DIALLEL ANALYSIS FOR GRAIN YIELD AND MINERAL ABSORPTION RATE OF SOYBEANS GROWN IN ACID BRAZILIAN SAVANNAH SOIL[1]

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ABSTRACT - High available aluminium and low levels of calcium below the ploughed zone of the soil are limiting factors for agricultural sustainability in the Brazilian Cerrados (Savannahs). The mineral stresses compound with dry spells effect by preventing deep root growth of cultivated plants and causes yield instability. The mode of inheritance for grain yield and mineral absorption ratio of a diallel cross in soybeans [*Glycine max* (L.) Merrill] grown in high and low Al areas was identified. Differences among the genotypes for grain yield were more evident in the high Al, by grouping tolerant and non-tolerant genotypes for their respective arrays in the hybrids. A large proportion of genetic variance was additive for grain yield and mineral absorption ratio in both environments. High heritability values suggest that soybeans can be improved by crosses among Al-tolerant genotypes, using modified pedigree, early generation and recurrent selection schemes.

Index terms: aluminium, calcium, cultivar, additive, dominance, breeding.

ANÁLISE DIALÉLICA DA PRODUÇÃO DE GRÃOS E TAXA DE ABSORÇÃO MINERAL NA SOJA CULTIVADA EM SOLO ÁCIDO DOS CERRADOS BRASILEIROS

RESUMO - A presença de alumínio e reduzidos níveis de cálcio abaixo da camada arável do solo são fatores que ameaçam a sustentabilidade agrícola nos cerrados brasileiros. Esses fatores limitantes agravam o efeito de estresses hídricos, por reduzir o crescimento radicular em profundidade nas plantas cultivadas, e resultam na instabilidade produtiva. Identificou-se o modo de herança da produção de grãos e a taxa de absorção de nutrientes em soja [*Glycine max* (L.) Merrill], com cruzamento dialélico entre nove cultivares, sob baixa e elevada disponibilidade de alumínio. As diferenças entre os genótipos mostraram-se mais evidentes nesta última, pelo agrupamento dos respectivos híbridos no dialelo. Grande proporção da variância genética para a produção de grãos e taxa de absorção mineral é devida a efeitos aditivos. A elevada herdabilidade sugere a possibilidade de selecionar por produtividade em presença dos estresses minerais nos cruzamentos entre genótipos tolerantes, com o uso dos métodos genealógico modificado, teste em gerações iniciais e seleção recorrente.

Termos para indexação: alumínio, cálcio, variedade, aditivo, dominância, melhoramento genético.

INTRODUCTION

The Brazilian Savannahs (Cerrados) cover vast areas of ferralsols in the tropics, which have free aluminium (Al) and scarcity of calcium (Ca) below the ploughed zone of the soil. These major constraints, that prevent deep root growth of cultivated plants, compounded by bad rainfall distribution, can cause yield fluctuations. The genetics of tolerance to these hindrances must be understood to achieve yield stability of cultivated plants (Spehar, 1994c, 1994d, 1995b).

Amendments tend to concentrate in the ploughed layer of cultivated savannah soils and only in the long run nutrients leach down into the subsoil, given there is no physical impediment. Cultivated plants, selected in these environments, possess some tolerance to toxic Al and to low levels of Ca, for deep root growth (Foy et al., 1992; Spehar, 1994a, 1995a). If the genetic factors that condition Al and low-Ca tolerances are identified, it is expected that yield in more tolerant cultivars will be buffered to weather instability.

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Controlled environment experiments that comprise the use of problem-soils and of nutrient solution have been used in varietal screening and in genetic and breeding studies as an indirect means to improve plants to mineral stress tolerance. In field selection of Al-tolerant cultivars, there are major concerns on mineral element interactions and the confounding effects of uncontrolled environmental factors, e.g., erratic rainfall distribution and frequency to dry spells, even though natural selection has contributed to crop adaptation (Foy et al., 1992; Spehar, 1994c). It can be questioned whether Al affects grain yield by reducing root growth and absorption of nutrients; or, if its interaction with Ca and magnesium (Mg) diminishes their absorption and movement in the plant, causing reduction in photosynthetic rate and, consequently, grain yield (Ohki, 1986; Devine et al., 1990; Foy et al., 1992; Rengel, 1992; Wilkinson & Duncan, 1993; Spehar, 1995a). Genotypic differences to Al tolerance have been identified by measuring mineral element absorption and root growth in hydroponics (Spehar, 1994c, 1995a).

