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Diallel analysis for mineral element absorption in tropical adapted soybeans [*Glycine max* (L.) Merrill]

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Abstract The Brazilian tropical adapted soybeans contains, in addition to superior morphological characters, genetic factors for tolerance to cultivation in acidic, mineral-stressed soils. However, the selection process for these hindrances has been empirical, and information on the genetics of mineral element uptake by the plant is necessary. The objective of this investigation was to identify the mode of inheritance for the absorption of phosphorus, potassium, calcium, magnesium, iron, aluminium, manganese, zinc and copper in a 9×9 diallel cross. General combining ability (GCA) was higher than specific combining ability (SCA), with the exception of copper, manganese and zinc, indicating predominantly additive effects. The ratios of GCA/SCA varied between 3.4 (calcium) and 8.5 (magnesium). The regression of covariance (W_r) on variance (V_r) showed that the additive-dominance model explained the genetic differences in this germ plasm. However, the detection of overdominance could be related to possible heterozygosity in the parental varieties for mineral absorption. Broad-sense heritability values were higher than narrow sense heritability values for aluminium, iron, potassium, calcium and magnesium, being in the range of 67.9–86.9% and 42.0–56.6%, respectively. This is an indication that soybeans can be further improved to efficient utilisation of nutrients and to tolerate toxic factors in the soil.

Key words Mineral stress · Nutrient efficiency · Aluminium tolerance · Inheritance · Genetics · Breeding

Introduction

Many tropical regions, like the Brazilian Savannas (Cerrados), have been the borderline of agricultural areas due to acidic and low fertile soils. Lime and fertiliser are nec-

essary to improve them before farming. Modern soybean cultivation in these environments has played an important role in the development of sustainable agricultural systems (Spehar et al. 1993). However, the identification of genetic variability for plant cycle, disease resistance and seed quality has been essential in the acquisition of new soybean varieties to suit the farmer's demand in these low latitude environments (Kiihl and Garcia 1989).

The crossing of contrasting parents has allowed the genetics of simple inherited traits, e.g. genes for lateness and juvenility, to be identified while aiming at selecting a desirable genotype. For genetic studies of multigene traits, however Yates (1947) employed a series of crosses in all possible combinations amongst parental lines. This diallel cross scheme has been used for studying more complex traits and for selecting new varieties. (Gibori et al. 1978; Perry et al. 1986). To be successfully employed it has to enhance the expectancy of genetic gain relative to that of the more empirical classic breeding (Hanson 1987).

The theory of diallels was developed by Jinks and Hayman (1953) and expanded by Dickinson and Jinks (1956). It allows genetic analysis to be carried out by tests of the adequacy of the model, which implies diploid segregation, no reciprocal differences, independent action of non-allelic genes, absence of multiple allelism, homozygous parents and independent distribution of genes. When the mode of inheritance is at least digenic, non-allelic interaction may be present, and this can also be estimated by the model. The estimates of genetic parameters guides the breeders in the selection of a given trait.

The inference to be drawn on the mode of gene action in diallel analysis is highly dependent on how far apart the genotypes being used in the cross are and how large their number is. If a small number is used, the genetic estimates are related only to the parents and crosses and not to a larger population (Mather and Jinks 1982). The practical importance is the identification of lines or varieties in the crosses that most contribute to desirable traits in order to use them in breeding programmes.

Diallel crosses were also analysed by Griffing (1956), who expanded the system of single-cross tests in maize de-

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veloped by Sprague and Tatum (1942). Through this approach, general and specific combining ability (GCA, SCA) effects have been calculated, and inferences have been made on whether the gene effects are additive or non-additive. The author presented the analysis according to two models, random and fixed effects, and suggested that the choice between the models depended on the nature of the parental material. When a particular set of varieties is used, Eberhart and Gardner (1966) suggested that the fixed model be utilised such that the information obtained is restricted to their genetic material. According to Cockerham (1980) for self-fertilising species our interest lies in measuring the effects of genes that are in the homozygous state. This implies that previously identified pure lines are used in the crosses and that for them only conclusions about genetic mechanism will be made.

