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Environmental and genotypic factors associated with genotype by environment interactions in soybean

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ABSTRACT - *The aim of this study was to quantify the influence of some environmental and genotypic variables on genotype by environment (GE) interactions in soybean. Mean yield data from eighteen test genotypes in eleven experiments in Goiás State, Brazil, were used and analyzed by AMMI method. To identify environmental and genotypic variables related to the GE interaction, simple linear correlations were estimated between the means of these variables and the scores of the first AMMI principal component of the interactions. Successive simple linear regression analyses were also carried stepwise, in order to relate the GE interaction of each genotype to the observed environmental factors. The environmental factors that influenced the GE interactions most were altitude, maximum temperature, end-of-cycle disease complex, total rainfall and soil fertility. The genotypic variables days to maturity and reaction to end-of-cycle disease complex were most associated with GE interactions.*

Key words: *Glycine max*, AMMI analysis, environment variables, yield adaptation.

INTRODUCTION

To be able to understand and exploit the interaction of genotypes with environments (GE interaction), in a breeding program, a lot of information is required on the determinant factors of the differentiated genotype response to environmental variables (Kang et al. 1989). The possibility of exploiting the GE interaction effects depends on the understanding of traits related to the interaction expression, of the genotypes, as well as of environments (Van Eeuwijk et al. 1996). When qualitative or quantitative variable interactions associated to the genotypes or environments are available, their effects on the interaction, under certain conditions, can best be evaluated.

Qualitative variables associated to the genotypes, for example, can be pedigree, geographic origin, classes of disease and pest resistance, maturation group, among others. Some of the quantitative variables are cycle (measured in continuous scale), plant height, resistance to diseases, among others. Amongst the qualitative environmental variables we can cite: soil class, technology level, planting season, geographic region. Altitude, latitude, temperature, rainfall and levels of chemical elements in the soil exemplify quantitative variables associated to the environments (Chaves 2001). This author adds that studies of correlation among these variables and GE interaction would be helpful to broaden the understanding of this interaction in support of future cultivar recommendations.

Bearing this in mind, some authors have mentioned the contribution of different environmental variables to the GE interactions (Saeed and Francis 1984, Kang and Gorman 1989, Margari and Kang 1993, Ramasamt et al.

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1996). Ramasamt et al. (1996) observed in peral millet that the contribution of environmental variables to this interaction was mainly determined by rainfall. This factor contributed more to the magnitude of the interaction sum of squares than any other environmental variable under study.

Kang and Gorman (1989) evaluated the effects of the variables maximum temperature, minimum temperature, rainfall and relative air moisture on GE interaction in maize. They concluded that rainfall explained 1.4% of this interaction, while the variables maximum temperature, minimum temperature and relative humidity explained a percentage considered negligible. Some studies, show that the effect of each environmental variable on GE interaction sum of squares is low, in most cases. This fact is expected in view of the multiplicity of factors involved in the environmental characterization. Nevertheless, the quantification of these effects may represent an important contribution to the understanding GE interaction nature and in the determination of genotypes with adaptability to specific environments.

Methods to evaluate the relative contribution of environmental variables and of other factors to GE interaction are available. Van Eeuwijk et al. (1996) describes a series of them, being that the most simple way is to fit the interaction as a genotypic regression to each environmental covariate. Chaves (2001) also described this procedure and illustrated it with a numeric example.

The objective of this study was to quantify the influence of some environmental and genotypic variables on the GE interaction in soybean, aiming at a more in-depth understanding of this so relevant phenomenon in the context of genetic plant breeding programs.

MATERIAL AND METHODS

Data of eleven trials (environments) carried out in three counties (Goiânia, Itumbiara and Jataí) of Goiás State were used. The trials included four sowing periods (11/28, 12/04, 12/11 and 12/18) of the planting season 2000/2001. The sites varied in climatic conditions, as well as soil fertility, due to the localization (Table 1). Eighteen genotypes were evaluated in each experiment, four of them commercial cultivars (controls). The experiments were designed in complete randomized blocks with three replications.