The mode of inheritance for important agronomic traits has been identified by hybridisation schemes, one of them is the diallel analysis. Griffing (1956) developed the analysis into combining ability evaluation, whereas Mather & Jinks (1982) method enables to estimate genetic components and heritability.

In diallel cross, Al-free, field experiments with maize (Gorsline et al., 1968), sorghum (Gorz et al., 1987) and soybeans (Spehar, 1995a), differential absorption of nutrients by the plant has shown quantitative inheritance as measured by the additive-dominance model.

Diallel analysis for Al tolerance experiments in maize indicated quantitative inheritance, with additive effects more important than dominance in both cases (Pandey et al., 1994). In soybeans, predominant additive effects for mineral composition suggested the use of modified pedigree and recurrent selection schemes for crop improvement (Spehar, 1994c, 1995a). The genetics of grain yield and its relationship to mineral element absorption in soybeans, however, remain to be studied (Foy et al., 1992; Spehar, 1995a).

This study aimed to identify the mode of inheritance for grain yield in soybeans by an experiment with a diallel cross in a high and in a low Al areas and relate it to mineral absorption ratio.

MATERIAL AND METHODS

The soybean cultivars IAC-2, IAC-5, IAC-7, IAC-8, IAC-9, UFV-1, Vx5-281.5, Biloxi and FT-Cristalina were chosen for a diallel cross, based on their performance in field and hydroponics experiments (Spehar, 1994a, 1994d). Their genealogy and reaction to Al has already been described (Spehar, 1995b). The F_1's were advanced into F_2's and seeds of true crosses, identified by marker genes, were pooled together for every cross among the cultivars. The experiment was conducted on hill plots, using 15 F_2 seeds per hill, in two levels of liming, with three replications of randomised complete-block design.

The two experimental areas were limed and fertilised in the following manner: 1) 500 kg/ha dolomitic limestone (100% $CaCO_3$ equivalent), 150 kg/ha P, 75 kg/ha K and 40 kg/ha of slow release micronutrients source, FTE-BR-12; 2) 4000 kg/ha dolomitic limestone (100% $CaCO_3$ equivalent) and the other sources of nutrients in the same amounts as in the first case. All amendments were broadcast applied and incorporated into the soil with a rotovator up to 20 cm depth. The chemical analyses of soil samples collected after the experiment, at 0-20 cm depth, indicated pH (H_2O 1:1) 5.1 and 5.7; Al 0.97 and 0.10 $cmol_c$/kg; Ca+Mg 1.65 and 3.56 $cmol_c$/kg; P 3.1 and 3.4 mg/kg; K 0.13 and 0.15 $cmol_c$/kg, respectively. Calcium carbonate equivalent is the acid neutralising capacity of lime expressed as weight percentage of calcium carbonate (Tisdale et al., 1985).

Foliar samples were collected, according to a method previously described, to eliminate possible differences of leaf position on the plant (Spehar, 1995a). At maturity the plants in each plot were harvested separately for both high and low Al experiment. The leaf mineral composition ratios (high/low Al) and grain yield/plant data of the two environments and their ratio were statistically analysed, according to Griffing (1956) and Mather & Jinks (1982) procedures. Due to absence of maternal effect, the data were analysed as half diallel and the reciprocals provided another set of replications for mineral element absorption rate.

