Genetic analysis of soybean resistance to *Cercospora sojina* Hara

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ABSTRACT

The genotypic variability of the resistance to *Cercospora sojina* can be used in breeding programs to develop soybean resistant cultivars. The characterization of progenitors and the genetic system involved allow the breeder to select the best progenitors, breeding method and selection procedure to be used. In this study a diallel of four soybean cultivars including the parents and all possible hybrids but the reciprocals were tested. Three resistant cultivars (Cristalina, Paraná and Uberaba) and a susceptible one (Bossier) and their F_1 populations were inoculated with the monosporic isolate identified as race 4. Results demonstrate that the resistance to *C. sojina* is controlled by a dominant gene or a gene-block; additive genetic effect and dominance are involved; the contribution of the environmental variation is minimum; and the interaction among the genes ranges from the partial to the complete dominance type, depending on the characteristic used in the evaluation of the resistance.

KEY WORDS: Diallel, frogeye leaf spot, *Glycine max*, resistance.

INTRODUCTION

The Frogeye Leaf Spot caused by the fungus *Cercospora sojina* Hara is one of the most important soybean (*Glycine max* (L.) Merrill) diseases in Brazil, and has caused great losses in several regions in the country. The development of new cultivars resistant to C. *sojina* is a priority in breeding programs, since this is the most efficient and economical method of control.

The genotypic variability of resistance to *C. sojina* may be used in breeding programs to help the development of resistant soybean cultivars. The selection performed on segregating generations derived from hybridizations is a common practice in soybean improvement programs, although the selection efficiency depends on the nature of the genetic system involved and on the degree in which the environment influences the expression of a given characteristic. The knowledge of the type and importance of the gene effects will help the breeder to choose the best selection procedure, improvement method and segregating population management. Higher genetic gains are expected with this information than with the empirically improvement methods based solely on the breeder's observation ability.

Diallel analysis is one of the biometric methods used in genetic analysis. It allows the evaluation of the genetic system that controls the specific characteristic under study, provides the necessary information for selecting progenitors as well as the choice of an improvement method and of a selection procedure. The methodology of diallel-cross analysis proposed by Hayman (1954) has been used to obtain the understanding of the genetic control of quantitative characteristics in self-pollinated species, such as the obtained inheritance of quantitative characteristics in maize (Silva et al., 1992), pepper (Oliveira, 1997), white clover (Caradus et al., 1992), rice (Chaubey et al., 1994) and soybean (Arias et al., 1996).

This work aimed at studying the genetic control of resistance to *Cercospora sojina* Hara in soybean on a diallel-cross using the methodology proposed by Hayman (1954).

MATERIAL AND METHODS

Four soybean cultivars, which were selected based on their reactions to *Cercospora sojina* Hara, were crossbred under a diallel-cross system, and all the possible hybrids were obtained except for the reciprocals. Three resistant cultivars (Cristalina, Paraná and Uberaba) and a susceptible one (Bossier) were involved in the crosses.

The experiment was carried out in a greenhouse in a completely randomized design with ten treatments (parents and F_1's) and 26 replicates. The plants were evaluated 20 days after the pathogen artificial inoculation with a suspension of 40,000 conidia/mL. The obtaining, replication, maintenance, preparation and inoculation of the fungus were performed according to the methodology adapted by Braga (1987), Cordeiro (1986) and Veiga (1973). Based on the more infected plant leaflet, the following characters were evaluated: infection level based on the visual note (VN), number of lesions per leaflet (NLL), average lesion diameter (ALD), number of lesions per square centimeter (NLC), injured leaf area (ILA), percentage of the injured leaf area (PILA) and disease index (DI), (Cordeiro, 1986; Braga, 1987 and Martins Filho et al., 1990).

