Genetic control of soybean resistance to brown spot (*Septoria glycines*): first studies

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ABSTRACT

Knowledge of the genetic effects that control a trait is essential to direct the breeding program for gains in the selection process. The main objective of this study was to investigate the genetic control of soybean resistance to brown spot. Two tolerant cultivars (FT-2 and Dourados) and two susceptible cultivars (Davis and Paraná) and the segregant F_2 and F_3 generations derived from the crosses between these cultivars were assessed for reaction to the disease after inoculation. Genetic models were adjusted to the means and variances of the generations. It could be concluded that the trait is governed by various genes with lesser effect, has low to medium heritability and selection should be made always using progeny from the F_3 generation and can be made during the initial stages of soybean growth, based on the mean of at least two trifoliate leaves.

KEY WORDS: Soybean, *Septoria glycines*, heritability, genetic effects.

INTRODUCTION

The occurrence of diseases in soybean has increased every year and has caused severe losses in the fields, requiring quick responses from research and in the development and application of control techniques. One of these diseases, that occurs from the beginning to end of the soybean cycle is the brown spot, caused by the *Septoria glycines* fungus, which is disseminated to all the Brazilian soybean producing regions, differing in importance from one region to another.

This disease occurs at the same period of Cercospora leaf blight caused by the *Cercospora kikuchii* fungus and due to the difficulties that individual assessments present, they are considered as a late season diseases complex. Therefore brown spot field assessments are not accurate and cannot be used for more detailed studies such as the study of genetic heritability. However, as septoriosis is also expressed early in the soybean cycle, a part of these problems can be solved by artificial inoculations made in a greenhouse and assessment of the genotypes at the initial growth stages. According to Arias et al. (1999) there is variability at this initial phase and it correlates with the soybean reaction at the end of the cycle.

No studies have been published on the genetic control of soybean resistance to this disease to date and this is the main objective of this study. Furthermore, disease assessment strategies and for carrying out the breeding program for resistance are defined.

MATERIAL AND METHODS

Two experiments were carried out in a greenhouse at Embrapa Soybean (Londrina, Paraná, latitude 23º22´S). Plants representing the F_2 and F_3 segregant populations were used, derived from the crosses between four soybean cultivars, two tolerant (FT-2 and Dourados) and two susceptible (Davis and Paraná). Each experiment consisted of 15 individuals of each parental line, 50 F_2 individuals and 30 F_3 families (each family represented by five individuals) of each cross distributed along a completely randomized design. The plot consisted of one plant. The seeds were sown in plastic 20 cm diameter pots and each pot contained two randomized genotypes in the experiment besides the genotype used as susceptibility standard (Davis). Inoculation was performed at the V_3-V_4 soybean growth stage by spraying a spore suspension at the concentration of 5 x 10^6 spores/ml. The level of infection was assessed at the first three trifoliate leaves, using a score scale from 0 to 10 (Brogin, 2001).

The data generated after the assessments were submitted to analysis of covariance, using the standard susceptibility cultivar as covariable in the statistic model, according to methodology by Steel and Torrie (1960). The data were then corrected for the covariable and the means and variances of each generation were calculated. The genetic models were fitted to the means and variances, according to methodologies proposed by Cavalli (1952), Hayman (1960) and Mather and Jinks (1982) using joint data of the two experiments, for each trifoliate leaf separately and also the mean of the trifoliate leaves.

Broad sense heritability based on the F_3 progeny was calculated from the components of variance of the F_3 families of each generation, using the formula:

$$h^2 = \sigma^2_g / (\sigma^2_g + \sigma^2/n)$$

where h^2 corresponds to heritability in the broad sense, σ^2_g to genetic variability, σ^2 to environmental variability and n is the harmonic mean of the number of individuals that form each one of the families in each generation. The estimates of these components of variation were obtained by analysis of variance of the F_3 progeny in each cross.

RESULTS AND DISCUSSION

The plants were assessed when the level of infection of the three trifoliate leaves of the standard susceptible cultivar was between six and eight. This interval was defined from data in preliminary experiments as the most suitable for assessment due to the greater differentiation among tolerant and susceptible genotypes (Brogin et al., 2000).