RESULTS AND DISCUSSION

The combining ability analysis of variance for grain yield in the high Al, in the low Al and the ratios between the two environments for both grain yield and mineral absorption are presented in Table 1. The general combining ability (GCA), which measured the additive effects of genes, was superior in magnitude to the specific combining ability (SCA). The ratio GCA/SCA was largest in the low Al environment, and lowest in the high Al environment and in the ratio high/low Al. Despite the difference in magnitude of the ratios, these results suggest that inheritance for grain yield in soybeans is controlled largely by additive effects. The ratio, which excluded a possible interference of varietal yielding potential,

TABLE 1. General and specific combining abilities (GCA, SCA) for grain yield in high Al (H), in low Al (L) and the ratio (H/L*100) for yield and mineral absorption of the diallel cross.

Character	Source of variation	D.F.	M.S.	F	p	GCA/SCA
			Grain yield			
High Al (H)	GCA	8	23.09	13.54	<0.001	
	SCA	36	7.97	4.67	0.001	2.9
	Error	44	1.70			
Low Al (L)	GCA	8	89.93	22.56	<0.001	
	SCA	36	10.93	2.74	0.004	8.2
	Error	44	3.98			
H/L	GCA	8	338.17	7.91	<0.001	
	SCA	36	112.10	2.70	0.003	3.0
	Error	44	1.70			
			Mineral absorption			
Potassium	GCA	8	176.70	5.79	0.006	
	SCA	36	73.11	2.40	0.005	2.4
	Error	132	30.50			
Calcium	GCA	8	472.90	9.14	0.001	
	SCA	36	138.30	2.67	0.004	3.4
	Error	132	51.70			
Magnesium	GCA	8	358.30	13.28	<0.001	
	SCA	36	63.01	2.33	0.004	5.7
	Error	132	27.00			
Iron	GCA	8	6763.61	6.73	0.003	
	SCA	36	2726.90	2.71	0.004	2.5
	Error	132	1004.42			
Aluminium	GCA	8	16920.03	7.69	0.002	
	SCA	36	5722.70	2.60	0.004	3.0
	Error	132	2200.61			
Manganese	GCA	8	20488.12	1.97	0.150	
	SCA	36	17800.10	1.71	0.025	1.1
	Error	132	10403.00			
Zinc	GCA	8	4046.51	12.83	<0.001	
	SCA	36	991.30	3.14	0.002	4.1
	Error	132	315.40			
Copper	GCA	8	1031.33	4.73	0.012	
	SCA	36	756.00	3.47	0.002	1.4
	Error	132	217.02			

confirms the predominance of additive effects. Similarly, Pandey et al. (1994) found larger additive than dominance effects for Al tolerance in maize, measured by grain yield.

The mean value for the grain yield in both environments and the ratios for both grain yield and mineral element absorption are presented in Table 2.

The arrays whose common parent was Biloxi had a great range for grain yield, although the mean was low in both environments. This result may be explained by its low agronomic performance in the cerrados. The lowest value for UFV-1 and the highest for IAC-9, in the high-Al area, confirms the reaction of respective parental cultivar to Al (Spehar, 1994a, 1994c). However, the array with Biloxi as a common parent did not provide clear cut results and yet it has shown to be Al-tolerant (Foy et al., 1992). This is interpreted that the gene combinations for yield are independent from the ones for Al-tolerance, as shown by the result in the absence of Al and the ratio high/low Al. In the latter IAC-9 and Biloxi gave highest results as compared to the lowest by UFV-1 and suggest that it is more accurate to use (Foy et al., 1992) if only Al tolerance is the character being selected. Thus, it is expected that crossing among adapted, high-yielding genotypes shall enhance soybeans to mineral stresses.

The higher absorption ratios for Al and iron in all genotypes, including intolerant UFV-1, than for tolerant Biloxi, confirmed, in part the results of previous work (Spehar, 1995a). This suggests that the roots grow deep in the subsoil, thus absorbing more Al, although IAC-9, another tolerant cultivar, did not show the same trend in all crosses. For Ca and Mg, however, the results between UFV-1 and the tolerant cultivars Biloxi and IAC-9 were more contrasting. UFV-1 and its crosses suffered possible Al damage in the roots, explaining the lower Ca and Mg absorption by hybrids of this cultivar in the high-Al environment. When Al was not a limiting factor in the ploughed layer of the soil, the roots of susceptible genotypes were more active and differences among the crosses expected to be less evident (Spehar, 1995a). The average ratios for K, Cu, Mn and Zn were not associated with specific array but with hybrid combination.