Data of altitude, total rainfall, rainfall in the reproductive period of the crop (from flowering to physiological grain maturation), soil fertility (basis saturation level), latitude and maximum and minimum temperatures were considered as environmental variables. The genotypic variables were number of days to flowering (NDF), number of days to maturity (NDM) and reaction to diseases resistance as powdery mildew and end-of-cycle disease complex (ECD).

Mean grain yield data of the experiment group were, statistically treated by AMMI analysis. This analysis consists in the sequential fitting of a model of joint analysis of experiments, initially by analysis of variance (additive fitting of the main effects) and then by analysis of principal components (multiplicative fitting of the effects of interaction). The analysis was implemented by SAS software with the routine available by Duarte and Vencovsky (1999).

For the identification of environmental and genotypic variables related to GE interaction, simple linear correlations were estimated between the means of these variables and the scores of the first AMMI principal component of interaction (IPCA1). Another approach to the evaluation of the specific effects of environmental factors on GE interaction was the use of successive analyses of simple linear regression, in a stepwise procedure. In each analysis, the sum of squares of the interaction ($SS_{G \times E}$, with $DF_{G \times E}$ degrees of freedom) is partitioned in: i) linear effect associated to the environmental variable (with g-1 degrees of freedom, where g is the number of genotypes); and ii) residues of the

Table 1. Mean characteristics of the three sites in Goiás State, Brazil

Site/Goiás	**Altitude** (m)	**Latitude**	**Maximum temperature** (°C)	**Mininum temperature** (°C)	**TR**[1] (mm)	**RR**[2] (mm)	**V**[3] (%)
Itumbiara	449	18° 25’	32	20	685.53	406.35	44
Goiânia	730	16° 41’	31	23	851.30	472.20	37
Jataí	708	17° 53’	31	19	837.93	423.65	36

[1] Total rainfall from the sowing period until physiological maturation
[2] Rainfall in the reproductive period of the crop (R1 the R7)
[3] Soil basis saturation

linear regression, with $DF_{G \times E}$-(g-1) degrees of freedom. The data of the environmental variables were thus successively included in the following model of analysis: $Y_{ij} = \mu + g_i + a_j + \beta_i z_j + (ga)'_{ij} + \bar{e}_{ij}$, where: Y_{ij}: mean response of the genotype i (i = 1, 2, ..., g) in the environment j (j = 1, 2, ..., a); m: overall trial mean; g_i: fixed genotype effect i; a_j: fixed environment effect j; $\hat{a}_i$: regression coefficient that measures the response of interaction effects of genotype *i* to variable Z; $(ga)'_{ij}$: residual effect of classic interaction; $\bar{e}_{ij}$: pooled experimental error.

In this approach, the interaction of genotype i with environment j, $(ga)_{ij}$, currently described in a traditional joint analysis model is partitioned in the sum: $\beta_i z_j + (ga)'_{ij}$. The first part is related to the linear effects ($\hat{a}_i$) of the environmental variable Z (with Z_j observations, *j*=1,2,...,a) on $(ga)_{ij}$ interaction, and the second, $(ga)'_{ij}$, represents a residue related to the other environmental factors not, leaved in account in the model (Van Eeuwijk et al. 1996, Chaves 2001).

The estimates of $\hat{a}_i$ were obtained by assuming each row of the GE interaction table or matrix as dependent variable and the respective environmental values of variable Z as independent variable. Initially the estimates of the interactions were obtained by ordinary least squares (OLS): $\hat{(ga)} = Y_{ij} - \bar{Y}_{i.} - \bar{Y}_{.j} + \bar{Y}_{..}$, where $\bar{Y}_{i.}$, $\bar{Y}_{.j}$ and $\bar{Y}_{..}$ are the genotype i, environment j and overall mean, respectively. So we have: $\hat{\beta}_i = b_i = \sum_j \hat{(ga)}_{ij} z_j / \sum_j z_j^2$, with $z_j = Z_j - \bar{Z}_.$, where $\bar{Z}_.$ is the mean of the Z_j values.

The sum of squares associated to linear regression of $\hat{(ga)}_{ij}$ on the environmental variable Z was determined by: $SQ_Z = \left(\sum_j \hat{(ga)}_{ij} z_j\right)^2 / \sum_j z_j^2$. This allows to obtain a analysis of variance with partitioning of the GE interaction, sum of square.