The genetic control of soybean resistance to *Cercospora sojina* Hara was analysed by the diallel analysis methodology proposed by Hayman (1954), under the assumption of homozygous progenitors, diploid segregation, absence of multiple allelism, independent genes distributed in the parents, absence of differences among reciprocal crosses and absence of interaction among non-allelic genes. The following statistics were estimated: $\hat{V}_{0L0}$ (progenitor variance), $\hat{V}_r$ (variance at the r-th line or column), $\hat{V}_{1L1}$ (average of variances in the lines or columns), $\hat{V}_{0L1}$ (variance of line averages), $\hat{W}_r$ (covariance of the progenitors and the r-th line), $\hat{W}_{0L01}$ (average of the covariances between progenitors and the r-th line) and $(M_{L1} - M_{L0})^2$, the squared difference between the total average (M_{L1}) and the progenitors average (M_{L0}). The adequacy of the data to the dominant-additive model was verified by evaluating the homogeneity differences $\hat{W}_r - \hat{V}_r$, by means of the following tests: 1) testing the significance of the slope (H_0:b=1 *vs* H_a:b≠1) of the linear regression of $\hat{W}_r$ on $\hat{V}_r$ by the t test, with p-2 degrees of freedom, where p is the number of progenitors involved in the diallel; and 2) weighing the average values of and by 45° rotation of the axis represented by these statistics and testing the slope of the linear regression after the rotation (H_0:b' = 0 *vs* H_a:b' ≠ 0) by the F (= t^2) test with 1 and p-2 degrees of freedom.

With the verification of the dominant-additive model sufficiency to explain the segregation pattern of the evaluated characteristics, the variance analysis was interpreted and the statistics obtained from the diallel table were used to estimate the components of the genetic variation $\hat{D}$, $\hat{H}_1$, $\hat{H}_2$, $\hat{h}^2$ and $\hat{F}$. On the model,

is the measure for the variation caused by the additive gene effects; and are the measures for the variation caused by dominance effects (theoretically, $\hat{H}_1 - \hat{H}_2 \geq 0$; if $\hat{H}_1 - \hat{H}_2 = 0$, the genes with positive and negative effects are present at equal frequency); is a measure for the variation caused by the dominance effects, referring to the squared difference between the average of the ½ n(n+1) elements of the diallel table and the average of progenitors; and is a measure of the average covariance between the additive and the dominance gene effects, working as an indicator of the allelic gene frequencies in the population. F is positive when the dominant alleles are more frequent, and negative when the recessive alleles are more frequent. The significance of the estimated variation components was evaluated by the t test at a 5% significance level, according to Singh and Chaudhary (1979). The standard deviations of each component were calculated according to Ferreira (1985).

Other functions between components of genetic variation were also used to estimate parameters and interpret some of the results. So, $(\hat{H}_1/\hat{D})^{1/2}$ is a measure of the average degree of dominance in all loci; $\hat{H}_2/4\hat{H}_1$ is a measure for the average value of the products of the positive and negative effect alleles frequencies at loci exhibiting dominance, with a maximum value of **0.25; $K_D/K_R = [(4\hat{D}\hat{H}_1)^{1/2} + \hat{F}] / [(4\hat{D}\hat{H}_1)^{1/2} - \hat{F}]$** is a measure of the type of allele in higher frequency, where estimates near 1 indicate equality between the number of dominant and recessive alleles in the progenitors; / is a measure of the gene or gene-block number controlling the characteristic and exhibiting some degree of dominance; $\hat{h}_A^2 = (\hat{D} - \hat{F} + \hat{H}_1 - ½\hat{H}_2)/(\hat{D} - \hat{F} + \hat{H}_1 - ½\hat{H}_2 + 2\hat{E})$ is a measure of the genotypic determination coefficient in a broad sense; and $\hat{h}_R^2 = (\hat{D} - \hat{F} + \hat{H}_1 - \hat{H}_2)/(\hat{D} - \hat{F} + \hat{H}_1 - ½\hat{H}_2 + 2\hat{E})$ is a measure of the genotypic determination coefficient in a narrow sense.

In addition, the regression of $\hat{W}_r$ on $\hat{V}_r$ was used to obtain two other important pieces of information: the average degree of dominance and the relative genetic constitution of the progenitors. So, in the case of overdominance the straight line will intercept the coordinate $\hat{W}_r$ below the origin; when complete dominance occurs, the interception will be at the origin; in the case of incomplete dominance, it will be above the origin; and in the absence of dominance, the straight line lies tangent to the limiting parabola established by $\hat{W}_r^2 = \hat{V}_{0L0} \hat{V}_r$. The position of the cultivars along the regression line will indicate if they have more dominant genes (when are near the