The results of the regression analysis for covariance (W_r) by variance (V_r) indicate that the test for b (the regression slope) was significantly different from one and that the additive-dominance model is not sufficient to explain the genetic differences in these genotypes for grain yield in both environments and the ratio. The mineral element absorption ratios were explained by the model for K, Mg, iron (Fe), Al, and Zn (Table 3). Ca, similarly

TABLE 2. Array means for grain yield (g/plant) in high Al (H), low Al (L) and the ratio (H/L*100) for yield and mineral absorption.

Character	Array								
	IAC-9	IAC-2	UFV-1	IAC-5	IAC-8	Vx5-281-5	IAC-7	Biloxi	FT-Cristalina
					Grain yield				
H	13.36	12.51	10.1	11.85	11.52	11.50	12.47	10.93	12.25
L	22.96	22.62	20.62	22.97	21.83	20.60	23.63	17.53	23.83
H/L	58.53	55.38	49.13	52.45	53.20	57.52	53.57	61.93	51.78
					Mineral element absorption ratio				
K	110.7	107.7	113.8	110.1	110.0	110.7	107.7	107.4	110.8
Ca	89.8	93.1	81.0	88.7	90.4	87.9	88.4	87.1	86.5
Mg	80.8	83.5	73.2	79.2	79.2	79.0	78.6	81.1	77.3
Fe	168.9	174.2	162.0	166.6	164.5	149.5	176.5	139.5	148.0
Al	212.3	225.7	204.1	212.0	202.9	187.7	223.4	168.3	180.0
Mn	394.7	449.3	433.8	428.1	421.7	393.0	424.4	377.1	376.2
Zn	184.7	163.2	169.4	183.8	194.7	169.4	190.5	172.3	175.1
Cu	147.4	141.1	138.4	138.8	137.3	143.8	147.4	133.3	133.6

to field and hydroponics experiments, showed to be fully explained by a more complex model (Spehar, 1989).

The estimates of genetic parameters are listed in Table 4. Negative values of H_1-H_2 indicated that there was no difference between allele frequency in the high and the ratio high/low Al for grain yield, whereas unequal allele frequency over all loci was found for mineral absorption ratios. The estimate of the type of allele with most frequency was given by the ratio $[(4DH_1)^{½} + F]/[(4DH_1)^{½} - F]$; values greater than one indicate more dominant than recessive alleles in both environments but not in the ratio high/low Al for grain yield. For K, Fe and Al, more dominant than recessive alleles predominated for mineral composition in the nine cultivars of the diallel. The square root of H_1/D, that measures the degree of dominance, had values higher than 1, indicating presence of overdominance, except for the low Al environment.

These data, apparently contradicting the expected more additive than dominance effects, found in the combining ability analysis, show that gene expression for grain yield and mineral absorption

TABLE 3. Regression of covariance (W_r) on Variance (V_r) for grain yield and mineral composition of the diallel cross.

Character	Regression equation	t-test (b=1)	p
	Grain yield		
High Al (H)	$0.46 - 0.50V_r$	7.49	<0.001
Low Al (L)	$4.88 + 0.40V_r$	2.28	0.060
H/L	$2.04 + 0.40V_r$	2.85	0.025
	Mineral absorption		
Potassium	$-10.06 + 0.71V_r$	1.76	0.130
Calcium	$10.35 + 0.15V_r$	2.99	0.023
Magnesium	$-4.76 + 0.91V_r$	0.33	>0.500
Iron	$-54.52 + 0.39V_r$	1.79	0.130
Aluminium	$13.89 + 0.41V_r$	1.70	0.150
Manganese	$-28.67 - 0.01V_r$	7.56	<0.001
Zinc	$-147.43 + 0.73V_r$	0.96	0.380
Copper	$110.59 + 0.41V_r$	6.99	<0.001

TABLE 4. Estimates of genetic and environmental components for grain yield in high Al (H), in low Al (L) and the ratio (H/L*100) for yield and mineral absorption of the diallel cross.

