

GENERATION MEAN ANALYSIS OF ROOT GROWTH UNDER ALUMINIUM-STRESS HYDROPONICS IN THE SOYBEANS (*GLYCINE MAX* (L.) MERRILL)¹

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ABSTRACT - There are vast areas in the tropics which are limited in their use by mineral stresses such as aluminium and low available nutrients. The grain crops shall be further adapted if breeding programmes include identification and use of the genetic factors to these hindrances. Three soybean families originated from crosses, selfing and backcrosses among the varieties IAC-2, IAC-7, IAC-9 and Biloxi were used in scaling tests to identify their genetic differences to aluminium tolerance by evaluating root growth in Al-stress hydroponics. The results indicated that this is a polygene trait with predominantly additive effects. However, the epistatic effect is also present and should be taken into account in a breeding programme. Recurrent selection is feasible because the method is non-destructive and selected individuals can be advanced for progeny testing and crossing.

Index terms: genetics, breeding, variety, additive, dominance, interaction, genetic model.

ANÁLISE DE GERAÇÕES PARA O CRESCIMENTO RADICULAR DA SOJA (*GLYCINE MAX* (L.) MERRILL) SOB ESTRESSE DE ALUMÍNIO EM SOLUÇÃO NUTRITIVA

RESUMO - Há vastas áreas nos trópicos que apresentam limitação no seu uso devido a estresses minerais como toxidez de alumínio e baixa disponibilidade de nutrientes. As culturas graníferas serão mais adaptadas se nos programas de melhoramento estiver incluída a identificação dos fatores genéticos que condicionam tolerância a esses limitantes. Três famílias (cruzamentos, autopolinização e retrocruzamentos) originárias das variedades IAC-2, IAC-7, IAC-9 e Biloxi foram utilizadas em testes de gerações para identificar as suas diferenças genéticas na tolerância ao alumínio, pela avaliação do crescimento radicular em cultura hidropônica. Os resultados indicaram que esta é uma característica poligênica, com efeitos predominantemente aditivos. Contudo, epistasia também está presente e deve ser considerada em um programa de melhoramento. Seleção recorrente torna-se possível devido à não-destrutibilidade da avaliação, pois os indivíduos selecionados podem produzir sementes para testes de progênie e novos cruzamentos.

Termos para indexação: melhoramento genético, variedade, aditividade, dominância, interação, modelo genético.

INTRODUCTION

When few genes are involved in the control of a particular trait, simple chi-square calculations have

been used to assess the goodness of fit expected Mendelian ratios. By using this approach, Camargo (1983) identified two major genes for aluminium tolerance in wheat. Similarly, Rhue et al. (1978) concluded that a dominant gene with multiple alleles would explain tolerance to aluminium in maize, as tolerant lines behaved differently when backcrossed to intolerant. The simplicity of this method needs to be backed by previous tests with parental lines and plants within lines to assure that they are perfectly homozygous. Also, it is essential that distinct clas-

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ses of segregation be identified in the population, in order to apply chi-square tests to their ratios.

In genetic studies, one approach that contributes to determine the magnitudes of gene effects is the use of scaling tests or generation mean analysis. This has been described by Mather & Jinks (1982), based on Cavalli's method (1952). Their theory was developed for diploid organisms, whose genes segregate independently and are homozygous in the parent lines. Given different generations of the same cross between individuals and their backcrosses, it is possible to evaluate, based on Mendelian segregation ratios, the additive, dominance and interaction (epistasis) effects of the genes.

The genetic contribution which is additive is fixable and that which is dominant is the unfixable heritable variation. Testing the departure of observed from expected values is simply carried out by chi-square procedure. Using the data on the parental lines, their F_1 , F_2 , F_3 , ..., F_n , and backcross generations to the parents has allowed to identify the mode of gene action for important traits in many breeding programmes.

The statistical analysis use specification matrix and parameter vector to provide a simple and compact method to present the relevant equations, while, in the computation of the estimates of genetic parameters, the weighted least squares have been used on any combination of generation means (Basford & DeLacy, 1979; Rowe & Alexander, 1980; Mather & Jinks, 1982).