origin) or more recessive genes (when they are far from the origin), based on the principle that the parents concentrating the dominant genes present lower and values, when they are crossed to other parents. The correlation (r) between $\overline{Y}$ (the average of the parent values) and $\hat{W}_r + \hat{V}_r$, (the indicator of the relation between favorable alleles and dominance), was also calculated. When r is positive and close to 1, the dominant genes act predominantly towards diminishing the character. When r is close to –1, the dominant genes act in an opposite direction. The theoretical selection limit established upon a cultivar which is completely dominant, given by $\hat{Y}_D$, or recessive, given by $\hat{Y}_R$, for the segregating genes in the diallel was estimated by the regression of $\overline{Y}$ on $\hat{W}_r + \hat{V}_r$. All analyses were performed with the aid of the Genes software (Cruz, 2001).

RESULTS AND DISCUSSION

In this work, infection level was considered the most important indicator of soybean resistance to *Cercospora sojina* Hara. However, other characteristics related to resistance were also evaluated.

Table 1 contains the results of two different tests applied in order to check the adequacy of the additive-dominant genetic model to the data. The adequacy of the model is an essential condition considering the restrictions imposed for the validity of the diallel method used in the analysis (Hayman, 1954). The genetic model was validated by both tests for all the evaluated characteristics. Therefore the diallel analysis was performed to assess the genetics of soybean resistance to *C. sojina* Hara.

Estimates of the components of genetic and non-genetic variation for the evaluated characteristics are presented in Table 2. The signals of the estimated differences between the average of the ½ n(n+1) elements in the diallel table (M_{L1}) and the average of the parents (M_{L0}) indicate that the dominance deviations occur towards the lowest average values. This confirms what was expected, since the majority of the genes studied in plant reactions to a pathogen is dominant and tends to reduce the values of those characteristics related to resistance, given the scale used for their measurement. Besides dominance, the variation of additive nature also contributed to the genetic variability between parents and F_1, since most the dominance component $\hat{H}_1$ and the additive component estimates $\hat{D}$ were significantly different from zero (Table 2). The positive and significant estimate of $\hat{D} - \hat{H}_1$ for VN (Table 2) shows the greater importance of the additive effects upon this characteristic and indicates a partial dominance relation among the alleles of non-fixed genes. In fact, the average degree of dominance estimated by $\left(\hat{H}_1/\hat{D}\right)^{1/2}$ statistics is inferior to unity, and the regression straight line of $\hat{W}_r$ on $\hat{V}_r$ intercepts the ordinate above the origin (Table 3 and Figure 1). However, for the other characteristics, there was no predominance of one particular type of gene effect

Table 1. Tests for sufficiency of the genetic additive dominant model based on linear regression analysis of $\hat{W}_r$ on $\hat{V}_r$ for visual note (VN), number of lesions per leaflet (NLL), average lesion diameter (ALD), injured leaf area (ILA), percentage of the injured leaf area (PILA), number of lesions per square centimeter (NLC) and disease index (DI) according to Hayman (1954).

Characteristics	Regression $\left[\hat{W}_r = \frac{1}{4}(\hat{D} - \hat{H}_1) + \hat{b}\hat{V}_r\right]$		
	$\hat{b}$ [1/]	t (H_0:b=1) [2/]	F = t² (H_0:b'=0) [3/]
VN	1.0255 ± 0.15	0.17 ns	0.10 ns
NLL	0.9998 ± 0.23	-0.01 ns	0.05 ns
ALD	0.7489 ± 0.47	-0.53 ns	0.00 ns
ILA	0.9693 ± 0.11	-0.29 ns	0.03 ns
PILA	0.9490 ± 0.11	-0.45 ns	0.11 ns
NLC	0.9903 ± 0.22	-0.05 ns	0.03 ns
DI	0.9693 ± 0.10	-0.29 ns	0.03 ns

[1/]slope estimates ± standard deviation; ns: non-significant at 5% probability ([2/] by t test; [3/] by F test); [3/] F test, weighing the average values of $\hat{W}_r$ and $\hat{V}_r$ by 45° rotation of the axis represented by these statistics.

Table 2. Estimates of the components of genetic and non-genetic variations with their respective standard deviations and the differences between the averages of the $[n(n+1)]/2$ elements of the diallel table (M_{L1}) and of n cultivars (M_{LO}) for visual note (VN), number of lesions per leaflet (NLL), average lesion diameter (ALD), injured leaf area (ILA), percentage of the injured leaf area (PILA), number of lesions per square centimeter (NLC) and disease index (DI), obtained according to Hayman (1954).