Thereafter, the same regression analysis was implemented considering the AMMI estimates of the GE interactions as dependent variable. These estimates were obtained based on the scores of the first principal component of interaction (IPCA1). The choice of this procedure with a single principal axis is supported in literature, by the possibility of an enhanced information quality on the GE interaction estimated by AMMI analysis, comparatively to the estimates of ordinary least squares (Kempton 1984, Mandel 1971, Gauch and Zobel 1996). Furthermore, recently the exploitation only of the first main axis has been defended, of the predictive point of view, even so when models of order higher (AMMI2, AMMI3...) if show statistically significant (Pacheco 2005).

RESULTS AND DISCUSSION

In the first cycle of stepwise regression analyses, the variables altitude, maximum temperature, end-of-cycle disease incidence, total rainfall and soil fertility, in this rank, were the ones with the strongest association to the GE interaction, with significant effects at 1% probability (Table 2). The respective sums of squares of these variables represented 23.4, 20.1, 16.7, 15.6, and 14.0% of the $SS_{G \times E}$ original.

These results indicate that one should include the linear effect of the variable altitude in the general description model of the phenotypic responses Y_{ij}. After the fitting a residue of the original $SS_{G \times E}$ was left over which was investigated, sequentially, for the presence of effects of the other environmental variables. In the second cycle of analyses, now modeling the linear effect of the altitude separately, an inversion was therefore observed in the ranking of importance of the environmental variables with

Table 2. Percentage of GE interaction sum of squares explained by the linear effects of environmental variables in four cycles of linear regression analyses (stepwise)

Environmental variables	Cycle of Analyses			
	1	2	3	4
Altitude	23.39 **	-	-	-
End-of-cycle disease	16.71 **	16.77 **	-	-
Powder mildew	7.35	12.81	14.90	-
Minimum temperature	10.30	13.92 *	12.42	12.53
Rainfall in the reproductive period of the crop[1]	10.02	9.42	10.50	11.65
Latitude	9.08	10.60	9.57	11.19
Soil fertility	14.03 **	5.25	6.55	7.455
Maximum temperature	20.10 **	4.18	5.98	7.367
Total rainfall	15.58 **	5.66	5.95	6.999

** and * significant at 1% and 5% probability, respectively
[1] Rainfall in the reproductive period of the crop (R1 to R7)

Table 3. Analysis of variance considering the effects of the environmental variables altitude, end-of-cycle disease complex and powdery mildew on the original GE interaction

Source of variation	DF	SS	MS	F	Pr > F	$SS_{G \times E}$ (%)
GE interaction	151	12891459.05	85373.90	1.77	0.0001	-
Altitude	17	3015549.99	177385.29	3.67	0.0000	23.39
GE residue	134	9875909.06	73700.81	1.52	0.0030	-
End-of-cycle disease complex	17	1655924.52	97407.32	2.01	0.0118	16.77
GE residue	117	8219984.54	70256.28	1.45	0.0094	-
Powdery mildew	17	1224869.68	72051.16	1.49	0.1002	14.90
GE residue	100	6995114.86	69951.15	1.45	0.0133	-
Pooled error [1]	216	-	48375.58	-	-	-

[1] The number of degrees of freedom for pooled error was adjusted by the method of Cochran (1954), due to heterogeneity among the residual mean squares

regard to the explanation of the residual $SS_{G \times E}$ (Table 2). The variables end-of-cycle disease incidence, and minimum temperature came to contribute more effectively to the GE interaction, representing 16.8 and 13.9%, respectively. On the other hand, the variables maximum temperature, total rainfall and soil fertility contributed least to the explanation of the residual $SS_{G \times E}$. This shows that these variables are correlated to the altitude, suggesting that if the effect of this latter is removed, the effect of the former is removed as well.

Actually the effect of altitude on soybean cultivar recommendation has been acknowledged by breeders exactly because of its relation with the temperature (higher altitudes, lower temperatures). Although the residue of the original GE interaction was still significant after the removal of the effects of altitude and the end-of-cycle disease index (Table 3), from the third cycle of analyses onwards, the individual contribution of each evaluated variable was no longer significant (Table 2). This brought the successive investigation process of the effects of environmental variables for this dataset to a close.