In studying the genetic control of resistance to cucumber mosaic virus, Pink (1987), compared the Mendelian analysis with the biometrical method previously described; five generations were used (F_1 was excluded from calculations), namely, P_1 , P_2 , F_2 , BCP_1 and BCP_2 of crosses between resistant and susceptible varieties and concluded that more generations were needed to assess the genetic control for that trait since there was no consistent pattern in those generations to fit simple expected Mendelian ratios. However, dominance for susceptibility was found to explain the genetics for that trait by the biometrical method. Additive effect was significant and explained by the effects of gene dosage in the mid parent. Epistasis was also identified when models of increasing complexity were employed.

Thus, departure from Mendelian ratios due to gene interaction is very likely to happen in practice, and makes justifiable the use of scaling tests in the rationalization of breeding efforts.

Generation mean analysis was employed by several authors studying the genetics of mineral nutrition efficiency. Baker (1968) found that in root beets, efficiency in potassium utilization was heritable with partial dominance. O'Sullivan et al. (1974) found that the genetic model which included the additive x additive interaction explained the inheritance for nitrogen utilization in tomatoes. Makmur et al. (1978) found that additive gene effects made the major contribution for potassium efficiency in tomatoes. Giordano et al. (1982), on a calcium efficiency study in tomatoes, employed three efficient and three inefficient lines in generation tests for estimation of gene effects. For two crosses the additive-dominance model was adequate to explain gene effects on total plant weight but that was inadequate for the other four crosses. When their model was expanded to include digenic interaction, additive x additive and additive x dominance gene effects made a major contribution to the genetics of calcium efficiency, while dominance had a minor effect.

The literature is abundant on differential response of soybean varieties to aluminium tolerance (Armiger et al., 1968; Sapra et al., 1982; Foy et al., 1992; Spehar et al., 1994) but little has been done in elucidating its genetics to fully explore the variability for this important trait. Hanson & Kamprath (1979), after screening soybeans for aluminium tolerance, using root growth rate in nutrient solution, interbred selected lines to produce cycles of selection, top crossing twelve susceptible and twelve tolerant lines with the same genetic stock, pure line D49-2491, which showed a degree of tolerance. Selected plants were backcrossed to a tolerant line and initiated a new cycle of selection. This allowed the estimation of heritability for aluminium tolerance on root growth rate which was found to be high, although tests in acid soil did not always confirm these results. On the other hand, Spehar (1989) on diallel cross among tropical adapted varieties found high heritability values for the same trait.

The main objective of this study was to identify the mode of gene action for aluminium tolerance in the soybeans, by testing three sets of generation families, to further improve tolerance of tropical adapted cultivars.

MATERIALS AND METHODS

Three soybean families were used in this study for root growth under aluminium stress. Four soybean varieties, namely, 'IAC-2', 'IAC-7', 'IAC-9' and 'Biloxi', representing a range of tolerance to aluminium according to relative seed yield evaluation in the field, were chosen for genetic studies in hydroponic experiments (Spehar, 1989). Relative seed yield indicated that 'IAC-7' was intolerant and this variety was crossed and backcrossed to the other three. However, based on nutrient solution testing, it was verified that the variety IAC-2 was less tolerant than 'IAC-7' (Spehar, 1989).

Hybridization was carried out in the Centro de Pesquisa Agropecuária dos Cerrados, EMBRAPA-CPAC, Planaltina, Brazil. The procedure was described by Spehar, 1989. F_1 seeds were grown to generate the F_2 generation and for backcrossing with parental lines. To assure maximum utilization of hybrid, clonal propagation of hybrid plants and sowing several batches of parental lines were conjugated (Spehar & Galwey, 1990). Due to scarcity of seeds, the F_1 generation was not included in the experiments. Initially, the tests were conducted with five generations, i.e., tolerant and susceptible parents, backcross to tolerant parent, backcross to susceptible parent and F_2 generation. With the seeds of the F_3 available, another test was carried out to include one more generation, and thus, to expand the test for more complex genetic models.