There are many examples in the literature of genetic variability for differences in mineral nutrition or toxic elements in plants (Foy et al. 1978, 1992; Spehar 1994a, b, c). However, only a few have assessed the mode of inheritance to these factors. Boye-Goni and Marcarian (1985) utilised a half diallel cross of sorghum involving three varieties susceptible to aluminium and three tolerant 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. In a diallel study of differential accumulation of calcium, magnesium and potassium in maize, Gorsline et al. (1968) indicated that the gene effects were more additive, and no relation amongst these elements was found. Moreover, diallel analysis in hybrid forage sorghum indicated that general GCA effects exceeded SCA effects for the minerals nitrogen, magnesium, silicon, phosphorus, sulphur, chlorine, potassium, calcium, manganese, iron, copper and zinc (Gorz et al. 1987).

Since the genetics of tolerance to mineral element toxicity and efficient nutrient utilisation is of importance in a breeding programme to fully adapt the soybean crop to the agricultural systems in the Brazilian Savannahs (Cerrados), a diallel cross among field-selected varieties was planned. The main objectives of the experiment described here were:

- 1) to assess the genetics of nutrient uptake in the soybean and the interaction with aluminium;
- 2) to establish methods of field screening of segregating populations to select for differential mineral element uptake;
- 3) to identify parental varieties efficient in mineral element utilisation to be used in breeding programmes in order to improve the soybeans for cultivation in subsoil limiting environments.

Materials and methods

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 were chosen to

Table 1 Genealogy of the soybean varieties used in the diallel cross, with relative contribution (%)^a of ancestor parental lines

Variety	Genealogy
IAC-2	PI 60406 (25), Tanloxi (25), PI 95727 (25), PI 40658 (12.5), Mammoth Yellow (12.5)
IAC-5	Selection in Florida Bulk 59-1
IAC-7	Bilomi 3 (25), CNS (12.5), Roanoke (12.5), Arksoy (12.5), Tokyo (9.37), PI 54610 (9.37), Illini (6.25), Dunfield (6.25) Haberlandt (6.25)
Vx5-281.5	Improved Pelican (50), CNS (12.5), Illini (12.5), PI 60406 (12.5), Tanloxi (12.5)
IAC-8	Bilomi 3 (25), CNS (18.75), Illini (18.75), PI 54610 (9.37), Tokyo (9.37), Dunfield (6.25)
UFV-1	CNS (25), Illini (25), PI 60406 (25), Tanloxi (25)
IAC-9	The same genealogy as IAC-7
Cristalina	CNS (18.75), Roanoke (12.5), PI 60406 (12.5), Tanloxi (12.5), PI 54610 (12.5), Dunfield (12.5), Illini (9.37), Arksoy (9.37)
Biloxi	American introduction from Tangsi, China

^a Adapted from Hiromoto and Vello (1986)

Table 2 Origin of the common ancestors of the soybean germ plasm utilised in diallel cross for aluminium tolerance

Ancestor ^a	Origin
PI 60406	Southern China
Tanloxi	
Pi 95727 (Nanda)	Sariwon, Korea
PI 40658 (Laredo)	Southern China
Mammoth Yellow	USA
PI 240664 (Bilomi 3)	Philippines
PI 71569 (CNS)	Southern China
PI 71597 (Nanking)	Nanking, China
PI 37335 (Arksoy)	Pingyang, Korea
PI 8424 (Tokyo)	Yokohama, Japan
PI 54610	Northeastern China
S-100 (Illini)	Northeastern China
PI 36846 (Dunfield)	Manchuria, China
PI 6396 (Haberlandt)	Pingyang, Korea
Improved Pelican	USA
PI 23211 (Biloxi)	Tangsi, China

^a Source: Hiromoto and Vello (1986); Morse et al. (1949)

represent a range of variability for aluminium tolerance and, with the exception of 'Biloxi', are adapted to the low latitudes of Central Brazil (Spehar 1994c). A brief description of their genealogy is presented in Table 1, and the origin of their ancestors is presented in Table 2 (Hiromoto and Vello 1986; Morse et al. 1949). Aluminium-tolerant 'Biloxi' (Foy et al. 1969) has not contributed to the gene pool of the Brazilian soybean varieties. All possible combinations of hybrids, including reciprocals, were made in a glasshouse, in EMBRAPA-CPAC, Planaltina, Brazil. These varieties belong to distinct maturity groups and, to allow coincidence of flowering, several weekly sowing batches were used, beginning with the most late varieties of this group, namely, 'IAC-7', 'IAC-9' and 'Cristalina'. A well-fertilised mixture of soil and compost was used in 2-l pots in which five seeds were sown. These seeds had been obtained by selfing single plants of the parent varieties and advancing their progeny through single-seed descent (Brim 1966). The selfed lines exhibited the main morphological traits that characterised the original varieties. The technique for hybridisation was adapted from the one described by Fehr (1980).