Characteristics	Genetic and Environmental Components[1]							
	$\hat{D}$	$\hat{H}_1$	$\hat{H}_2$	$\hat{h}^2$	$\hat{F}$	$(\hat{D}-\hat{H}_1)$	$\hat{E}$	$M_{L1} - M_{L0}$
VN	2.74±0.15[2]	1.71±0.51[2]	1.26±0.45[2]	0.62±0.28[2]	2.05±0.39[2]	1.04±0.44[2]	0.01±0.07ns	-0.40
NLL	4316.10±419.51[2]	3548.24±1366[2]	2613.09±1230[2]	941.94±759.84ns	3660.71±1059[2]	767.86±1203ns	34.08±201.79ns	-15.60
ALD	0.03±0.01[2]	0.01±0.01ns	0.01±0.01ns	0.01±0.01ns	0.02±0.01[2]	0.01±0.01ns	0.00±0.01ns	-0.04
ILA	39.79±2.41[2]	40.90±7.84[2]	30.98±7.05[2]	24.67±4.36[2]	39.38±6.08[2]	-1.10±6.91ns	0.23±1.16ns	-2.49
PILA	118.03±8.06[2]	125.10±26.26[2]	95.79±23.63[2]	84.02±14.59[2]	116.82±20.36[2]	-7.06±23.12ns	1.13±3.88ns	-4.61
NLC	1.23±0.10[2]	0.90±0.33[2]	0.65±0.30[2]	0.24±0.19ns	0.92±0.26[2]	0.33±0.29ns	0.01±0.05ns	-0.25
DI	64.51±3.90[2]	66.31±12.71[2]	50.23±11.43[2]	39.99±7.06[2]	63.84±9.85[2]	-1.79±11.19ns	0.37±1.88ns	-3.18

[1] Estimates ± standard deviation, if appearing; [2] The estimate is significant at 5% probability; ns The estimates is non-significant at 5% probability.

Table 3. Estimates of the genetic parameters for the visual note (VN), number of lesions per leaflet (NLL), average lesion diameter (ALD), injured leaf area (ILA), percentage of the injured leaf area (PILA), number of lesions per square centimeter (NLC) and disease index (DI) obtained according to Hayman (1954).

Characteristics	Estimates of the genetic parameters									Average increasing order [1]	Dominance decreasing order
	$\left(\hat{H}_1/\hat{D}\right)^{1/2}$	$\hat{H}_2/4\hat{H}_1$	K_D/K_R	$\hat{h}^2/\hat{H}_2$	$\hat{h}^2_R$	$\hat{h}^2_A$	r	$\hat{Y}_D$	$\hat{Y}_R$		
VN	0.78	0.18	2.80	0.49	0.63	0.98	0.87	1.29	4.75	2(1.0), 3, 1, 4(4.60)	1, 2, 3, 4
NLL	0.91	0.18	2.76	0.36	0.54	0.98	0.89	4.13	149.34	2(0.0), 3, 1, 4(139.60)	1, 2, 3, 4
ALD	0.75	0.20	2.50	0.56	0.66	0.98	0.54	0.07	0.64	2(0.0), 3, 1, 4(0.35)	1, 2, 3, 4
ILA	1.01	0.19	2.91	0.80	0.39	0.98	0.97	0.66	13.93	2(0.0), 3, 1, 4(13.26)	1, 2, 3, 4
PILA	1.03	0.19	2.85	0.88	0.38	0.97	0.96	1.50	25.06	2(0.0), 3, 1, 4(23.08)	1, 2, 3, 4
NLC	0.85	0.18	2.56	0.37	0.61	0.97	0.83	0.11	2.53	2(0.0), 3, 1, 4(2.38)	1, 2, 3, 4
DI	1.01	0.19	2.91	0.80	0.39	0.98	0.97	0.84	17.73	2(0.0), 3, 1, 4(16.88)	1, 2, 3, 4

[1] (1) Paraná, (2) Cristalina, (3) Uberaba, (4) Bossier. The values within parenthesis refer to the characteristic average.

since was not significant (Table 2). For ILA, PILA and DI the estimates of evidenced interactions among the non-fixed alleles of complete dominance type, which was confirmed by the average degree of dominance estimate, $\left(\hat{H}_1/\hat{D}\right)^{1/2}$, near unity and the regression line of $\hat{W}_r$ on $\hat{V}_r$ intercepting the ordinate also near the origin (Tables 2 and 3; Figures 2, 3 and 4). Furthermore, for NLL, ALD and NLC the average degree of dominance lower than unity indicates a partial dominance among the non-fixed alleles, confirmed by the regression of on intercepting the ordinate above the origin (Table 3 and Figures 5, 6 and 7).

