.43	34.19	43.09

**Table 5** Estimates of genetic and environmental components for root growth of soybean in the 9 × 9 diallel

Character	Aluminium treatment		F <sub>3</sub>
	F <sub>2</sub>	F <sub>3</sub>	
	2 mg/l	4 mg/l	2 mg/l
$V_p$	0.2383	0.0977	0.650
$V_r$	0.1702	0.0318	0.211
$V_e$	0.0993	0.0204	0.095
$\bar{W}_r$	0.1409	0.0420	0.236
E	0.0296	0.0196	0.103
D	0.0296	0.0782	0.547
F	-0.2918	-0.0230	0.708
H <sub>1</sub>	0.8831	0.0112	1.269
H <sub>2</sub>	0.7074	0.0253	1.418
H <sub>1</sub> - H <sub>2</sub>	0.1757	-0.0141	-0.199
H <sub>2</sub> /4H <sub>1</sub>	0.2003	0.5655	0.279
(H <sub>1</sub> /D) <sup>1/2</sup>	2.0567	0.3783	1.523
((4H <sub>1</sub> ) <sup>1/2</sup> + F)/((4H <sub>1</sub> ) <sup>1/2</sup> - F)	0.4927	0.4408	2.476
Heritability			
Broad Sense	89.16	69.50	66.28
Narrow Sense	72.98	67.04	59.03

absorption and root growth (Spehar 1995 b). This would explain the results when the progeny performed better than both parents.

Broad-sense heritability varied from medium for calcium to high for the other elements, with the exception of manganese. The narrow-sense heritability varied from low for potassium, calcium, iron, aluminium and manganese to high for magnesium. Both broad- and narrow-sense heritabilities were high for root growth (Tables 4 and 5). The high values indicate the possibility of genetic gain in selection for Al tolerance based on root growth and mineral element absorption by soybeans.

The present varieties and their hybrids illustrate the power of natural selection to mould plant species to

specific environmental components such as high aluminium in the soil (Foy et al. 1992; Spehar 1994 c). Moreover, further varietal improvement for this hindrance needs a combination of hydroponics and field work to exploit both the additive and dominance genetic variability in the hybrids. These results emphasize the use of modified pedigree and recurrent selections to increase genetic gain for this character that shall contribute to achieve genotypic stability in acid soil cultivation.

## Conclusions

The detection of more additive than dominance effects for mineral element absorption and root growth in the presence of aluminium ensures opportunity for progress in the selection of soybeans to mineral stresses. The use of hydroponics to select for aluminium tolerance is an efficient means to obtain genetic gain if conjugated with field evaluations for desirable agronomic characters in tropical-adapted soybeans.

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