The following genetic markers were used to verify, in the F_1 generation, if harvested seeds were crossed: colour of the flower and hypocotyl (purple dominant to white), pubescence colour (brown dominant to grey), pod colour (brown dominant to tan), growth habit (indeterminant dominant to determinate), maturity (long cycle dominant to short cycle), seed colour (yellow dominant to brown) and hilum colour (black dominant to brown).

The F_1 seeds were advanced into F_2 s to generate a larger bulk of seeds for the diallel experiment in the field. To ensure that a large number of seeds was produced per hybrid, plants were grown in a glasshouse under a 16-h daylength regime. Thirty days after emergence the plants were exposed to a short photoperiod to induce flowering. The hybrid plants were observed from emergence to maturity. The selfed plants were rogued out on the basis of the marker genes mentioned above.

The field experiment was conducted in a cerrado Dark Red Latosol, a variation on Oxisol (Typic Haplustox, fine, kaolinitic, isohyperthermic in the U.S. soil taxonomy), that had been previously limed to supply calcium and magnesium and neutralize any available aluminium and fertilised with phosphorus, potassium and micronutrients. To allow testing of all crosses, a hill plot scheme was used (Spehar 1989). Ten F_2 plants per hill were grown, and these constituted one replicate. Three replications of randomised complete blocks were used. The hills were 0.70 m apart in one direction and 1.00 m in the other, which was sufficient to avoid interplot competition. Foliar samples were collected for mineral analysis, a change from the method described by Spehar (1989). The populations segregated for flowering, and sampling was carried prior to that date. To avoid this leaf position interference, the 7th and 8th fully expanded leaves from the bottom were harvested, with petioles, from each plant. One composite sample of 20 leaves was collected per replicate.

The samples were washed twice in distilled water to remove dust and rain-splashed soil particles from the leaves. They were drained and placed in an oven with forced ventilation for 72 h at 100°C. After cooling, the samples were milled. The finely ground material was placed in glass vials to aid further drying in an oven overnight at 80°C. After the samples cooled they were transferred to a silica-gel desiccator for 3 h. A subsample of 0.25 g was transferred to volumetric Pyrex tubes for wet digestion. A mixture of perchloric (60%) and nitric (concentrated) acids was used in the proportions 1:4 (v/v). The tubes stood for 3 h to allow the beginning of oxidation and were then transferred to a block digester connected to a programmer that progressively activates the digester first to 60°C, then to 100°C, 120°C, and 190°C, taking 11 h for full digestion. Next, 5 ml of 25% HCl was pipetted into the tubes and swirled with a spin mixer. The samples were heated to 80°C for 30 min, cooled down and the tubes were filled with deionized water up to the 25 ml mark. Aliquots were pipetted for mineral analysis into the Inductively Coupled Plasma Emission Spectrometer (ICPES).

The diallel analysis for leaf mineral composition was performed according to the Mather and Jinks (1982) and Griffing (1956) models, respectively.

In the first procedure, the statistical method enabled V_p , V_r and W_r to be calculated, which are the variance of the parents, the variance of an array and the covariance of the offspring in an array with the non-recurrent parents, respectively. There were nine arrays and each consisted of nine families, i.e. the parent and its eight crosses with the other parents. Since no reciprocal differences were found, the data were analysed as a half diallel, and the reciprocals provided another set of replications. The linear regression of W_r on V_r has a slope that is not significantly different from 1, given by a *t*-test, if the additive-dominance model is able to explain the genetic pattern of segregation for the observed characters.

A test of significance was conducted on the estimates of the components: the a , b , b_1 , b_2 and b_3 defined by Mather and Jinks (1982). These components measure the magnitude of additive gene effect (a), the magnitude of dominance gene effect (b), deviations of the hybrids from their mid-parental value (b_1), difference in mean dominance deviation of the hybrid from mid-parental values within each array when compared to the other arrays (b_2) and deviations unique to each hybrid (b_3). For the tests of significance, ratios were obtained between each individual effect and its interaction with the block ef-

fect. The variance of the parents (V_p), the mean variance of arrays (\bar{V}_r), the variance of array means (V_r) and the mean covariance (\bar{W}_r) were used to calculate the coefficients D , H_1 , H_2 , and F . The first coefficient measures additive effects; H_1 and H_2 measure dominance effects. A positive value of F indicates that there are more dominant than recessive alleles. The relationships amongst these coefficients were also used in the interpretation of the results. The square root of H_1/D measures the degree of dominance; the ratio $H_2/4H_1$ measures the average value of dominant/recessive alleles over all loci. Broad sense heritability and narrow sense heritability were calculated using the same coefficients.