The variation of infection level in the plants of the standard suceptibility cultivar (Davis) both in the first and second experiment caused a significance of the covariable in the statistical model, justifying its use for correction of part of the environmental effects. The response to these micro-environmental variations was not uniform, and no direct relationship was observed between the regression coefficient estimates and reaction to the disease, in the different genotypes (Table 1). Therefore, a linear regression coefficient was used for each generation to correct the data for the covariable even when the coefficient was not significant. The data of each plant was corrected using the equation:

$$\hat{y}_{ijk} = y_{ijk} - \hat{\beta}_i(x_{ijk} - \bar{x})$$

where $\hat{y}_{ijk}$ corresponds to the estimated value of the score for the infection level in the trifoliate leaf of the k-eth individual, in the j-eth family of the i-eth generation after correction by the covariable; y_{ijk} is the score given in the assessment for the infection level in the trifoliate leaf of the k-eth individual, in

Table 1. Linear regression coefficients for the first, second and third trifoliate leaves, obtained by analysis for the covariable.

Generation	1º Experiment			2º Experiment		
	1º Trif.leaf	2º Trif.leaf	3º Trif.leaf	1º Trif.leaf	2º Trif.leaf	3º Trif.leaf
Parental						
Paraná	$0.20^{n.s.}$	$0.50^{2/}$	$0.87^{2/}$	$1.01^{2/}$	$-0.23^{n.s.}$	$-0.15^{n.s.}$
FT-2	$0.57^{n.s.}$	$0.25^{n.s.}$	$0.10^{n.s.}$	$0.50^{n.s.}$	$0.67^{n.s.}$	$0.23^{n.s.}$
Dourados	$-0.22^{n.s.}$	$0.08^{n.s.}$	$0.16^{n.s.}$	$0.37^{n.s.}$	$1.06^{2/}$	$0.11^{n.s.}$
Davis	$1.08^{2/}$	$1.04^{2/}$	$0.38^{n.s.}$	$0.04^{n.s.}$	$0.77^{n.s.}$	$0.28^{n.s.}$
F_2						
Paraná x FT-2	$0.73^{2/}$	$0.50^{2/}$	$0.42^{2/}$	$0.28^{n.s.}$	$0.20^{n.s.}$	$0.06^{n.s.}$
Paraná x Dourados	$0.49^{2/}$	$0.52^{2/}$	$0.39^{2/}$	$0.34^{1/}$	$0.32^{n.s.}$	$0.07^{n.s.}$
Paraná x Davis	$0.68^{2/}$	$0.71^{2/}$	$0.61^{2/}$	$0.12^{n.s.}$	$-0.06^{n.s.}$	$0.40^{1/}$
FT-2 x Dourados	$0.33^{1/}$	$-0.03^{n.s.}$	$0.25^{1/}$	$0.47^{2/}$	$0.22^{n.s.}$	$0.14^{n.s.}$
FT-2 x Davis	$0.46^{2/}$	$0.77^{2/}$	$0.37^{1/}$	$0.21^{n.s.}$	$0.24^{n.s.}$	$0.25^{n.s.}$
Dourados x Davis	$0.79^{2/}$	$0.57^{2/}$	$0.32^{1/}$	$0.74^{2/}$	$0.23^{n.s.}$	$0.36^{1/}$
F_3						
Paraná x FT-2	$0.42^{2/}$	$0.47^{2/}$	$0.37^{2/}$	$0.35^{2/}$	$0.31^{2/}$	$0.28^{2/}$
Paraná x Dourados	$0.48^{2/}$	$0.46^{2/}$	$0.37^{2/}$	$0.49^{2/}$	$0.45^{2/}$	$0.26^{1/}$
Paraná x Davis	$0.43^{2/}$	$0.55^{2/}$	$0.55^{2/}$	$0.27^{2/}$	$0.31^{2/}$	$0.23^{1/}$
FT-2 x Dourados	$0.32^{2/}$	$0.24^{2/}$	$0.29^{2/}$	$0.27^{2/}$	$0.29^{2/}$	$0.22^{1/}$
FT-2 x Davis	$0.55^{2/}$	$0.40^{2/}$	$0.32^{2/}$	$0.32^{2/}$	$0.37^{2/}$	$0.07^{n.s.}$
Dourados x Davis	$0.75^{2/}$	$0.51^{2/}$	$0.60^{2/}$	$0.48^{2/}$	$0.28^{2/}$	$0.17^{n.s.}$

^{ns}, $^{1/}$ e $^{2/}$: not significant at the 0.05 probability level and significant at the 0.05 and 0.01 probability levels, respectively, by t test.

the j-eth family of the i-eth generation; β_i is the estimated regression parameter of the i-eth generation; x_{ijk} is the value of the covariable corresponding to the k-eth individual in the j-eth family of the i-eth generation; and x is the general mean of the covariable in the experiment.

