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ARTICLE

Epistatic effects on grain yield of soybean [*Glycine max* (L.) Merrill]

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Abstract – *Studies addressing the estimation of genetic parameters in soybean have not-emphasized the epistatic effects. The purpose of this study was to estimate the significance of these effects on soybean grain yield, based on the Modified Triple Test Cross design. Thirty-two inbred lines derived from a cross between two contrasting lines were used, which were crossed with two testers (L_1 and L_2). The experiments were carried out at two locations, in 10 x 10 triple lattice designs with 9 replications, containing 32 lines (P_i), 64 crosses (32 P_i x L_1 and 32 P_i x L_2) and controls. The variation between ($\overline{L}_{1i} + \overline{L}_{2i} - \overline{P}_i$) revealed the presence of epistasis, as well as an interaction of epistasis* x *environment. Since the predominant component of epistasis in autogamous species is additive x additive (i type), we suggest postponing the selection for grain yield to later generations of inbreeding in order to exploit the beneficial effects of additive x additive epistasis.*

Key words: *Gene action, modified triple test cross, epistasis × environment interaction.*

INTRODUCTION

In soybean breeding programs [*Glycine max* (L.) Merrill], inbred lines are developed in a continuous process to release new cultivars, which is one of the strategies that has contributed most to increase yield and sustainability in modern agriculture. Most of the traits with an economic impact on the different species are quantitative. Genetic studies are usually based on a simplified model that defines the phenotypic value as a result of the genotypic plus the environmental effect. Johannsen was the first to demonstrate that the observed phenotypic variation results from the combined effect of genetic variation and environmental variation (Allard 1971), so that the environmental effect always represents an uncertainty factor in the estimation of genetic parameters (Ramalho et al. 2000).

With the advancement of quantitative genetics, the population structure was better understood by the genetic components of variation, resulting from the allelic and non-allelic action and interaction (epistasis). The term epistasis was first proposed by Bateson (1909) to designate the interaction between alleles from different loci. In 1918, Fisher partitioned the genetic variance in additive (average effects of alleles), dominant (interactions between alleles of the same locus) and epistatic (interactions between alleles of different loci), of which the latter was considered the most complex for trait inheritance studies (Fisher 1984). According to Bernardo (2002), epistatic effects exist when the sum of the individual effects of the loci are larger or smaller than the overall effect thereof; in other words, in the absence of epistatic effects, a single additive-dominant model would fully explain the expression of a character. On the other hand, when epistasis is present, it can bias the estimates of additive and dominant genetic components, resulting in inaccurate estimates of important genetic parameters, such as heritability and expected response to selection.

Although epistasis is already known since the first genetic studies, discussions about the importance for quantitative traits have repeatedly emerged in the literature, without consistent results. Currently, there is a growing interest in epistasis, mainly because the epistatic effects are involved in the genetic basis of heterosis and inbreeding depression (Primomo et al. 2005). For autogamous species, the most important are possibly the additive x additive epistatic effects, since inbred lines are developed by natural and artificial selection.

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There are many examples of epistasis for qualitative traits, but this does not apply to the quantitative traits, where relatively complex designs are required to detect epistasis. Mather (1949) proposed a method based on the analysis of generation means; however, the additive, dominant and epistatic genetic effects that constitute the model cannot be tested independently, preventing an individual interpretation of each effect. The method of Cockerham (1954) allows testing the genetic effects of the model independently; however, for being based on variance components, the error is larger than of the mean components. Moreover, the method involves a more complex genetic-statistical approach, limiting its applications. The Triple Test Cross (TTC) design proposed by Kearsey and Jinks (1968), which is a modification of the "North Carolina III" design, has been widely used because it allows an accurate detection of the presence of epistasis, regardless of the allele frequency, inbreeding level and occurrence of linkage disequilibrium in the population. Later, Jinks et al. (1969) proposed a modification, known as Modified Triple Test Cross, which is better suited for autogamous species.