The estimates of ratios lower than 0.25 (Table 3) indicate that the frequency of positive and negative

alleles is asymmetric in the parent group. In Table 2, the estimates indicate that the average frequencies of dominant alleles in loci affecting the characteristics are higher than those of the recessive alleles, which is verified by K_D/K_R values higher than unity in Table 3, evidencing a higher frequency of dominant alleles in the parents. This result was already expected, since the crosses involved three resistant and one susceptible cultivar.

In Table 3, the estimates of $\hat{h}^2/\hat{H}_2$ statistics for VN and other evaluated characteristics indicate the presence of either a gene or a gene block which shows dominance. However, Cruz and Regazzi (1994) explain that these statistic estimates do not give good
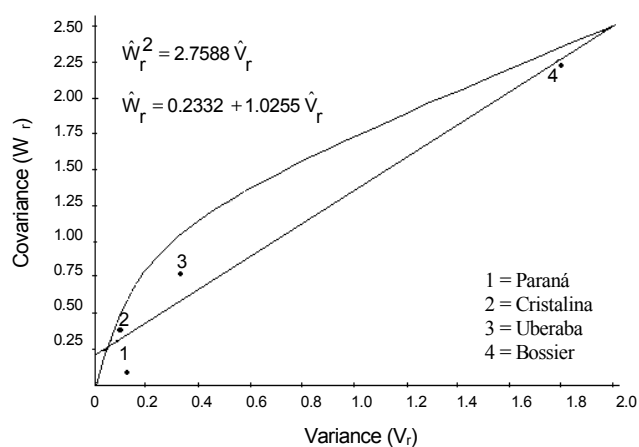
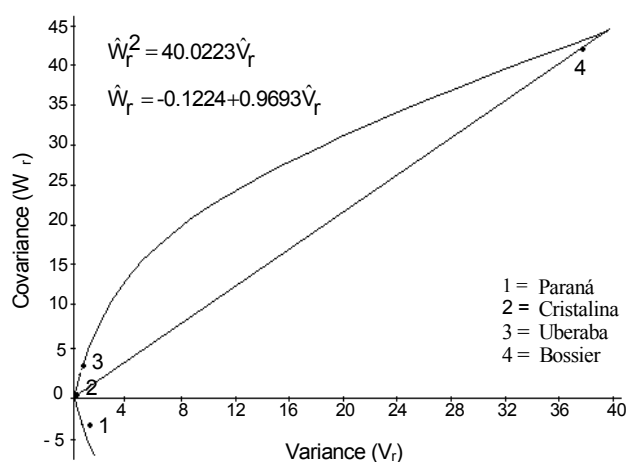**Figure 1.** Regression of $\hat{W}_r$ on $\hat{V}_r$ of the visual note (VN).

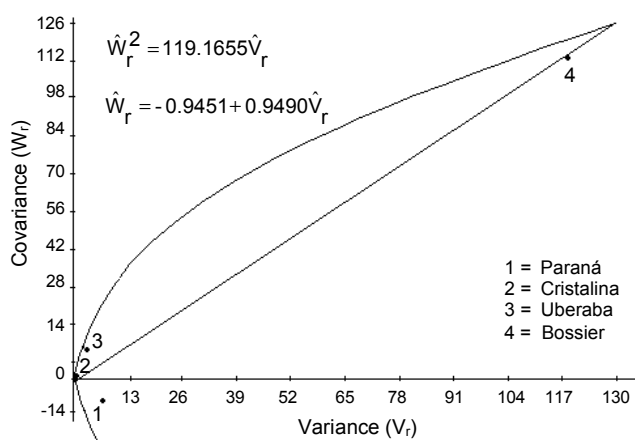**Figure 2.** Regression of $\hat{W}_r$ on $\hat{V}_r$ of the injured leaf area (ILA).