After correcting the data for the covariable, the means and the variances for each generation (parental, F_2, F_3) were obtained. Comparing these results with the original data analysis (data not presented) in all cases there was reduction in variance, that is, part of the microenvironmental effects were removed from the phenotypic variance of each generation. The values of the mean squares of the residues, obtained by analyses of variance of the data corrected for the covariable, were 5.77, 6.02 and 7.40 for the first experiment and 9.36, 7.12 and 7.34 for the second experiment respectively for the first, second and third trifoliate leaves. Therefore, the data from the first and second experiments could be analyzed together, because the homogeneity of variances of the residues for the three trifoliate leaves was ascertained. The coefficient of variation (CV%) for the first experiment ranged from 32.72% to 59.94% and in the second experiment, from 45.41% to 53.35%. All the genetic analyses were carried out using data from the joint analysis of the experiments.

Genetic Analyses

Table 2 shows the means, variances and degrees of freedom of the parental, F_2 and F_3 generations used to obtain the genetic parameters of mean and variance of the reaction to brown spot trait. This table presents the data for the three trifoliate leaves separately and the mean of the three trifoliate leaves.

All the fitted models presented degrees of freedom available for the model adherence test (χ^2) and were not significant (p>0.05) in any of the cases, indicating that the models were satisfactory to explain the variability found. All the genetic components of mean and variance of the fitted models were significant at the minimum probability level of 0.05 by the Student t test.

Mean Models

Significant additive effects [d] were detected in most of the crosses (Table 3) except for the crosses Paraná x Dourados and Paraná x Davis in the first trifoliate leaf, Paraná x Davis in the second trifoliate leaf and Paraná x Dourados in the third trifoliate leaf. With the use of the mean of the three trifoliate leaves, the additive effects estimated were significant in all the crosses. The largest [d] estimates were observed in the crosses involving the FT-2 cultivar with more susceptible cultivars (Paraná and Davis). Even in the cross between susceptible genotypes (Paraná x Davis), significant additive genetic effect was detected for the third trifoliate leaf and for the mean of the trifoliate leaves, indicating the presence of different susceptibility levels.

Non-allelic interaction of the additive x additive type [i] which indicates interaction among loci in homozygosis, was detected in the Paraná x FT-2 and FT-2 x Davis crosses in the first trifoliate leaf, presenting negative sign in both cases that indicates interaction between genes that results in the reduction of the infection level or that are dispersed in the parents; Paraná x FT-2 and Dourados x Davis in the third trifoliate leaf in the sense of reducing the trait in the cross Paraná x FT-2 and of increase in the Dourados x Davis cross. In the models fitted to the second trifoliate leaf no epistatic effects were observed in any of the crosses. Using the mean of the three trifoliate leaves to fit the models, this type of effect was detected in the Paraná x FT-2 and Paraná x Davis crosses both in the sense of reducing the infection level. The [i] magnitude was relatively higher in the Paraná x FT-2 cross while in Paraná x Davis both [d] and [i] were small. FT-2, considered tolerant to brown spot, when in hybrid combination with the susceptible cultivars Paraná and Davis, presented a tendency to reduce the infection level of the resulting progeny, probably because it has a greater number of genes that condition resistance to *S. glycines*. Although the Paraná cultivar is considered susceptible, it probably must possess genes that confer resistance because when crossed with the Davis cultivar, also susceptible, it presented significant interaction among homozygotic genes in the sense of reducing the infection level or these genes are dispersed in the parents. This did not happened with the Dourados cultivar that, although considered tolerant, probably has genes with lesser effects for resistance compared to FT-2.