The seeds of five genetic families, namely P_1 , P_2 , BCP_1 , BCP_2 and F_2 , for each cross, were used in the first test for aluminium tolerance in a hydroponics experiment conducted in a growth cabinet. The temperature was set to $25 \pm 1^\circ\text{C}$ and the day length was 16 hours. Seeds were germinated in lay-tag beads in the cabinets and transferred to treatment solution on the third day, after being soaked for one hour in distilled water. The solution was 1/4 normal concentration, phosphorus absent, (Moore et al., 1977) and contained 2 mg/l Al. Five seedlings per family were grown for five days in Styrofoam cups filled with 180 ml of treatment solution. For each set of crosses there were 10 seedlings of each parent, 30 seedlings of each backcross and 40 F_2 seedlings. The solution was replaced every day, during the experiment and the pH measured. Plants were

harvested and stored in a cold room at a temperature of 5°C , for root measurement. The longest secondary root formed entirely in the presence of aluminium was measured. For the second experiment, the same numbers of seedlings were used, with the inclusion of 40 F_3 seedlings. The F_3 seeds were obtained by selfing two randomly chosen F_2 plants.

The biometrical analysis on the generation means was based on Cavalli's proposal to estimate the magnitude of gene action in the additive-dominance model. Mather & Jinks (1982) illustrate the use of this method and present the computational steps taking into account the different gene effects as follows: mean (m), additive (d), dominance (h), additive x additive (i), additive x dominance (j) dominance x dominance (l).

Six parameters corresponding to main effects of genes and their interactions, i.e., epistatic effects, are analyzed and six means are available for their estimation. The F_3 generation was employed in the analysis and the new biometrical model was modified from the one suggested by Mather & Jinks (1982), to obtain the specification matrix to calculate for the six generations.

If the simple gene effects and their interactions are all to be calculated, no test of goodness of fit is possible for the model. The observed values are tested against the expected values for a given model through the chi-square test. But in the complete model there are no degrees of freedom left for the test, as there are six parameters to be estimated and five or six genetic families in the present experiments. The alternative is to start with simple additive model and subsequently, add the other effects making the model more complex, testing the goodness of fit at each stage. The biometrical model of increasing complexity allows estimation of the contribution for each of the gene effects and their interactions and was used by several authors (Giordano et al., 1982; Delaney & Lower, 1987; Ginkel & Scharen, 1987; Bjarko & Line, 1988).

The methods employed in the two present experiments were as follows: a weighted least squares procedure was used to fit models of increasing complexity, starting with the mean and, by the addition of a new genetic parameter, chi-square values were obtained to assess its goodness of fit. The mean + additive effects (d) was tested; then the dominance term (h) was added to the model, tested and compared to the preceding simpler model; then the homozygous x homozygous (i), homozygous x heterozygous (j) and heterozygous x heterozygous (l) interactions were alternatively added to verify the epistatic gene effects on the model.

When a parameter was added to the new model, a new chi-square value was obtained and, by calculating the difference between the two values, it was possible to

quantify the contribution of each gene effect. The calculation of chi-square statistics was done adapting the computational procedure suggested by Rowe & Alexander (1980).

RESULTS AND DISCUSSION

The results for the chi-square tests, mean root length, standard deviation and coefficient of variation for the five generation means are presented in Tables 1 and 2. By the inclusion of the additive term for the cross IAC-7 x Biloxi, only 25% of the chi-square was explained. It was obvious that the model could not fully explain the genetic differences between the two varieties. By adding the dominance term, the chi-square increased little, indicating that the simple additive-dominance model was also insufficient. Only by the inclusion of the additive x additive interaction was the model made adequate.

The genetic effects of the cross IAC-7 x IAC-2 were not fully explained by any of the models tested. However the additive effects alone seemed to play an important role in the genetic difference between the two genotypes as measured by the explained chi-

-square. The mean + additive model explained 85% of the chi-square. The lack of fit for the simple additive-dominance model indicated that epistatic effects play a role in the genetics of aluminium tolerance in these two varieties. The model which included the additive x additive interactions seemed to explain the genetic differences, but inclusion of additive x dominance produced similar result. However, the chi-square value for the deviations from the former model had a degree of significance and this indicated that a model more complex than the four term should be tested, which cannot be done in a set of five families.

The analysis of IAC-7 x IAC-9 cross indicated a similar pattern, i.e., the simple gene effects did not produce any substantial contribution towards explaining the chi-square. The four term model, which included the additive x additive interaction, mostly explained the genetic differences between the two varieties.

The results for the tests with the inclusion of F_3 generation, where the dominance effect and the dominance x dominance interaction were halved

TABLE 1. Chi-square values for the genetic models and probabilities (p) using five generation means (F_2 , BCP₁, BCP₂, P₁, P₂).

