Diallel analysis for frogeye leaf spot resistance in soybean[1]

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Abstract – Seven soybean cultivars (Bossier, Cristalina, Davis, Kent, Lincoln, Paraná and Uberaba), with different levels of resistance to *Cercospora sojina*, were crossed in a diallel design to determine the general (GCA) and specific (SCA) combining abilities relative to the inheritance of the resistance. Race 04 of the fungus was inoculated in the parents and in the 21 F_1 hybrids in a greenhouse in a completely randomized design, with 12 replications. The reactions to the disease were evaluated 20 days after the inoculation, always on the most infected leaflet. Both GCA and SCA were significant for all the evaluated characters, being inferred that, for the expression of the characters, the additive, dominant and, possibly, epistatic genic actions were important. The largest values of estimated SCA effect ($\hat{s}_{ij}$) were observed in the hybrid combinations where at least one parent presented high GCA. Cristalina, Davis and Uberaba cultivars showed the largest estimates for GCA effect ($\hat{g}_i$), and from the analysis of $\hat{S}_{ii}$, the contribution of these parents to heterosis of their hybrids will be towards the reduction of the disease symptoms. Therefore, these cultivars are indicated as parents in breeding programs that seek the development of soybean cultivars with resistance to frogeye leaf spot.

Index terms: *Glycine max*, *Cercospora sojina*, combining ability, heterosis, genetic resistance, genetic parameters.

Análise dialélica da resistência à mancha olho-de-rã em soja

Resumo – Sete cultivares de soja (Bossier, Cristalina, Davis, Kent, Lincoln, Paraná e Uberaba) com diferentes níveis de resistência à *Cercospora sojina* foram cruzadas de modo dialélico para avaliar as capacidades geral (CGC) e específica (CEC) de combinação quanto à herança da resistência. A raça 04 do fungo foi inoculada nos progenitores e nos híbridos F_1, em casa de vegetação, num delineamento inteiramente casualizado, com 12 repetições. As avaliações da reação à doença foram feitas 20 dias após a inoculação, sempre no folíolo mais infectado. Ambas, CGC e CEC, foram significativas quanto a todos os caracteres avaliados, inferindo-se que, para a expressão dos caracteres, as ações gênicas aditivas, dominantes e, possivelmente, interações epistáticas foram importantes. Os maiores valores dos efeitos da CEC estimados ($\hat{s}_{ij}$) foram observados nas combinações híbridas dos cruzamentos em que pelo menos um progenitor apresentou alta CGC. As cultivares Cristalina, Davis e Uberaba apresentaram as maiores estimativas do efeito de CGC ($\hat{g}_i$) e, pela análise de $\hat{S}_{ii}$, a contribuição desses genitores para a heterose de seus híbridos será no sentido de redução dos sintomas da doença. Portanto, essas cultivares são indicadas como genitores em programas de melhoramento que visem à obtenção de cultivares de soja com resistência à mancha olho-de-rã.

Termos para indexação: *Glycine max*, *Cercospora sojina*, capacidade combinatória, heterose, resistência genética, parâmetro genético.

Introduction

Soybean (*Glycine max* (L.) Merrill) is cultivated in several parts of the world where it constitutes an important source of vegetable protein and oil. In Brazil, the cultivated area has increased in the last years and so has the incidence of diseases, which are now responsible for losses of about two billion dollars, annually. Amongst the diseases, cercospora leaf spot, also known as frogeye leaf spot, is distin-

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guished (Yorinori, 1997). It is caused by the fungus *Cercospora sojina* Hara and it is primarily a disease of the foliage, although, infections can also occur on stems, pods and seeds (Sinclair & Backman, 1989). The incidence of the disease is favored by hot and humid environment and its influence in the reduction of the productivity derives from the reduction of the photosynthetic area, premature defoliation and damages to the seeds (Akem & Dashiell, 1994).