The particular effects of an environmental variable on the relative sensitivity of each genotype (specific GE interaction effects) can be evaluated through estimates of the regression coefficients (b_i) (Table 4). For example, positive b_i values for altitude indicate an adaptation of the genotype to higher, and negative b_i values to lower altitudes. Cultivar FT-2000, for example, was especially adapted to high altitude environments of (b=3.12), while line L-7 (b=-0.91) to lower altitudes. Cultivar Conquista was adapted to environments of higher altitudes and tolerated lower fertility indexes and a higher incidence of end-of-cycle diseases. The biplot (Figure 1) obtained by the AMMI analysis confirms this performance, demonstrating that the cultivar was especially adapted to the Jataí location (altitude of 708 m, maximum temperature of 31 ºC and basis saturation of 36%), in all planting periods. This result was also discussed by Oliveira et al. (2003). These environments were among those of highest altitudes, where soil fertility varies from low to moderate and milder temperatures.

The investigation about the effects of environmental variables on the GE interaction estimated by AMMI analysis was motivated by the expectation of an enhanced information quality of the AMMI1 estimates, compared to ones of ordinary least squares. As Zobel et al. (1988) and Gauch and Zobel (1988) argue, the AMMI method can capture agronomic and statistically important patterns in the GE interaction, which are explained mainly by the first

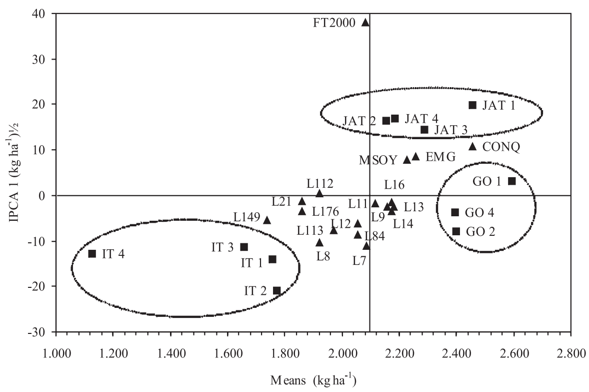

Figure 1. AMMI1 biplot for data of soybean grain yield (kg ha-1) of 18 genotypes (▲) in 11 environments (■) in Goiás State (IT: Itumbiara; GO: Goiânia, and JAT: Jataí)

Table 4. Estimate of linear regression coefficients (b_i) of the effects of the GE interaction in function of the environmental variables, in a first cycle of stepwise analyses

Genotypes	ALT[1]	MAX T	ECD	TR	B SAT	MIN T	RR	LAT	P MIL
Conquista	0.88	-218.09	168.87	0.73	-14.73	-2.61	0.57	-43.50	-39.32
Emgopa 315	0.71	-175.49	135.88	0.59	-11.85	-2.10	0.46	-35.00	-31.64
FT-2000	3.12	-776.27	601.09	2.61	-52.42	-9.30	2.03	-154.83	-139.97
L-7	-0.91	225.03	-174.25	-0.76	15.19	2.70	-0.59	44.88	40.58
L-8	-0.85	211.85	-164.04	-0.71	14.30	2.54	-0.55	42.26	38.20
L-9	-0.19	48.37	-37.46	-0.16	3.27	0.58	-0.13	9.65	8.72
L-11	-0.14	35.64	-27.59	-0.12	2.41	0.43	-0.09	7.11	6.43
L-112	0.04	-10.48	8.12	0.04	-0.71	-0.13	0.03	-2.09	-1.89
L-113	-0.64	158.65	-122.85	-0.53	10.71	1.90	-0.42	31.64	28.61
L-12	-0.50	123.81	-95.87	-0.42	8.36	1.48	-0.32	24.70	22.33
L-13	-0.21	52.22	-40.43	-0.18	3.53	0.63	-0.14	10.42	9.42
L-14	-0.28	70.49	-54.58	-0.24	4.76	0.84	-0.18	14.06	12.71
L-149	-0.44	110.11	-85.26	-0.37	7.44	1.32	-0.29	21.96	19.85
L-16	-0.12	30.31	-23.47	-0.10	2.05	0.36	-0.08	6.05	5.47
L-176	-0.28	70.20	-54.35	-0.24	4.74	0.84	-0.18	14.00	12.66
L-21	-0.11	27.30	-21.14	-0.09	1.84	0.33	-0.07	5.45	4.92
L-84	-0.72	178.18	-137.97	-0.60	12.03	2.14	-0.47	35.54	32.13
MSOY-8001	0.65	-161.84	125.32	0.54	-10.93	-1.94	0.42	-32.28	-29.18