Cross	Model	Chi-square		D.F.	P
		Explained (D.F. = 1)	Residual		
IAC-7 x Biloxi	m		99.71	4	<0.001
	m [d]	26.26	73.45	3	<0.001
	m [d] [h]	3.20	70.25	2	<0.001
	m [d] [h] [i]	68.13	2.11	1	0.180
	m [d] [h] [j]	4.43	69.02	1	<0.001
IAC-7 x IAC-2	m		61.73	4	<0.001
	m [d]	52.94	8.79	3	0.002
	m [d] [h]	0.56	8.22	2	0.003
	m [d] [h] [i]	4.52	4.27	1	0.041
	m [d] [h] [j]	5.05	3.73	1	0.055
IAC-7 x IAC-9	m		32.41	4	<0.001
	m [d]	1.48	30.93	3	<0.001
	m [d] [h]	4.41	26.52	2	<0.001
	m [d] [h] [i]	21.44	5.08	1	0.025
	m [d] [h] [j]	11.19	15.33	1	<0.001

TABLE 2. Mean root length, standard deviation (S.D.) and coefficient of variation (C.V.) for the five generations.

Cross	Generation	Mean (cm)	S.D.	C.V. (%)
IAC-7 x Biloxi	P1	2.52	0.402	15.95
	P2	3.29	0.419	12.73
	F2	3.64	0.656	18.02
	BC1	2.53	0.705	27.87
	BC2	2.64	0.711	26.93
IAC-7 x IAC-2	P1	2.52	0.402	15.95
	P2	1.78	0.336	18.88
	F2	2.38	0.574	24.12
	BC1	2.50	0.496	19.84
	BC2	1.81	0.411	22.70
IAC-7 x IAC-9	P1	2.52	0.402	15.95
	P2	2.55	0.407	15.96
	F2	3.07	0.578	18.82
	BC1	2.80	0.480	17.14
	BC2	2.48	0.569	22.94

relative to the F_2 , are presented in Tables 3 and 4. The cross IAC-7 x Biloxi showed a substantial reduction of the residual chi-square by the inclusion of the additive term into the model. This increased importance of the additive term apparently contradicted the results with five generations, when its magnitude was less apparent. The reason to this could be the inclusion of more individuals for the parental varieties, reducing error variation. The simple additive model was sufficient to explain three quarters of the genetic variability. When the dominance effect was included into the model there was virtually no reduction on the chi-square value. Similarly to the five generation analysis for the same two varieties, the simple additive-dominance model was not sufficient to explain the genetic differences between these two varieties.

More complex models which included digenic interactions were tried, first with the three possible four-term models, which were made by alternatively adding the interactions. A reduction in the absolute chi-square value was obtained when the model included the additive x additive gene interaction. The other four-term models, which included additive x dominance and dominance x dominance interactions did not show any improvement in fit.

The five-term model which produced a non-significant chi-square and therefore best explained the differences between these two varieties was the one which included the additive x additive and dominance x dominance interaction.

For the cross IAC-7 x IAC-2 the simple mean + additive model explained three quarters of the genetic differences between the two genotypes, although it was not sufficient to make the chi-square significant. Also for this cross the five-term model which included the additive x additive and dominance x dominance interactions produced the least chi-square value, although still highly significant.

The third set of six families originated from the cross IAC-7 x IAC-9 was also tested for models of different complexity. The small chi-square value obtained by the mean + additive effects confirmed the results for the same cross using five generations. The three-term mean + additive + dominance model was not sufficient to explain the genetic differences and a four-term was then tested. Likewise, three five-term models were tested and the model which explained the genetic differences in this cross was the one that had the additive x additive and dominance x dominance interactions.

TABLE 3. Chi-square values for the genetic models and probabilities (p) using six generation means (F_2 , F_3 , BCP_1 , BCP_2 , P_1 , P_2).