The effects of dominance [h] were significant only for the Paraná x Davis cross in the first trifoliate leaf, and FT-2 x Davis, in the second trifoliate leaf, always with positive sign, that is, the dominance found was in the sense of increasing the infection level. For the third

Table 2. Joint degrees of freedom (d.f.), means ($\overline{x}$) and variances (Var.) for the two experiments, using data corrected to the covariable, for the trait infection level in the first, second and third trifoliate leaves and for the mean of the trifoliate leaves, in the parental, F_2 and F_3 generations of six soybean crosses.

Generation	1º Trif.leaf			2º Trif.leaf			3º Trif.leaf			Mean of the Trif.leaves		
	d.f.	$\overline{x}$	Var.	d.f.	$\overline{x}$	Var.	d.f.	$\overline{x}$	Var.	d.f.	$\overline{x}$	Var.
Parental[1/]												
Paraná (S)	23	7.30	6.13	27	6.08	4.38	27	5.59	7.16	27	6.32	2.45
FT-2 (T)	26	4.30	5.91	27	2.45	2.23	28	1.85	2.17	28	2.88	1.99
Dourados (T)	24	6.65	11.23	26	3.96	6.30	26	4.19	7.45	26	4.92	5.18
Davis (S)	24	7.75	5.02	24	6.26	2.93	24	7.80	4.39	24	7.27	2.29
F_2												
Paraná X FT-2	88	7.08	7.50	95	5.15	7.98	97	5.02	8.87	97	5.74	5.48
Paraná X Dourados	86	7.46	8.25	93	4.73	7.83	94	4.94	8.65	94	5.69	4.81
Paraná X Davis	96	8.45	3.79	97	6.52	6.50	95	6.67	7.29	97	7.22	2.75
FT-2 X Dourados	84	5.83	9.52	89	3.48	6.95	94	3.46	5.40	95	4.26	4.07
FT-2 X Davis	90	6.71	8.57	92	5.31	5.86	92	5.53	9.31	93	5.85	4.78
Dourados X Davis	91	6.77	6.91	91	4.94	7.35	91	5.12	8.40	91	5.61	4.34
F_3												
Paraná X FT-2												
Between	59	7.11	9.92	59	4.59	8.54	59	4.90	8.70	59	5.57	6.46
Within	212		7.13	225		6.63	223		7.90	230		4.23
Total	271		7.76	284		7.04	282		8.07	289		4.69
Paraná X Dourados												
Between	59	7.37	10.34	59	5.28	11.35	59	5.23	13.53	59	5.95	8.38
Within	209		6.84	226		6.95	223		8.09	227		4.03
Total	268		7.67	285		7.89	282		9.26	286		4.95
Paraná X Davis												
Between	59	8.17	6.07	59	6.65	6.30	59	6.91	6.77	59	7.24	2.59
Within	220		5.80	222		6.05	224		7.01	226		3.34
Total	279		5.86	281		6.10	283		6.96	285		3.18
FT-2 X Dourados												
Between	59	5.10	10.31	59	3.28	8.32	59	3.23	6.46	59	3.86	5.80
Within	205		9.07	220		4.95	224		4.95	228		3.56
Total	264		9.36	279		5.68	283		5.27	287		4.03
FT-2 X Davis												
Between	59	6.79	11.66	59	4.79	10.37	59	4.97	11.18	59	5.52	8.38
Within	216		7.81	223		7.68	220		7.88	226		4.93
Total	275		8.66	282		8.26	279		8.60	285		5.66
Dourados X Davis												
Between	59	6.53	8.80	59	5.12	9.47	59	5.27	11.71	59	5.64	6.61
Within	217		8.17	218		6.92	221		8.06	223		4.47
Total	276		8.31	277		7.48	280		8.85	282		4.93

[1/](S) and (T): respectively susceptible and tolerance to brown spot.

trifoliate leaf, no significant dominance effects were detected. Interaction among loci in heterozygosis [l] was not observed in any cross, corresponding to dominant x dominant interaction. For the mean of the three trifoliate leaves the dominance effect was significant only for the FT-2 x Davis cross in the sense of increasing the trait. The dominance sense increasing susceptibility of the plants to septoriosis indicates that this disease was not important in the evolutionary process of this species.