In Brazil, this disease is currently under control through genetic resistance; its occurrence is sporadical and limited to the South of Balsas in the State of Maranhão and North of Niquelândia in the State of Goiás. More than 23 races have already been identified in Brazil and new epidemics are likely to occur (Yorinori & Klingelfuss, 1999).

The chemical control with fungicides is expensive and it is not the most efficient way to control the disease. The use of resistant cultivars and the incorporation of resistance genes into susceptible commercial cultivars are the most economic and efficient ways to control frogeye leaf spot. So, it is important to know the genetic mechanisms and parameters underlying resistance to this disease (Cruz & Regazzi, 2001).

The genetic parameters necessary for predictions are relatively easy to obtain and are usually estimated in the initial phases of a breeding program. Although some complicators such as epistasis, linkage disequilibrium, genotype vs. environmental interactions and deviation from normality can interfere with the prediction. These complicators, with the exception of epistasis, will not cause serious difficulties to the breeders (Jinks & Perkins, 1972).

The diallel cross analysis, a genetic-statistical method used at this stage of the breeding process, is an efficient instrument in the genetic analysis of quantitative characters. The applications of this method were discussed by Jinks & Hayman (1953), in works carried out on maize.

Several methods for analysis and interpretation of diallel crosses have been suggested (Hayman, 1954; Griffing, 1956; Gardner & Eberhart, 1966). The method proposed by Hayman (1954) allows the identification of the type of predominant genic action and gives a general idea of the genetic control of quantitative characters by means of estimates of variances and covariances. According to Kurek et al. (2001), this type of information is less useful for the breeder of autogamous plants in comparison to the methods of Griffing (1956) and Gardner & Eberhart (1966). These two methods deal with the estimation of components of the means. The method of Gardner & Eberhart (1966) makes a detailed study of heterosis and that of Griffing (1956) supplies information on the combining abilities of the parents and the additive and non-additive variances can be estimated from them.

The general combining ability (GCA) refers to the average behavior of an inbred parent in a series of hybrid combinations, and it is associated to the additive action of the genes. The specific combining ability (SCA) refers to those instances in which certain hybrid combinations are either better or poorer than would be expected on the average performance of the inbred parents considered, and it is associated to the effect of dominance (Rojas & Sprague, 1952). Both GCA and SCA are affected by epistatic effects (Miranda et al., 1988). The diallel analysis allows the evaluation and identification of more promising crosses to develop superior segregating lines or to be used to generate hybrid populations. The identification of superior hybrid combinations among the parents is important to efficiently carry on breeding programs that aim at the introduction of resistance to frogeye leaf spot into cultivated soybean.

The objective of this work was to determine the general and specific combining abilities for resistance to *C. sojina* of seven soybean cultivars.

Material and Methods

Seven soybean cultivars (Bossier, Cristalina, Davis, Kent, Lincoln, Paraná and Uberaba) were used. Two of them (Kent and Lincoln) were supplied by Embrapa-Centro Nacional de Pesquisa de Soja, Londrina, PR. The Gene Bank of Departamento de Fitotecnia da Universidade Federal de Viçosa, Viçosa, MG, supplied the other five cultivars (Table 1). These cultivars were chosen because they present different levels of resistance to *C. sojina*.

By means of compatible artificial crossings between each pair of parent cultivars, 21 F_1 hybrid combinations were obtained. The hybrids and the seven parents were evaluated on the basis of six characters associated with the disease, in a completely randomized design with 12 replications. This work was carried out on 2001, in a greenhouse of the Departamento de Fitotecnia, Universidade Federal de Viçosa, Viçosa, MG.

The *C. sojina* race 04 was supplied by Embrapa-Centro Nacional de Pesquisa de Soja. Multiplication of *C. sojina* isolate was made in Petri dishes, containing agar-tomato juice culture medium, prepared similarly to the V8-agar medium, just substituting the V8 by tomato juice.