The importance of epistasis has been reported in several species for many economically important traits, e.g. yield, using the TTC or Modified TTC, especially in recent years. However, few papers deal with epistasis in soybean. In addition, few studies have addressed the interaction between epistatic effects and environments. The purpose of this work was to study the epistatic influence on grain yield and the epistasis x environment interaction in soybean.

MATERIALS AND METHODS

The plant material used in this experiment consisted of inbred lines of a soybean population derived from the cross between lines PI-123439 and PI-239235. From the F_2 generation of this cross, the population was inbred without selection, by the single-seed descent (SSD) method up to generation F_8, to develop a set of completely inbred lines. From this population, 32 lines were randomly chosen (P_i, with $i = 1, 2, ..., 32$) and two others were selected (the most contrasting for grain yield) as testers (L_1 and L_2), according to the Modified TTC method (Jinks et al. 1969).

The 32 lines were crossed with the two testers, i.e., 32 ($P_i \times L_1$) crosses and 32 ($P_i \times L_2$) crosses, resulting in a total of 64 crosses. From the F_1 seeds, the F_2, F_3 and F_4 generations were obtained for the 64 crosses, by harvesting all plants of each cross in bulk. This procedure was applied to increase the number seeds of each cross, and allows performing experiments with a large number of replications. For this purpose, the experimental evaluations were carried out in the F_4 generation.

In the 2006/7 growing season, experimental evaluations were carried out at two locations: Location 1: Experimental Station of the Department of Genetics, in Piracicaba, São Paulo, and Location 2: Experimental Station of Anhumas, in Piracicaba, São Paulo, both of which belong to the Department of Genetics, ESALQ/USP. These locations differ primarily in the soil type (Location 1-clay soil, and Location 2- sandy soil).

A 10 x 10 triple lattice design (nine replications) was used, with 100 treatments: 32 ($P_i \times L_1$) crosses and 32 ($P_i \times L_2$) crosses; 32 original lines (P_i); two commercial controls (IAC-100 and IAC-8); plus two experimental lines. The last two were only included to complete 100 treatments. The plots consisted of 2-m-rows spaced 0.5 m apart, with 35 plants each after thinning. The grain yield (GY) was evaluated in g $plot^{-1}$ at maturity.

The experimental data were subjected to analysis of variance by location and then to combined analysis of variance, according to the following mathematical model, in which the treatment effect was considered as random and the location effect as fixed: $Y_{ijkl} = \mu + t_i + r_{j(l)} + b_{k(jl)} + l_l + tl_{il} + \varepsilon_{ijkl}$, where Y_{ijkl} is the observed value of treatment i in block k of replication j at location l; μ is the general mean; t_i is the effect of treatment i, with i varying from 1 to 100; $r_{j(l)}$ is the effect of replication j within location l, with j ranging from 1 to 9; $b_{k(jl)}$ is the effect of block k within replication j and location l, with k ranging from 1 to 10; l_l is the effect of location l, with l ranging from 1 to 2; tl_{il} is the interaction effect of treatmenti i and location l; and ε_{ijkl} is the experimental error associated with the plot $ijkl$. In all analyses, the grain yield (GY) data were corrected according to the stand (number of surviving plants per plot).

Then, the treatment means were subjected to analysis of variance according to the modified TTC method (Jinks et al. 1969). This method tests epistasis based on the variance between ($\overline{L}_{1i} + \overline{L}_{2i} - \overline{P}_i$) for $i = 1, 2,... 32$, where L_{1i} is the mean of the cross of the i^{th} line with tester L_1; L_{2i} is the mean of the cross of the i^{th} line with tester L_2; and P_i is the mean of the i^{th} line *per se*. As there are 32 contrasts, the mean square has 31 degrees of freedom and is tested with the error of the analysis of variance. If the variation between these contrasts is non-significant, the conclusion is that there is no epistasis, whereas significance of the variation between the contrasts shows the existence of epistasis; in this second case, the genetic variances estimated by the additive-dominant model may be biased (Jinks et al. 1 969).