[1] ALT: Altitude; MAX T: Maximum temperature; ECD: End-of-cycle disease complex; TR: Total rainfall from the sowing period until physiological grain maturation; B SAT: Basis saturation index; RR: Rainfall in the reproductive period of the crop (R1 to R7); MIN T: Minimum temperature, LAT: Latitude, and P MIL: Powdery mildew

principal component of the analysis. There, precision is gained in the estimates allowing one understand the true GE interaction effects.

Owing to the number of environments, the original GE interaction can be partitioned by AMMI analysis in ten principal components (rank of the interaction matrix), of which only the first term (IPCA1) was significant ($P < 0.01$). Furthermore, the residues of this model (AMMI1) were non-significant ($P > 0.01$), confirming the choice of only the first principal axis of GE interaction. Oliveira et al. (2003) justify the use of the significance level at 1% probability in the Snedecor's F test applied to the selection of AMMI models. The tendency in GE interaction studies has been to exploit only the first principal axis, even when models with more multiplicative terms are statistically significant

Table 5. Percentage of the GE interaction sum of squares (SS_{GxE}) captured by the AMMI1 model and significances of F explained by the linear effects of environmental variables in a cycle of stepwise regression analyses

Environmental variables[1]	$SS_{G \times E}$ (%)	F	Environmental variables	$SS_{G \times E}$ (%)	F
Altitude	57.21	3.28**	Latitude	4.02	0.23
Maximum temperature	36.25	2.08**	RR	2.99	0.17
Soil fertility	29.85	1.71*	Powdery mildew	1.74	0.10
Total rainfall	28.20	1.62	Minimum temperature	1.39	0.08
End-of-cycle disease complex	24.47	1.40	-	-	-

** and *: significant at 1 and 5% probability, respectively
[1] RR: Rainfall in the reproductive period of the crop (R1 to R7)

(Gauch 1992, Ebdon and Gauch 2002). In the present study the GE interaction pattern (described by AMMI1 model) was, therefore, explained by approximately 36% of $SS_{G \times E}$, despite not using more than 20% of the original degrees of freedom.

The proportion of $SS_{G \times E}$ captured by the AMMI1 model and explained by the linear effects of the environmental variables, in the first cycle of stepwise regression analyses are presented in Table 5. In this cases, the variables altitude and maximum temperature contribute with the highest percentages of explanation, as well. There was also a change in the rank of explanation of environmental variables in relation to the analyses with the GE interaction estimated by least squares. This was particularly true for soil fertility with the AMMI1 model, which came to be the third variable that most explained $SS_{G \times E}$. The variables reaction to end-of-cycle diseases and rainfall did not explain a significant portion of the $SS_{G \times E}$ by AMMI1, as discussed above (Table 2).

The partitioning of the $SS_{G \times E}$ plot captured in the AMMI analysis, taking into account to the linear effect associated to the variable altitude is showed in Table 6. If the portion considered here should represent the effects of the GE interaction more realistically, we can say that the altitude represented not less than 57% of this sum of squares. The significance of the corresponding residues yet evidences that the altitude separately does not explain the significant pattern of the GE interaction. That os, it indicates that other environmental factors are co-responsible for the interaction. In the case of this second analysis, we cannot realize a second cycle of analyses in an attempt to isolate the effect of other variables, due to the low number of degrees of freedom for the AMMI component of the SS_{GxE}. As Chaves (2001) described, each variable need (*g-1*) degrees of freedom for this analysis (number of $\hat{a}_i$ coefficients). The second round of analyses would therefore affect the degrees of freedom available for the residual interaction (Table 6).