The simultaneous presence of the [d] and [h] components was observed only in the FT-2 x Davis cross, in the second trifoliate leaf and in the mean of the trifoliate leaves, among the fitted models for all the crosses. If the trait was monogenic, it could be stated that there is complete dominance among the alleles because there was no differences between the estimates of these two parameters indicating that [d] =[h]. However, as it is probably a polygenic trait, the [d] and [h] estimates are results of the algebraic sum of the effects of each one of the genes involved in the trait control and it cannot be stated with certainty that there is complete dominance. If the [d] estimate were lesser than that of [h], it could be stated that the genes are dispersed in the parents or that there is overdominance. However, these suppositions cannot be proved based only on the genetic means models, and should be analyzed together with the components of variance.

Models of Variance

In the models fitted to the first trifoliate leaf, single environmental effects (E) were detected in all the crosses and there was no interaction between genotype and microenvironment (E1 and E2) (Table 4). This did not occur in the models fitted to the second trifoliate leaf where this type of interaction was detected in most of the crosses except in the Dourados x Davis cross. For the third trifoliate leaf

Table 3. Genetic parameters fitted to the mean of the joint analysis of the experiments for the inflection level in the first, second and third trifoliate leaves and for the mean of the infection level in the three trifoliate leaves, in six soybean crosses.

Genetic parameters, χ^2 test, degrees of freedom and probability	Paraná X FT-2	Paraná X Dourados	Paraná X Davis	FT-2 X Dourados	FT-2 X Davis	Dourados X Davis
1º Trifoliate leaf						
m	7.10 ± 0.15	7.35 ± 0.14	7.70 ± 0.24	5.31 ± 0.15	6.77 ± 0.16	6.67 ± 0.14
[d]	1.50 ± 0.33	-	-	1.11 ± 0.37	1.73 ± 0.31	0.76 ± 0.36
[h]	-	-	1.62 ± 0.72	-	-	-
[i]	-1.30 ± 0.36	-	-	-	-0.74 ± 0.35	-
[l]	-	-	-	-	-	-
χ^2	0.01	1.28	0.99	3.88	0.05	2.63
d.f.	1	3	2	2	1	2
P	0.93	0.73	0.61	0.14	0.83	0.27
2º Trifoliate leaf						
m	4.65 ± 0.13	5.13 ± 0.14	6.59 ± 0.12	3.30 ± 0.12	4.32 ± 0.26	5.08 ± 0.14
[d]	2.06 ± 0.31	1.08 ± 0.45	-	0.80 ± 0.30	1.89 ± 0.32	1.15 ± 0.41
[h]	-	-	-	-	1.93 ± 0.83	-
[i]	-	-	-	-	-	-
[l]	-	-	-	-	-	-
χ^2	3.78	2.83	1.11	0.41	0.02	0.28
d.f.	2	2	3	2	1	2
P	0.15	0.24	0.78	0.82	0.88	0.87
3º Trifoliate leaf						
m	4.93 ± 0.15	5.12 ± 0.15	6.83 ± 0.13	3.25 ± 0.11	5.03 ± 0.13	5.23 ± 0.15
[d]	1.87 ± 0.30	-	1.08 ± 0.33	1.30 ± 0.25	3.05 ± 0.24	1.81 ± 0.34
[h]	-	-	-	-	-	-
[i]	-1.21 ± 0.33	-	-	-	-	0.76 ± 0.37
[l]	-	-	-	-	-	-
χ^2	0.12	4.60	0.75	1.37	3.34	0.19
d.f.	1	3	2	2	2	1
P	0.72	0.20	0.69	0.50	0.19	0.66
Mean of the three trifoliate leafs						
m	5.61 ± 0.11	5.84 ± 0.10	7.23 ± 0.09	3.95 ± 0.10	5.10 ± 0.17	5.70 ± 0.10
[d]	1.72 ± 0.20	0.62 ± 0.25	0.48 ± 0.21	1.04 ± 0.23	2.20 ± 0.20	1.31 ± 0.25
[h]	-	-	-	-	1.56 ± 0.60	-
[i]	-1.01± 0.23	-	-0.44 ± 0.23	-	-	-
[l]	-	-	-	-	-	-
χ^2	0.40	1.84	0.01	2.88	0.08	2.58
d.f.	1	2	1	2	1	2
P	0.53	0.40	0.92	0.24	0.78	0.28

in most of the crosses a single E was estimated, except in the crosses FT-2 x Dourados and FT-2 x Davis. In the models of variance fitted with the data of the mean of the three trifoliate leaves in all the crosses single estimates of the environmental variance were observed. The presence of genotype x microenvironment interaction indicates that the parents involved in the crosses in question did not present the same performance in the conditions of a same experiment.