The original methodology is based on the evaluation of the crosses (L_{1i} and L_{2i}) in the F_1 generation, but in this study the F_4 generation was assessed. The progeny means in the F_4 generation, based on a model of two loci with two alleles (data not shown), indicated that only the coefficients of the dominant component changes by inbreeding (from 1 in F_1 to 1/8 in F_4), in other words, the detection of epistasis was not impaired.

Following the recommendation of Ketata et al. (1976), the *t*-test was also used to compare the significance of the overall mean of the epistatic deviations, based on the contrasts among populations. According to these authors, the reason is that when ($\overline{L}_{1i} + \overline{L}_{2i} - \overline{P}_i$) for $i = 1, 2, ..., n$, have similar magnitudes and equal sign, the *F* test cannot detect the presence of epistasis. The *t*-test is performed using the error degrees of freedom of the analysis of variance.

RESULTS AND DISCUSSION

The experimental precision of the experiments at both locations was satisfactory, with coefficients of experimental variation (CV%) for GY (Table 1) similar to those reported in the literature for the same plot size used in this study (Barona et al. 2009, Colombari-Filho et al. 2010). The overall mean was 144.1 g plot^{-1} for Location1 and 203.4 g plot^{-1} for Location 2, which is the reason for the higher CV% at Location 1 (32.3%) than at Location 2 (23.6%), since the mean squares of the error of both locations were similar. This difference between locations can also be shown in the control (IAC-100 and IAC-8) means, which were about 20% higher at Location 2.

Table 1. Analysis of variance for grain yield (GY, g plot^{-1}) of soybean at two locations. Modified Triple Test Cross design, assessed in two 10 x 10 triple lattice experiments with nine replications

Sources of variation	Location 1			Location 2		
	df	MS		df	MS	
Replications (R)	8	20,267.0	**	8	68,991.0	**
Blocks/R	81	2,705.0		81	9,401.6	**
Treatments	-		-	-	-	
Crosses (L_{1i})	31	9,609.6	**	31	8,568.9	**
Crosses (L_{2i})	31	4,523.9	**	31	5,525.0	**
Lines (P_i)	31	10,037.0	**	31	17,827.0	**
Intra-block error	686	2,174.9		676	2,432.9	
Mean		144.1			203.4	
CV%		32.3			23.6	
IAC-100		203.6			237.8	
IAC-8		106.9			127.0	

** significant ($p \leq 0.01$) by the *F* test, respectively.

Significant differences ($p \leq 0.01$) among treatments were observed at both locations (Table 1). When the variation among treatments was partitioned in crosses L_{1i}, crosses L_{2i} and lines P_i, the occurrence of significant differences ($p \leq 0.01$) for GY was observe d at both locations for all sources, indicating the occurrence of high variability for crosses and lines considered. This variation can be easily observed by the treatment means (Table 2). The means of the 32 lines ranged from 729 - 2,318 kg ha^{-1} (Location 1) and 650 - 2,921 kg ha^{-1} (Location 2). For crosses with Tester 1, means ranged from 847 - 2,488 kg ha^{-1} (Location 1) and 1,702 - 3,331 kg ha^{-1} (Location 2), while for the crosses with Tester 2 means ranged from 888 - 1,899 kg ha^{-1} (Location 1) and 1,543 - 2,386 kg ha^{-1} (Location 2).