Specific and general combining abilities were calculated according to the fixed-effects model described by Griffing (1956). The nine genotypes, although they originated from a relatively wide range of germ plasm and had previously been tested for diversity, were not considered to be a random sample from the population. Thus, conclusions can be drawn only on the basis of the parental lines involved in the cross. However, inferences can be made about the population from which the lines were drawn. The observations for the parents and $p(p-1)$ crosses over three blocks were analysed.

Results and discussion

The analysis of variance for the mineral composition of the diallel is shown in Table 3, according to the statistical model proposed by Griffing (1956), for potassium, calcium, magnesium, iron, aluminium, zinc, copper and manganese. Phosphorus was not included in the analysis as there was only one replication available for that element. General combining ability variance ratios were larger than the SCA ratios for all of the elements. The ratio GCA/SCA was high for the elements potassium, magnesium, iron and aluminium. A relatively low ratio was found for calcium, indicating that the degree of specificity for this element could be related to a possible difference in the frequency of dominant genes in the parental lines. This could be confounded with the additive effects and mask the real magnitude of the dominant gene effects in the genetics of calcium. The evidence for genetic variability for calcium, magnesium and aluminium confirmed the association among these elements reported in the literature (Foy et al. 1969; Alva et al. 1986; Saneoka et al. 1986; Hecht-Buchholz and Schuster 1987). For the other elements there was reduced genetic variation as measured by GCA and SCA. As expected, the magnitude of the GCA/SCA ratio was small, but this should not be interpreted that specific hybrid combinations tended to produce superior genotypes in soybeans.

The means over arrays for mineral composition of the leaves from the diallel are presented in Table 4. In general, crosses involving the aluminium-susceptible variety 'UFV-1' showed less potassium in the leaves, suggesting that their roots may have concentrated their growth where acidity was reduced. The already low cation exchange capacity (CEC) in the ploughed layer of the soil may have caused more potassium to leach down to a less favourable environment to root growth. The range for differences among arrays varied within 0.3 g/kg from the lowest (common parent 'UFV-1') to the highest (common parent 'IAC-7'). It has been reported that the absorption of calcium and magnesium is negatively affected by aluminium

Table 3 General and specific combining abilities (GCA, SCA) for mineral composition of leaves from the 9×9 soybean diallel

Element	Source of variation	df	M.S.	F	P	Ratio GCA/SCA
Potassium	Blocks	5	0.423	14.10	<0.001	7.0
	GCA	8	0.394	13.13	<0.001	
	SCA	36	0.046	1.87	0.010	
	Error	220	0.030			
Calcium	Blocks	5	0.222	13.87	<0.001	3.4
	GCA	8	0.111	6.94	0.002	
	SCA	36	0.033	2.06	0.005	
	Error	220	0.016			
Magnesium	Blocks	5	0.0255	21.25	<0.001	8.5
	GCA	8	0.0210	14.75	<0.001	
	SCA	36	0.0021	1.75	0.025	
	Error	220	0.0012			
Iron	Blocks	5	22 627	1.92	0.220	5.8
	GCA	8	106 486	9.04	0.001	
	SCA	36	18 374	1.56	0.100	
	Error	220	11 781			
Aluminium	Blocks	5	92 150	0.38	n.s.	5.0
	GCA	8	208 578	8.58	0.001	
	SCA	36	41 851	1.72	0.025	
	Error	220	24 310			
Zinc	Blocks	5	58.0	1.56	0.300	1.4
	GCA	8	67.3	1.80	0.150	
	SCA	36	46.5	1.25	0.250	
	Error	220	37.3			
Copper	Blocks	5	8.32	2.31	0.180	1.4
	GCA	8	5.66	1.57	0.250	
	SCA	36	3.82	1.08	0.300	
	Error	220	3.60			
Manganese	Blocks	5	427.5	13.21	<0.001	1.2
	GCA	8	65.4	2.02	0.120	
	SCA	36	52.4	1.62	0.080	
	Error	220	32.3			

Table 4 Mean performance over arrays for common parent in the 9×9 diallel for mineral element absorption in soybeans