The use of the mean of the trifoliate leaves favored the occurrence of single environmental variance estimates even in the crosses where the genotype x microenvironment interaction was significant in the analyses for each trifoliate leaf individually. This occurred because there was reduction in the experimental error and consequent reduction in the estimates of environmental variance, that also contributed to the estimated additive genetic effects were more significant and detected with greater frequency in the adjusted models.

In the fitted models to the data for the first and second trifoliate leaves, significant additive effects (D) were detected only for the FT-2 x Davis cross, that was expected, because there are the most contrasting parents according to the means obtained in the experiment for each one. For the third trifoliate leaf, significant additive effects were detected in the Paraná x Dourados and FT-2 x Davis crosses. For the fitted models using the mean of the three trifoliate leaves significant additive effects of variance were observed in most of the crosses including: Paraná x FT-2, Paraná x Dourados, FT-2 x Dourados and FT-2 x Davis. The effects of estimated additive variance were not significant in the individual analyses for each trifoliate leaf in some of these crosses because the experimental errors associated with these estimates were of great magnitude.

Based on the analysis with the mean of the trifoliate leaves, the non significance of D for the Paraná x Davis cross confirmed that the additive genetic variability in this cross must be small and is not favorable for selection. The same occurred for the Dourados x Davis cross, where the Dourados cultivar is considered tolerant to brown spot, showing that the genetic variability was small and also did not favor the selection process. Although the Dourados and Davis cultivar present quite distinct genealogies and phenotypic characteristics, the variability generated in their cross for the trait was small and there was not transgressive segregation in the frequency distribution in the F_3 families. These facts were confirmed by the relatively small heritability values indicating that possible gains with selection will be small in this cross. However, in the Dourados x Paraná cross, besides the presence of significant additive variance in the models fitted for the third trifoliate leaf and for the mean of the three trifoliate leaves, heritability based on the F_3 progeny was high in all the analyses, indicating that there is enough genetic variability to obtain gains in selection for resistance to brown spot.

Significant effects of dominance were observed in the models fitted for the first trifoliate leaf in the Paraná x FT-2 and Paraná x Dourados (H1) crosses, characterizing in the latter the presence of linked genes. For the second trifoliate leaf, in the Paraná x Davis and FT-2 x Dourados crosses dominance effects among linked genes were also observed, but in the Paraná x Dourados cross there was dominance effect without the presence of genetic linkage. In the models adjusted to the third trifoliate leaf data, the effects of dominance were important for the Paraná x FT-2 and Dourados x Davis crosses without the presence of linkage among the genes. For the mean of the trifoliate leaves data, significant dominance effects were not observed in any of the fitted models.

Generally, the magnitude of the dominance effects (H) was always greater than that of the additive effects (D) in the analyses with individual trifoliate leaves. In the analyses with the means of the trifoliate leaves, all the complicating non-additive effects disappeared. No effects of genotype x microenvironment interaction, dominance or linkage were observed and only additive genetic and environmental effects predominated. It was clear that the trait resistance to *S. glycines*, that seemed very complex when assessed in individual leaves, became quite simple as long as care was taken with environmental effects. Thus the assessment of at least three trifoliate leaves with adequate infection levels is indicated for a better characterization of the genotype resistance.

Heritability

Heritability for the trait in the broad sense calculated based on F3 progeny in the six crosses (Table 4) ranged from 10.15% to 45.01% for the first trifoliate leaf, 2.16% to 42.69% for the second trifoliate leaf, 0.00% to 43.36% for the third trifoliate leaf and 0.00% to 52.08% for the mean of the three trifoliate leaves. Paraná x Dourados was the cross that presented the greatest heritability estimates and the Paraná x Davis cross presented the smallest. The largest heritabilities obtained were for the first trifoliate leaf and also for the means of the three trifoliate leaves. This indicates that in this case the selection for resistance to brown spot is more efficient if one of these two parameters is used.