Table 2. Means, in kg ha^{-1}, of 32 soybean lines ($\overline{P}_i$), 32 crosses of the lines with tester 1 ($\overline{L}_{1i}$), 32 crosses of the lines with tester 2 ($\overline{L}_{2i}$) and controls, at both locations, assessed in two 10 x 10 triple lattice design, with nine replications

Lines	Location 1			Location 2		
	$\overline{P}_i$	$\overline{L}_{1i}$	$\overline{L}_{2i}$	$\overline{P}_i$	$\overline{L}_{1i}$	$\overline{L}_{2i}$
1	729.0	1,327.8	1,279.3	1,802.1	2,091.3	2,076.0
2	1,314.1	1,700.9	1,270.1	1,732.5	1,796.7	2,359.2
3	1,811.5	2,073.4	1,418.8	1,898.7	2,018.9	2,102.7
4	1,158.8	1,595.6	1,288.3	1,447.3	2,156.3	1,596.2
5	1,380.9	1,180.9	1,259.4	2,210.4	2,258.0	2,357.2
6	1,456.7	1,533.0	1,443.8	1,751.6	1,964.6	1,977.6
7	1,303.0	1,162.7	947.1	1,872.7	2,228.0	2,144.3
8	1,131.1	2,018.8	1,092.7	1,807.2	2,468.7	1,543.5
9	992.3	1,618.8	1,288.0	1,508.5	2,026.3	2,062.3
10	1,466.1	1,634.3	1,104.8	1,950.6	2,691.7	2,006.2
11	1,568.4	1,989.1	1,374.3	1,961.8	1,837.0	1,902.1
12	1,557.5	1,609.5	1,173.2	1,475.6	2,510.9	1,974.6
13	1,099.7	1,715.8	1,458.7	1,838.1	2,077.1	2,313.9
14	1,465.8	1,804.3	1,037.6	924.4	2,073.8	1,973.0
15	1,207.8	1,653.7	1,143.9	650.2	2,155.9	1,988.5
16	1,608.6	1,277.2	1,326.6	2,306.8	2,256.7	2,011.0
17	1,050.4	1,355.9	1,072.5	1,671.1	2,325.0	1,607.8
18	1,297.1	1,679.3	888.0	1,765.0	2,161.7	1,832.9
19	1,384.9	1,273.9	1,542.5	2,162.0	1,789.7	1,621.1
20	786.6	1,453.5	1,275.5	1,679.4	1,743.3	1,552.0
21	1,393.4	1,656.9	1,406.2	2,216.6	2,033.6	1,802.3
22	1,195.2	847.7	1,899.6	2,301.9	2,191.3	2,373.8
23	1,316.1	2,001.7	1,422.3	2,376.8	2,716.9	1,891.2
24	1,336.6	1,284.2	1,235.4	1,797.5	1,877.4	1,961.1
25	1,883.3	1,412.9	1,534.6	2,921.8	1,702.9	1,957.0
26	1,551.2	1,481.6	1,397.8	2,164.7	2,430.4	1,774.6
27	2,205.4	2,272.2	1,886.4	2,695.0	3,331.6	1,770.7
28	1,753.2	1,718.8	1,869.2	2,685.4	2,190.5	2,386.1
29	2,318.6	1,631.9	1,331.4	2,601.7	2,478.7	1,937.9
30	1,399.8	2,488.1	985.5	2,109.2	2,281.6	1,571.7
31	817.8	1,922.6	1,428.2	1,876.2	2,486.7	2,260.7
32	1,531.4	1,443.8	1,113.3	2,418.0	2,074.9	1,897.9
IAC-100	2,036.5	-	-	2,378.0	-	-
IAC-8	1,069.5	-	-	1,270.0	-	-

In the combined analysis of variance (Table 3), significant differences ($p \leq 0.01$) between locations were detected, which are easily observed by the differences between the means of the populations and controls at both locations (Table 1). The occurrence of significant differences ($p \leq 0.01$) for the treatment effect of three types of populations was also observed, as already noted in the individual analyses. The interactions of the crosses (L_{1i} and L_{2i}) and lines (P_i) with locations were highly significant ($p \leq 0.01$), showing that the performance of crosses (L_{1i} and L_{2i}) and lines (P_i) was not consistent in both locations, indicating an already well-known fact: the occurrence of genotype x environment interaction, common in plant breeding. This fact is evident when comparing the means of the two locations (Table 2).