Figure 3. Regression of $\hat{W}_r$ on $\hat{V}_r$ of the percentage of the injured leaf area (PILA).

information when genes have little or no dominance, so the dominance should be considered as underestimated.

For all the evaluated characteristics, the positive and generally high-magnitude estimates of the correlation coefficient (r) between $\hat{W}_r + \hat{V}_r$ and the average of the parent cultivars (Table 3) indicate that the resistance to *C. sojina* Hara expressed by the lower averages is conditioned by dominant genes. Such a behavior may be confirmed by comparing the order of cultivar averages and of dominance estimates given by (Table 3 and Figures 1, 2, 3, 4, 5, 6 and 7). We could notice that while cultivars 1, 2 and 3 were resistant to the pathogen hence presenting reduced averages, they concentrated dominant genes (positioned closer to the origin of the regression of on graphic); cultivar 4, susceptible and hence with higher averages, concentrates recessive genes (positioned further from the origin of the regression of on graphic).

The reachable limits by selection in segregating populations derived from diallel, established by and , and presented in Table 3, indicate that it is possible to obtain pure lines which are resistant to *Cercospora sojina* Hara. This may be achieved by replacing those genes increasing the characteristic averages by their alleles, which diminish them, but neither of those lines will be better than "Cristalina" cultivar which does not present any symptom of the disease at all.

The broad-sense coefficients of genotypic determination estimates $(\hat{h}_A^2)$ were high for all characteristics, while those in the narrow sense $(\hat{h}_R^2)$ were generally low compared to those of broad sense (Table 3). In all the evaluated characteristics, the high magnitudes of $\hat{h}_A^2$ evidenced their low sensibility to the environmental variations. In fact, the component of the environmental variation was of no significance for all the $\hat{E}$ estimates (Table 2). The differences between and estimates reinforce that additive and dominant genes are affecting the resistance to the disease. Also, it should be emphasized that those values of and obtained from the studied population will only have some meaning when all of the gene set of the evaluated parental cultivars is used (Miranda, 1987).

The presence of the additive and dominant genetic variation in the evaluated characteristics of the studied population suggests that the genetic breeding programs for resistance to *C. sojina* Hara may be planned with reasonable success. In the case of
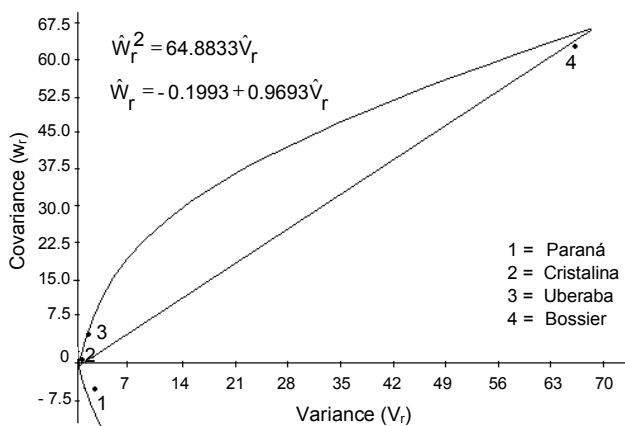
Figure 4. Regression of $\hat{W}_r$ on $\hat{V}_r$ of the disease index (DI).
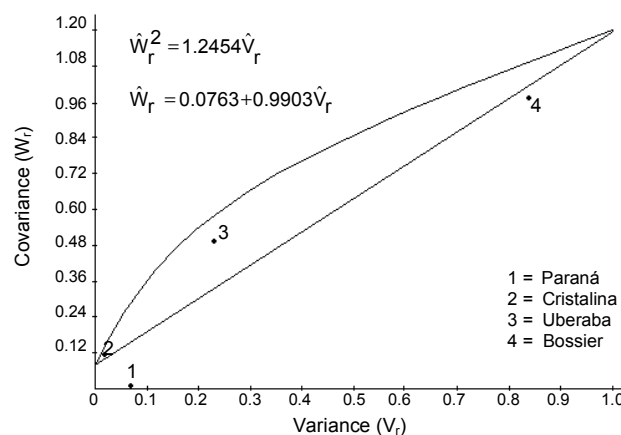