Array	Element								
	P g/100 g	K	Ca	Mg	Fe	Al mg/kg	Zn	Cu	Mn
Biloxi	0.369	3.094	1.090	0.516	406.3	540.8	37.1	7.5	28.0
Cristalina	0.368	3.109	1.022	0.488	378.1	502.1	36.4	7.3	29.1
IAC-2	0.355	3.085	1.025	0.483	302.8	382.9	38.9	7.1	26.6
IAC-5	0.358	3.068	0.980	0.486	331.0	419.2	35.3	7.1	27.5
IAC-7	0.373	3.164	1.019	0.478	305.4	392.5	35.9	6.9	27.8
IAC-8	0.357	3.014	1.033	0.454	364.1	460.8	34.5	7.3	29.7
IAC-9	0.365	3.054	1.065	0.479	342.3	448.4	36.4	7.2	30.3
UFA-1	0.345	2.920	1.090	0.491	336.3	438.4	36.8	6.8	27.6
Vx5-281.5	0.363	3.099	1.025	0.468	327.2	424.7	36.7	6.8	28.3

(Foy et al. 1992; Alva et al. 1986; Saneoka et al. 1986; Hecht-Buchholz and Schuster 1987; Hoddinott and Richter 1987). The differences were less evident for calcium and magnesium which are less mobile in the soil and were available to the plants by being abundant in the ploughed layer of the soil.

The analysis for aluminium indicated that, in general, its levels in the leaves are high; there was no clear trend in the ability of the genotypes to absorb it. However, crosses

involving tolerant variety 'Biloxi' had higher levels of aluminium in the leaves than crosses whose common parent was the intolerant variety 'UFV-1'. A possible explanation for aluminium being present in the leaves of soybeans at relatively high levels when its availability should have been reduced in the ploughed layer of the soil is that the roots of more aluminium-tolerant plants penetrated deeper layers of the soil profile where aluminium is still abundant.

Table 5 Results of the regression of covariance (W_r) on variance (V_r) for mineral compositions of soybean leaves

Element	Regression equation ($W_r - V_r$)	Test for $b = 0$		Test for $b = 1$	
		t	P	t	P
Phosphorus	$0.0001 + 0.4656 V_r$	1.547	0.162	1.776	0.120
Potassium	$0.0038 + 0.8320 V_r$	4.068	0.004	0.822	0.480
Calcium	$0.0019 + 0.2296 V_r$	0.874	0.450	2.841	0.025
Magnesium	$0.0003 + 0.7924 V_r$	2.203	0.072	0.577	>0.500
Iron	$-1294.1 + 1.1690 V_r$	3.818	0.006	0.552	>0.500
Aluminium	$-2792.0 + 1.0390 V_r$	2.294	0.076	0.087	>0.500
Manganese	$-1.345 + 0.3530 V_r$	1.216	0.270	2.230	0.070
Zinc	$0.952 + 0.0209 V_r$	0.142	>0.500	6.675	<0.001
Copper	$0.0256 + 0.2759 V_r$	0.684	>0.500	1.796	0.120

Table 6 Estimates of genetic and environmental components for mineral composition of soybean leaves of the F_2 diallel

Character	Element							
	Phosphorus	Potassium	Calcium	Magnesium	Iron	Aluminium	Manganese	Zinc
V_p	0.0007	0.0483	0.0098	0.0025	15 838	36 488	15.01	6.70
\bar{V}_r	0.0002	0.0120	0.0053	0.0006	4 160	10 220	8.41	5.04
V_r	0.0001	0.0053	0.0015	0.0003	1 383	3 089	1.71	1.21
\bar{W}_r	0.0002	0.0138	0.0032	0.0008	3 568	7 830	1.62	1.62
E		0.0049	0.0029	0.0002	788	2 285	18.96	4.94
D		0.0434	0.0070	0.0023	15 050	34 203	-3.95	1.77
F		0.0633	0.0025	0.0030	31 651	74 176	-28.79	-5.91
H_1		0.1099	0.0418	0.0055	64 056	158 810	-42.05	26.68
H_2		0.0678	0.0373	0.0040	38 130	95 816	-44.47	21.88
$H_1 - H_2$		0.0421	0.0045	0.0015	25 926	62 994	-86.52	4.80
$H_2/4H_1$		0.154	0.223	0.180	0.149	0.151	0.264	0.205
$(H_1/D)^{1/2}$		1.592	2.449	1.547	2.063	2.155	3.262	3.890
$((4DH_1)^{1/2} + F)/((4DH_1)^{1/2} - F)$		2.694	1.160	2.416	3.079	3.026	-0.055	0.398
Heritability								
Broad-sense		75.83	67.84	80.72	86.92	84.46	-	46.71
Narrow-sense		54.93	42.00	56.62	47.73	43.73	-	31.95