Analyzing the correlations of the environmental variables evaluated with the environmental scores of the first AMMI principal component (IPCA1), a conclusion may be drawn that besides the altitude, the

Table 6. Analysis of variance considering the effect of environmental variables (Z_j) on GE interaction estimated by the AMMI1 model

Source of variation	DF	SSz	MS	F	$SS_{GE/AMMI}$ (%)
GE interaction/AMMI1	26	4715627.11	181370.27	3.75**	-
Altitude	17	2697613.54	158683.15	3.28**	57.21
Residue GE/AMMI1	9	2018013.57	224223.73	4.64**	-
Mean error[1]	216	-	48375.58	-	-

[1] Mean experimental error; number of degrees of freedom adjusted by the method of Cochran (1954), due to the heterogeneity among the residual mean squares
** significant at 1% probability

Table 7. Estimates of correlation (r) between environmental and genotypic variables and the scores of the first AMMI principal component interaction (IPCA1)

Environmental variables[1]	r	Genotypic variables[2]	r
Altitude	0.756**	NDF	0.030
Latitude	-0.200	NDM	0.612**
Maximum temperature	-0.602*	Powdery mildew	0.221
Minimum temperature	-0.118	End-of-cycle disease complex	0.790**
Total rainfall	0.531*	-	-
RR	0.173	-	-
Soil fertility	-0.546*	-	-
Powdery mildew	-0.132	-	-
ECD	0.495	-	-

** and *: Significant at 1and 5% probability, respectively, by the t test (Student)
[1] RR: Rainfall in the reproductive period of the crop (R1 the R7)
[2] NDF: Number of days to flowering; NDM: Number of days to maturation

variables maximum temperature, soil fertility and total rainfall were most strongly associated to the GE interaction pattern (Table 7).

The following genotype variables were correlated with the IPCA1 component: days to maturation and reaction to end-of-cycle diseases (Table 7). It may be concluded that the duration of the physiological cycle of the crop and the resistance to these diseases are genetic factors related to the GE interaction pattern, in particular, to the set of genotypes and environments under evaluation. Similar results were reported by Zobel et al. (1988).

Given the importance of the GE interaction for cultivar recommendation and for the planning of the experimentation network, we reinforce the advice of literature that the characterization of the test environments should be continuously complemented (Kang and Gauch 1996, Chaves 2001). The same applies for the genotypes. Only this way it will be possible to make headway in the understanding of such an important and complex phenomenon as the GE interaction.

CONCLUSIONS

1. Among the evaluated environmental variables the altitude, maximum temperature and soil fertility were the factors which, separately, most influenced the GE interaction.

2. The evaluated genotypic variables that were most associated to the GE interaction were number of days to maturity and genotypic reaction to the of end-of-cycle diseases complex.

3. The commercial cultivars FT-2000, Conquista, Emgopa 315 and MSOY 8001 were especially adapted to higher altitudes, while most of the experimental lines showed specific adaptation to lower altitudes.

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Fatores ambientais e genotípicos associados à interação de genótipos com ambientes em soja

RESUMO - *O objetivo deste trabalho foi quantificar a influência de algumas variáveis ambientais e genotípicas sobre a interação genótipo x ambiente (GxA) em soja. Foram utilizados dados de produtividade média de dezoito genótipos testados em onze experimentos no Estado de Goiás, os quais foram submetidos à análise AMMI. Para identificação de variáveis ambientais e genotípicas relacionadas com a interação GxA, estimaram-se correlações lineares simples entre as médias dessas variáveis e os escores do primeiro componente principal de interação (IPCA1). Realizaram-se também análises sucessivas de regressão linear simples, via procedimento* stepwise, *buscando relacionar as interações GxA de cada genótipo com os fatores ambientais observados. A altitude, temperatura máxima, incidência de doenças de final de ciclo, precipitação total e fertilidade do solo foram os fatores que, isoladamente, mais influenciaram a interação GxA. As variáveis genotípicas mais associadas à interação GxA foram dias para maturação e reação ao complexo de doenças de final de ciclo.*

Palavras-chave: *Glycine max*, análise AMMI, variáveis ambientais, adaptação produtiva.

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