Resistance reactions to the pathogen were studied on parental and 21 F_1 hybrid combination generations. The inoculation was done in the greenhouse when the soybean seedlings presented the third trifoliate leaf completely developed, spraying about 10 mL per plant of a 40,000 conidia per milliliter suspension. Immediately after the inoculation, the pots were taken to a mist chamber where they remained for tree days under a relative humidity of 100%.

Twenty days after inoculation, when the disease symptoms were stablished, the following characters were evaluated: infection degree (ID), a visual evaluation of the symptoms and application of a grading scale, from 1.0, without apparent infection, to 5.0, the maximum infection degree; number of lesions per leaflet (NLF), on the most infected leaflet of the plant; lesion mean diameter (LMD), average of the 10 largest lesions of the most infected leaflet, in millimeters; number of lesions per square centimeter (NLC), the number of lesions per leaflet divided by the area of the leaflet; percentage of lesioned foliar area (PLFA), the lesioned foliar area divided by the area of the leaflet and multiplied by one hundred; and disease index (DI), the number of lesions per leaflet multiplied by the square of lesion mean diameter [DI = NLF x $(LMD)^2$]. All variables were evaluated in accordance with the methods used by Veiga (1973), Cordeiro (1986) and Martins Filho (1999).

Statistical and diallel analyses were carried out for each character, using the GENES software (Cruz, 2001).

Population means were compared by the Duncan's test and analyzed according to the fixed model method-2 diallel analysis of Griffing (1956). The treatment effect was considered fixed and decomposed into general (GCA) and specific (SCA) combining abilities, with p(p-1)/2 F_1 hybrid combinations, with no reciprocals, where p is the number of parents.

Griffing's model establishes that:

$$Y_{ij} = m + g_i + g_j + s_{ij} + e_{ij}, \text{where}:$$

Y_{ij} is the average value of the hybrid combination ($i \neq j$) or of the parent ($i = j$); m is the overall mean; g_i and g_j are GCA effect of the i-th and j-th parent, respectively; s_{ij} is the SCA effect for the cross between the i-th and j-th parent; and e_{ij} is the experimental error.

Results and Discussion

The analysis of variance of the data showed that the treatment (parents and their hybrid combinations) effect was significant at 1% probability by the F test for all evaluated characters (Table 2).

Table 1. Half diallel table, indicating the crosses performed among soybean cultivars.

Parents	Cristalina	Bossier	Davis	Kent	Lincoln	Paraná	Uberaba
Cristalina	Y_{11}	Y_{12}	Y_{13}	Y_{14}	Y_{15}	Y_{16}	Y_{17}
Bossier		Y_{22}	Y_{23}	Y_{24}	Y_{25}	Y_{26}	Y_{27}
Davis			Y_{33}	Y_{34}	Y_{35}	Y_{36}	Y_{37}
Kent				Y_{44}	Y_{45}	Y_{46}	Y_{47}
Lincoln					Y_{55}	Y_{56}	Y_{57}
Paraná						Y_{66}	Y_{67}
Uberaba							Y_{77}

Table 2. Analysis of variance (mean squares) and coefficients of variation for soybean reaction to *Cercospora sojina*. Viçosa, 2001(1).

Source of variation	df	ID	NLF	LMD	NLC	PLFA	DI
Treatments	27	23.68	6,563.75	31.40	3.15	750.25	310.65
Error	308	0.48	271.77	0.77	0.19	45.74	15.82
F test		49.61**	24.16**	41.01**	16.55**	16.40**	19.64**
CV (%)		31.90	93.29	53.45	102.05	137.87	139.29

(1)ID: infection degree; NLF: number of lesions per leaflet; LMD: lesion mean diameter; NLC: number of lesions per square centimeter; PLFA: percentage of lesioned foliar area; DI: disease index. **Significant at 1% probability level.