Cross	Model	Chi-square		D.F.	p
		Explained (D.F. = 1)	Residual		
IAC-7 x Biloxi	m		104.00	5	<0.001
	m [d]	69.59	34.41	4	<0.001
	m [d] [h]	-2.71	37.12	3	<0.001
	m [d] [h] [i]	19.90	20.22	2	<0.001
	m [d] [h] [j]	5.39	31.73	2	<0.001
	m [d] [h] [l]	7.06	30.06	2	<0.001
	m [d] [h] [i] [j]	0.24	19.98	1	<0.001
	m [d] [h] [i] [l]	20.03	0.19	1	0.686
	m [d] [h] [j] [l]	-9.53	29.75	1	<0.001
IAC-7 x IAC-2	m		96.50	4	<0.001
	m [d]	64.59	31.91	3	<0.001
	m [d] [h]	0.55	31.36	2	<0.001
	m [d] [h] [i]	5.86	25.50	1	<0.001
	m [d] [h] [j]	11.32	20.04	1	<0.001
	m [d] [h] [l]	0.66	30.70	1	<0.001
	m [d] [h] [i] [j]	10.40	15.10	1	<0.001
	m [d] [h] [i] [l]	15.88	9.62	1	0.002
	m [d] [h] [j] [l]	0	20.04	1	<0.001
IAC-7 x IAC-9	m		71.74	5	<0.001
	m [d]	21.39	50.35	4	<0.001
	m [d] [h]	-1.82	52.17	3	<0.001
	m [d] [h] [i]	32.88	19.29	2	0.001
	m [d] [h] [j]	27.52	24.65	2	<0.001
	m [d] [h] [l]	18.60	33.57	2	<0.001
	m [d] [h] [i] [j]	16.25	3.04	1	0.085
	m [d] [h] [i] [l]	5.50	13.79	1	<0.001
	m [d] [h] [j] [l]	12.35	12.30	1	<0.001

The additive forces seemed to play a major role in the genetics of aluminium tolerance both in the individual effects of genes and their interactions, although dominance had a role in these set of families, indicating that tolerance to aluminium is a multiple gene character in soybeans. At this point it is interesting to relate the single gene results obtained between hybridization of contrasting varieties by Rhue et al. (1978) and the polygene, with predominantly additive effects in a diallel cross in maize (Pandey et al., 1994). These apparently contradictory results may be related to the different genetic background likely to happen when varieties

with some degree of tolerance are crossed for crop improvement.

In hydroponics experiments with low-calcium stress on tomato hybrids, Giordano et al. (1982) found that in six sets of families, there were also contrasting genetic differences. For two of the sets the simple additive dominance model was adequate and for the remaining crosses more complex models including digenic interactions were sufficient to explain genetic differences. Likewise to what was found in the present study, the magnitude of additive gene effects surpassed that of dominant effects. In a study with low-potassium stress, Makmur et al.

TABLE 4. Mean root length, standard deviation (S.D.) and coefficient of variation for the six generations.

Cross	Generation	Mean (cm)	S.D.	C.V. (%)
IAC-7 x Biloxi	P1	2.54	0.432	17.00
	P2	3.25	0.575	17.69
	F2	3.26	0.698	21.41
	F3	3.10	0.506	16.32
	BC1	2.53	0.701	27.70
	BC2	2.80	0.602	21.50
IAC-7 x IAC-2	P1	2.54	0.432	17.00
	P2	2.05	0.362	17.66
	F2	2.58	0.604	23.41
	F3	2.33	0.569	24.42
	BC1	2.60	0.505	19.42
	BC2	1.82	0.416	22.86
IAC-7 x IAC-9	P1	2.54	0.432	17.00
	P2	3.11	0.571	18.36
	F2	3.07	0.578	18.82
	F3	3.22	0.558	17.33
	BC1	2.80	0.480	17.14
	BC2	2.57	0.506	19.69

(1978) found that additive gene effects made the major contribution to the genetics for efficiency in potassium utilization.

The present results are corroborated by a diallel analysis in soybeans for aluminium tolerance in which also additive effects were more prominent (Spehar, 1989). However, the effects due to dominance were still significant and on a minor scale contributed to the genetics of aluminium tolerance. It seems that favourable genes, accumulated in acid soil adapted soybeans, are scattered in the varieties. These can be further improved for the trait by modified pedigree and recurrent selections.

CONCLUSIONS

1. The simple additive-dominance model was insufficient to explain the genetics of aluminium tolerance in the present soybean germplasm.

2. The additive x additive and the additive x dominance interactions best defined the pattern for aluminium tolerance for the cross IAC-7 x Biloxi, whilst in IAC-7 x IAC-9 the best fit was given by the inclusion of additive x additive and dominance x dominance interactions.

3. Hybridizations among selected varieties, using modified pedigree and recurrent selection schemes, shall be successfully used in a breeding program to improve soybean for aluminium tolerance.

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