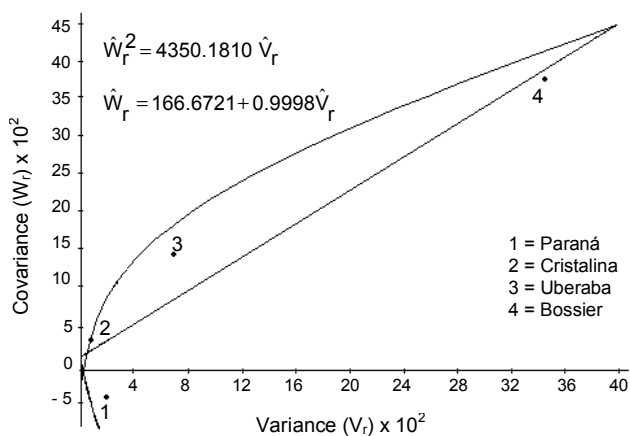**Figure 7.** Regression of $\hat{W}_r$ on $\hat{V}_r$ of the number of lesions per square centimeter (NLC).

Figure 5. Regression of $\hat{W}_r$ on $\hat{V}_r$ of the number of lesions per leaflet (NLL)
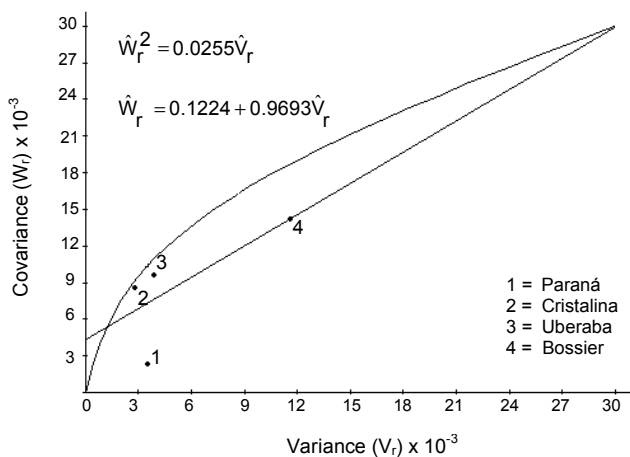

Figure 6. Regression of $\hat{W}_r$ on $\hat{V}_r$ of the average lesion diameter (ALD).

selection of pure lines for the resistance to the pathogen in segregating populations derived from diallel using the characteristics with partial and/or complete dominance, the results indicate that selection work may begin in the first segregating generation.

CONCLUSIONS

The additive-dominant genetic model is sufficient to evaluate the control of resistance to *Cercospora sojina* Hara in soybean and the contribution of the environmental variation is very small.

The resistance to *Cercospora sojina* Hara is conditioned by a dominant gene or a gene-block.

The average frequencies of dominant alleles in loci affecting the characteristics are higher than those of the recessive alleles.

The interaction among the genes ranges from partial to complete dominance type, depending on the characteristic used in the evaluation of the resistance.

It is possible to obtain pure lines which are resistant to *C. sojina,* and the selection may begin in the first segregating generation.

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RESUMO

Análise genética da resistência da soja a *Cercospora Sojina* hara

A variabilidade genotípica da resistência à *C. sojina* Hara pode ser usada num programa de melhoramento, com o objetivo de desenvolver cultivares de soja resistentes. A caracterização dos progenitores e o sistema genético envolvido permitem ao melhorista selecionar os melhores progenitores, o método de melhoramento e o procedimento de seleção a ser utilizado. Neste estudo foram testados em um sistema de cruzamentos dialélicos quatro cultivares de soja, incluindo os pais e todos os possíveis híbridos, excluindo os recíprocos. Três cultivares resistentes (Cristalina, Paraná e Uberaba) e um cultivar suscetível (Bossier) e a população F_1 originada destes cruzamentos, foram inoculados com um isolado monospórico, identificado como raça 4. Os resultados demonstram que a resistência ao patógeno estudado é governada por um gene dominante ou um bloco gênico; que estão envolvidos efeitos genéticos aditivos e de dominância, que a contribuição da variação ambiental é mínima e ainda, que a interação entre os genes é do tipo dominância parcial ou completa dependendo da característica utilizada na avaliação da resistência.

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