Because the fitted models using the means of the trifoliate leaves data were simpler, it is clear that the assessment by means is advantageous in this case.

In addition to heritability, in the broad sense, calculated based on F_3 progeny shown in Table 4, the estimates of genetic and environmental additive variances of the models adjusted to the mean of the trifoliate leaves were used for the heritability

Table 4. Genetic parameters fitted to the variances of the joint analysis of the experiments, for the infection level in the first, second and third trifoliate leaves and for the mean of the infection level of the three trifoliate leaves, in six soybean crosses.

Genetic parameters, χ^2 test, degrees of freedom, probability and heritability[1/]	Paraná X FT-2	Paraná X Dourados	Paraná X Davis	FT-2 X Dourados	FT-2 X Davis	Dourados X Davis
			1º Trifoliate leaf			
D	-	-	-	-	2.35 ± 1.06	-
H	10.57 ± 4.80	-	-	-	-	-
H1	-	12.44 ± 5.33	-	-	-	-
E	5.76 ± 0.85	7.15 ± 0.63	5.42 ± 0.37	9.22 ± 0.65	7.16 ± 0.70	8.28 ± 0.57
χ^2	0.02	4.31	3.48	3.02	4.45	3.90
d.f.	3	3	4	4	3	4
P	0.99	0.23	0.48	0.55	0.22	0.42
h^2	38.22	45.01	10.15	28.54	38.81	14.97
			2º Trifoliate leaf			
D	-	-	-	-	1.86 ± 0.93	-
H	-	9.99 ± 4.31	-	-	-	-
H1	-	-	7.41 ± 3.35	14.49 ± 4.30	-	-
E	-	-	-	-	-	7.90 ± 0.54
E1	12.21 ± 1.28	10.46 ± 2.27	10.44 ± 1.86	2.96 ± 0.75	3.60 ± 0.94	-
E2	3.14 ± 0.81	7.50 ± 1.85	6.73 ± 1.64	7.45 ± 1.07	15.15 ± 2.03	-
χ^2	4.60	5.08	5.84	2.03	4.37	3.81
d.f.	3	2	2	2	2	4
P	0.20	0.08	0.05	0.36	0.11	0.43
h^2	27.00	40.37	2.16	42.69	30.54	29.73
			3º Trifoliate leaf			
D	-	2.49 ± 1.14	-	-	2.14 ± 1.01	-
H	9.21 ± 4.70	-	-	-	-	11.18 ± 5.16
E	6.22 ± 0.86	8.11 ± 0.77	7.03 ± 0.48	-	-	6.39 ± 0.92
E1	-	-	-	2.41 ± 0.61	2.69 ± 0.69	-
E2	-	-	-	8.26 ± 0.91	11.26 ± 1.49	-
χ^2	7.85	3.41	2.14	2.17	6.11	2.30
d.f.	3	3	4	3	2	3
P	0.05	0.33	0.71	0.54	0.05	0.51
h^2	13.87	43.36	0.00	21.47	33.33	35.45
			Mean of the three trifoliate leaves			
D	1.46 ± 0.57	1.83 ± 0.64	-	0.92 ± 0.45	2.09 ± 0.67	-
E	3.72 ± 0.36	3.68 ± 0.37	2.99 ± 0.20	3.42 ± 0.32	3.82 ± 0.39	4.66 ± 0.32
χ^2	8.01	3.86	3.48	6.06	7.47	8.83
d.f.	3	3	4	3	3	4
P	0.05	0.28	0.48	0.11	0.06	0.07
h^2	35.47	52.08	0.00	36.35	42.55	35.02

[1/] Broad sense heritability, calculated from the components of variance of the F_3 progenies.

calculation, in the narrow sense, based on individual plants and also based on F_3 progeny. The results are shown in Table 5. It can be observed that heritability, based on individual plants, was always smaller, ranging from 11.86% to 21.48%. Also using the genetic models, heritability, based on F_3 families ranged from 39.23% to 56.59% presenting estimates always greater than those based on the generation variances in the broad sense, that ranged from 0.00% to 52.08%.