	H	L	H/L	Potassium	Calcium	Magnesium	Iron	Aluminium	Manganese	Zinc	Copper
V_p (variance of parents)	6.99	21.55	9.99	45.69	52.73	46.27	1560.76	3823.44	1249.12	285.79	204.45
V_r (mean var. of arrays)	4.38	8.60	65.82	16.22	40.06	19.95	749.95	1641.10	3900.76	315.64	190.82
V_r (var. of array means)	0.95	3.99	15.47	3.70	10.94	8.04	160.57	381.66	690.44	114.94	27.92
W_r (mean covariance)	2.37	8.35	28.65	7.17	16.66	13.41	238.77	686.30	-62.64	82.63	18.10
E	1.70	3.98	42.75	10.42	37.79	17.70	266.10	532.76	10353.50	213.86	157.76
D	5.28	17.56	48.23	35.27	14.94	28.57	1294.66	3290.67	-9104.33	72.05	46.59
F	2.13	3.47	-36.30	83.76	-73.51	7.02	3268.51	7672.29	-35916.00	-372.85	41.53
H_1	29.04	17.59	179.61	211.92	165.46	93.13	11465.31	24650.96	-46627.60	2496.38	1827.17
H_2	30.32	16.32	189.16	116.98	163.62	48.96	7301.25	15889.02	-31462.50	1501.29	1343.38
$H_1 - H_2$	-1.27	1.27	-9.54	94.93	1.85	44.17	4164.06	8761.94	-15165.10	995.09	483.79
$H_2/4H_1$	0.26	0.23	0.26	0.14	0.25	0.13	0.16	0.16	0.17	0.15	0.18
$(H_1/D)^{½}$	2.34	1.00	1.92	2.45	3.33	1.80	2.98	2.74	2.26	5.89	6.26
$((4DH_r)^{½} + F)/((4DH_r) - F)^{½}$	1.19	1.22	0.67	2.88	0.15	1.15	2.47	2.48	0.07	0.39	1.15
Heritability											
Broad sense	69.27	69.52	50.61	60.37	50.00	54.39	75.20	77.31	0.05	61.91	49.92
Narrow sense	35.13	61.73	36.96	32.56	35.19	46.50	32.69	35.02	0.23	45.19	23.28

ratio is highly dependent on the plant environment. Departure from additive was related to some crosses that had a better performance than the parents, when they were both tolerant, one intolerant and the other tolerant and both intolerant, for grain yield and mineral absorption ratio.

The calculated heritabilities for grain yield indicated that broad sense was high in each environment and intermediate in the ratio, while narrow sense was low except in the low-Al environment. High broad sense heritabilities were found for K, Al, Fe and Zn; for Ca, Mg and Cu, they had intermediate values; the genetic differences for Mn seemed rather complex. Narrow sense heritabilities were of low values for all elements. Similar results were obtained for mineral element uptake in maize, forage sorghum and soybeans (Gorsline et al., 1968; Gorz et al., 1987; Spehar, 1995a). The lack of fitness of the additive-dominance model may have been a consequence of possible residual heterozigosity in the parental cultivars. Indication of genetic variability for low-Ca tolerance within soybean cultivars has already been reported (Spehar & Galwey, 1997). However, despite the limiting factors, these results suggest that soybeans can be improved for high yield and tolerance to Al by using modified pedigree, early generation testing on hill plot and recurrent selection, following hybridisation of superior individuals (Spehar, 1994b).

The best recombinants can be identified in hydroponics experiments and shall form a gene pool to be employed in field tests for the acquisition of new cultivars to enhance the prospect for sustainable agricultural systems (Spehar, 1994d, 1995a).

CONCLUSIONS

1. Grain yield is an efficient evaluation of genetics to Al tolerance in soybeans and the ratio high-/low-Al allows to separate the intrinsic differences in yield among the genotypes.

2. The predominantly additive and, in a minor scale, dominance effects for grain yield and mineral absorption ratios is exploited by modified pedigree, early generation and recurrent selection schemes to improve soybeans for acid soil tropical cultivation.

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