Table 3. Combined analysis of variance (two locations) of grain yield (GY, in g plot^{-1}) in soybean. Modified Triple Test Cross design, assessed in two 10 x 10 triple lattice experiments, with nine replications

Sources of variation	df	MS	
Locations (L)	1	1,532,940.0	**
Replications (R)/L	16	44.629.0	**
Blocks /R/L	162	6,053.3	**
Treatments (T)	-	-	
Crosses (L_{1i})	31	12,680.0	**
Crosses (L_{2i})	31	6,058.1	**
Lines (P_i)	31	18,840.0	**
T x L	-		-
Crosses (L_{1i}) x L	31	5,344.2	**
Crosses (L_{2i}) x L	31	3,423.3	**
Lines (P_i) x L	31	6,306.7	**
Mean intra-block error	1,362	2,302.9	
General mean		173.62	

** significant at $p \leq 0.01$ by the *F* test.

In the analysis of variance of epistasis (Table 4), significant differences ($p \leq 0.01$) were detected for GY, indicating the occurrence of epistasis in the expression of this trait, which was reinforced by the significance of the *t* test, which tests the deviation of total epistasis. Therefore, results indicate that epistasis cannot be excluded from the model to estimate the genetic variance for GY in soybean (Jinks et al. 1969) or that the genetic variance for GY in soybean cannot be explained by only one additive-dominant model.

In the breeding of autogamous species, where the objective is to obtain inbred lines, additive x additive epistasis (*i* type) is possibly the most important because it is fixable in homozygous genotypes, contributing to the superiority of elite lines (Cockerham 1954, Goldringer et al. 1997). In this study, highly homozygous lines were used, which allows the conclusion that the detected epistasis is additive x additive (*i* type). Consequently, we suggest postponing the selection for grain yield to later generations of inbreeding (F_5 or F_6) in order to exploit the beneficial effects of additive x additive epistasis.

Table 4. Analysis of variance of epistasis for grain yield (GY, g plot^{-1}) of soybean at two locations, according to a Modified Triple Test Cross design

Sources of variation	Location 1			Location 2		
	df	MS		df	MS	
Epistasis	31	5,551.0	**	31	9,047.2	**
Error	686	2,174.9		676	2,432.9	
Deviation from total epistasis‡		154.8	**		220.1	**

** significant at $p \leq 0.01$ by the *F* test; ‡ significant at $p \leq 0.01$ by the *t* test.

Studies on the genetic variation in soybean using inbred lines, segregating populations, molecular markers (QTL) and several genetic analysis models (generation means, scaling tests and diallel crosses), among others (Toledo et al. 2000, Gravina et al. 2004, Vollmann et al. 2005, and Primomo et al. 2005), showed that additive variance is the main component of genetic variation, with a contribution of 60 - 90% for most agronomic traits, but that a large proportion is attributed to additive x additive epistatic variance (*i* type). According to Bernardo (2002), although the epistatic variation is present, there are certain difficulties to separate it from additive and dominance variation because it is smaller and the error associated with its estimation higher, compared to the error of additive and dominant variances.

The occurrence of epistasis for GY using the TTC or Modified TTC designs has been reported for other species, e.g., wheat (Ketata et al. 1976, Singh 1981), maize (Wolf and Hallauer 1997, Parvez et al. 2006), mung bean (Khattak et al. 2001, Khattak et al. 2002), cotton (Silva and Alves 1983, Bhatti et al. 2006), peanut (Upadhyaya and Nigam 1999), rice (Saleem et al. 2005, Subbsaraman and Ranagasamy 1989), flax (Sood et al. 2007), common bean (Moreto et al. 2012), soybean (Barona et al. 2009), and *Arabidopsis thaliana* (Kusterer et al. 2007). Interestingly, most of these studies were published in recent years.