The results on iron showed the same trend as that found for aluminium, with smaller differences for the crosses involving variety 'Biloxi' as a common parent when compared with the crosses whose common parent was 'UFV-1'. This suggests an association between aluminium and iron uptake by soybeans grown in the soils of the Brazilian Cerrados. It is not unexpected in view of the mineralogy of these soils. The clay fraction contains iron and aluminium oxides, from which the free aluminium is derived.

The reduced level of manganese confirmed its higher dependence on soil pH than available aluminium (Ritchey et al. 1982). The behaviour of copper was similar to that of manganese and zinc, with smaller differences among the arrays. However, for copper the array which had 'UFV-1' as the common parent was different from the array for 'Biloxi', with trends similar to those for calcium and magnesium.

The results for the variance (V_r)-covariance (W_r) regression analysis are presented in Table 5. The t -test for $b=0$ indicated that the additive-dominance model explained the genetic effects for potassium, magnesium, iron, aluminium, zinc, and copper but was not sufficient for phosphorus, calcium and manganese. The values of t for

$b=1$ (full adequacy of the model) confirmed the first test. These data suggested that the genetic relationship among these genotypes is more complex for calcium, manganese and zinc.

The analysis of the components a , b , b_1 , b_2 and b_3 , as described by Mather and Jinks (1982), confirmed the predominance of additive genetic variance detected by Griffing's model. The estimates of genetic and environmental components for leaf mineral composition of the F_2 diallel are presented in Table 6. With the exception of manganese, the positive values of H_1-H_2 indicated that there was unequal allele frequency over all loci. This is confirmed by the $H_2/4H_1$ ratio which was, in general, less than 0.25. The estimate of the type of allele with the most frequency was given by the ratio $((4DH_1)^{1/2} + F)/((4DH_1)^{1/2} - F)$. The values for this estimate were higher than 1, with the exception of calcium and manganese. This was an indication that more dominant than recessive alleles were present in the genotypes. The degree of dominance was measured by $(H_1/D)^{1/2}$. The values for this estimate were higher than 1 in all cases, which indicates an overdominance effect, but it is possible that the parental varieties, homozygous for morphological characteristics, were heterozygous for mineral element absorption. This

would explain the results when the progeny performed better than both parents. Some evidence of calcium segregation within the parental line has already been shown (Spehar 1989).

Heritability in the broad- and narrow-sense are presented in Table 6. There was only one replication for phosphorus and for this reason no information about heritability was obtained for this element. Broad-sense heritability varied from medium, in the case of calcium, to high, for the other elements, with the exception of manganese. The narrow sense heritability varied from low in the case of potassium, iron, aluminium and manganese, to high, for magnesium. For calcium it had a medium value. For aluminium and iron, two other elements closely associated, the broad-sense heritability values varied from medium to high. The high heritabilities indicate the possibility for genetic gain in mineral element absorption by the soybeans. The varieties used in this study originated from breeding programmes aimed at adapting soybean cultivation to mineral stress environments and can be used to illustrate the power of natural selection to mould plant species (Foy et al. 1978, 1992). However, the further improvement of genotypes for efficient nutrient utilisation needs to consider the proportion of dominant genetic variability in order to exploit it in the population. It is expected that recurrent selection with the intermating the superior segregants in large populations should be used in selection cycles to increase the frequency of favourable genes.

Conclusions

The predominance of more additive than dominance effects for most of the elements indicates an opportunity for progress in the selection process to further adapt the soybeans to mineral stresses by pedigree method or its modifications; recurrent selection may be a useful means by which to exploit the dominance fraction which seemed also important.

Aluminium-tolerant plants will have deep roots into the low-CEC soil and recover leached-down potassium, thus giving an indirect assessment of aluminium tolerance. Iron and aluminium are closely associated, even though the former did not reach toxic levels. This is supported by the mineralogy of these soils, which are rich in aluminium and iron oxides as a result of clay decomposition.

The genetic variability for the levels of the remaining minor elements in these soybean varieties, that is, copper, zinc and manganese, was small and that could be one cause for the lack of fitness to the additive-dominance model.

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