Selection for Resistance to Brown Spot

According to the heritability estimates presented previously and with the estimated effects in the mean and variance models (Tables 3 and 4) for crosses where there were significant additive genetic effects and heritability considered mean (30%<h2<60%), selection can be made on initial generations during the generation advancement process, such as in F_3/F_4. In these cases, selection can be efficient in obtaining plants resistant to brown spot.

Due to the environmental influence that acts on the trait and also to the complicating agents of the assessments in the field, such as the presence of other diseases, lack of moisture and even absence of the pathogen in the experimental location, selection for resistance to brown spot should be made under controlled conditions in a greenhouse, for a better differentiation of the genotypes for reaction to the disease and consequently, efficient selection.

Selection on individual plants in the F_2 generation, for example, is not recommended because heritability based on individual plants is very low (Table 5) that greatly decreases the selection efficiency. The ideal is selection on progeny from the F_3 generation with at least five individuals per progeny.

Another important aspect is on which trifoliate leaf to make the assessment. Normally, assessments in the field and in the greenhouse for reaction to several diseases are made on the most infected trifoliate leaf or by the general aspect of the plant or plot. According to the heritability estimates presented in Table 4, the greatest values were obtained for the mean of the three trifoliate leaves. As the use of the means of the trifoliate leaves in the analyses simplified the genetic models, it is recommended that at least two trifoliate leaves are assessed to obtain their mean.

The ideal moment to select for resistance to brown spot, under the same conditions in a greenhouse, is when the standard susceptibility cultivar presents infection level between 6 and 8. It is at this stage that the greatest differentiation among the genotypes being assessed occurs. If the selection is being made on a segregant generation, it is recommended that the parents used in the cross are also assessed for reaction to brown spot, serving as control to check the ideal moment for assessment that is where there is the greatest differentiation among the parents.

CONCLUSIONS

Heritability of resistance to brown spot in soybean is polygenic, with mean to low heritability, determined mainly by additive effects.

The resistance assessed in individual leaves can have complicating genetic effects in heritability, such as epistasis, genetic linkage and genotype x microenvironment interaction.

Working with the mean of at least two trifoliate leaves and increasing the environmental control by the use of progenies, the complicating effects of the trait are minimized.

Selection for resistance to brown spot should be made under controlled environmental conditions such as a greenhouse, and based on progenies starting at the F_3 generation, from crosses involving resistance sources.

Table 5. Heritability for the trait resistance to brown spot based on the variances of the progeny and on the genetic models of variance, using the means of the trifoliate leaves data.

	Heritability (%)		
Cross	$h^2 = \sigma^2 g / (\sigma^2 g + \sigma^2/n)$	$h^2 r = ½ D / (½ D + E)$	$h^2 r = ½ D / (½ D + E/n)$
Paraná x FT-2	35.47	16.40	46.87
Paraná x Dourados	52.08	19.91	54.32
Paraná x Davis	0.00	-	-
FT-2 x Dourados	36.35	11.86	39.23
FT-2 x Davis	42.55	21.48	56.59
Dourados x Davis	35,02	-	-

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RESUMO

Controle genético da resistência da soja à mancha parda (*Septoria glycines*): primeiros estudos

O conhecimento dos efeitos genéticos que controlam uma característica é essencial para direcionar o programa de melhoramento para que se tenha ganhos no processo de seleção. O objetivo principal deste trabalho foi estudar o controle genético da resistência da soja [*Glycine max* (L.) Merrill] à mancha parda. Duas cultivares tolerantes (FT-2 e Dourados) e duas suscetíveis (Davis e Paraná), além das gerações segregantes F_2 e F_3 derivadas dos cruzamentos entre as cultivares, foram avaliadas para a reação à doença após inoculação. Foram ajustados modelos genéticos às médias e variâncias das gerações. Pôde-se concluir, que o caráter é governado por vários genes de efeito menor, possui herdabilidade de média a baixa e a seleção deve ser realizada utilizando sempre progênies a partir da geração F_3, podendo ser efetivada nos estádios iniciais de crescimento da soja, com base na média do nível de infecção de pelo menos dois trifólios.

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