The effect of locations was significant ($p \leq 0.01$), indicating that the expression of GY depends on non-allelic interactions and that these two locations differed in the expression of epistasis (Table 5). Furthermore, epistasis x environment interaction was significant ($p \leq 0.01$) and therefore the sensitivity or non-consistent performance of epistasis of the GY-related loci between locations. It is noteworthy that interactions with environments depend on the number of loci involved in the trait inheritance, i.e., the higher the number of involved loci, the greater the possibility of environmental influence on trait expression, which

Table 5. Combined analysis of variance (two locations) of epistasis for grain yield (GY, in g plot^{-1}) in soybean, according to a Modified Triple Test Cross design

Sources of variation	df	MS	
Location (L)	1	204,575.8	**
Epistasis (E)	31	8,584.5	**
E x L	31	6,013.8	**
Mean error	1,362	2,302.9	

** significant at $p \leq 0.01$ by the *F* test.

is characteristic of quantitative traits. Also, mechanisms involved in the expression of a complex trait such as GY may differ, according to the environment. Thus, if the loci that determine GY in soybean participate in adaptation and interact with the particular environment, then epistasis will be environmentally variable and this could therefore be a possible explanation for the strong epistasis × environment interaction detected in this study.

Changes in the relative magnitudes of the variance components (additive, dominant and epistatic) between different environments can occur if the loci that determine the trait have different sensitivities for the environments considered (Jinks and Perkins 1970). Goldringer et al. (1997) estimated the epistatic variance for GY in wheat in two years and found that the interaction of epistasis with years was more consistent than the interaction of additive variance with years. Upadhyaya and Nigam (1999) reported the presence of epistasis for yield in peanuts in several environments and also found that the epistasis x environment interaction was more pronounced than interactions of additive and dominant effects with environments. Perkins and Jinks (1971) stated, for plant height in tobacco, that *i* type epistasis (additive x additive) is more sensitive to environmental effects than *j* type epistasis (additive x dominant). Variations in the pattern of epistasis x environment interaction between different traits were also reported by Khattak et al. (2002).

Although there are few reports on the epistasis x location interaction using TTC, the surveys conducted in various crops suggest that the results obtained may change across years and locations because of epistasis x environment interactions and that a series of experiments would be required to improve the efficiency of plant breeding procedures (Jinks et al. 1969, Ketata et al. 1976, Tefera and Peat 1997, Sood et al. 2007).

The results of this study therefore indicate that epistasis is present in yield expression in soybeans and, furthermore, that it interacts with environments, i.e., its expression is not consistent in different environments. Consequently, the genetic variance of this trait cannot be explained only by an additive-dominant model. In view of these facts, we suggest postponing the selection for grain yield to later generations of inbreeding as well as evaluating the inbred lines across several environments, to exploit the beneficial effect of additive x additive epistasis in each test environment of soybean breeding programs.

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Efeitos epistáticos para produção de grãos em soja [*Glycine max* (L.) Merrill]

Resumo - *Efeitos epistáticos não têm sido muito enfatizados em estudos envolvendo a estimação de parâmetros genéticos em soja. O presente trabalho teve por objetivo estimar a significância destes efeitos na produção de grãos para esta cultura utilizando-se o delineamento Triple Test Cross Modificado. Utilizaram-se 32 linhagens derivadas do cruzamento entre duas linhagens contrastantes, as quais foram cruzadas com dois testadores (L_1 e L_2). Os experimentos foram conduzidos em dois locais, em delineamentos em látice triplo 10 x 10 com nove repetições, contendo 32 linhagens (P_i), 64 cruzamentos (32 P_i x L_1 e 32 P_i x L_2) e testemunhas. A variação entre (L_{1i} + L_{2i} - P_i) revelou a presença de epistasia, bem como a ocorrência de interação epistasia x locais. Como em espécies autógamas o componente predominante de epistasia é aditiva x aditiva (tipo i), recomenda-se que a seleção para a produção de grãos seja feita em gerações mais avançadas de endogamia, para capitalizar os efeitos positivos deste tipo de epistasia.*

Palavras-chave*: A*ção gênica, *triple test cross modificado, interação epistasia x ambientes.*

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