Significant effects of treatments on ID, NLF, LMD, NLC, PLFA and DI characters are associated to the symptoms expression of the disease in the inoculated plants. It is important to remember that the values associated to these characters are inversely proportional to the resistance, that is, smaller values are associated to greater resistance. Although the characters evaluated in this study are correlated, ID can be considered as the reference because it took into account the general visual aspect of the infected leaf, involving a number of characters in its composition. Furthermore, ID presented the smaller coefficient of variation. Other authors also have taken this character as a reference (Martins Filho, 1991, 1999; Cordeiro et al., 1992; Barbieri et al., 2001).

The parents can be separated into three groups: cultivars Bossier and Lincoln presented reaction of high susceptibility to *C. sojina* fungus; Kent and Paraná showed intermediate reactions; and Cristalina, Davis and Uberaba were resistant (Table 3). F_1 hybrids derived from the parent crosses were highly different from each other regarding their reaction to *C. sojina*. Hybrids derived from crosses where at least one of the parents was resistant presented few or no symptom of the disease, indicating dominance. Hybrids from crosses between two susceptible cultivars or between cultivars with intermediate resistance presented more symptoms of the disease in the leaves.

Table 3. Estimated means for characters evaluated in the assay of soybean reaction to *Cercospora sojina*, involving seven parents and their 21 hybrid combinations of a diallel cross. Viçosa, 2001[(1)].

Treatment/	Character[(2)]					
genotype	ID	NLF	LMD	NLC	PLFA	DI
1. Bossier	4.88a	33.60cde	4.92a	0.93abcd	15.34b	6.95b
2. Cristalina	1.00c	0.00f	0.00j	0.00f	0.00d	0.00d
3. Davis	1.03c	0.17f	0.08ij	0.01f	0.01d	0.01d
4. Kent	2.33b	16.08ef	2.25de	0.45cdef	2.83cd	1.28cd
5. Lincoln	3.91a	35.00cde	3.50bc	0.80bcd	9.15bcd	4.94bcd
6. Paraná	1.73bc	8.33f	1.67efg	0.32def	0.92d	0.29d
7. Uberaba	1.23c	3.75f	0.75fghij	0.16f	0.21d	0.07d
1 x 2	1.07c	0.83f	0.25ij	0.02f	0.01d	0.01d
1 x 3	1.18c	2.00f	0.58ghij	0.09f	0.19d	0.04d
1 x 4	4.40a	69.08ab	4.00abc	1.26ab	17.84ab	12.59a
1 x 5	3.90a	56.50bc	4.50ab	1.01abc	25.72a	16.91a
1 x 6	4.12a	41.17cd	3.00cd	1.47a	11.69bc	4.99bcd
1 x 7	1.42bc	5.42f	1.33efghi	0.14f	0.52d	0.26d
2 x 3	1.00c	0.00f	0.00j	0.00f	0.00d	0.00d
2 x 4	1.00c	0.00f	0.00j	0.00f	0.00d	0.00d
2 x 5	1.05c	0.50f	0.33hij	0.01f	0.02d	0.01d
2 x 6	1.00c	0.00f	0.00j	0.00f	0.00d	0.00d
2 x 7	1.02c	0.08f	0.08ij	0.01f	0.01d	0.01d
3 x 4	1.58bc	14.75f	1.00fghij	0.44cdef	0.93d	0.39d
3 x 5	1.18c	1.08f	0.92fghij	0.03f	0.09d	0.04d
3 x 6	1.40bc	4.92f	1.17efghij	0.12f	0.50d	0.28d
3 x 7	1.00c	0.00f	0.00j	0.00f	0.00d	0.00d
4 x 5	4.04a	38.92cd	3.50bc	1.00abc	12.46b	6.56bc
4 x 6	3.98a	44.58c	3.00cd	1.35ab	11.02bc	4.88bcd
4 x 7	1.83bc	10.83f	1.58efgh	0.27ef	0.73d	0.37d
5 x 6	4.19a	82.77a	4.67ab	1.51a	25.22a	17.74a
5 x 7	2.27b	20.18def	2.00def	0.44cdef	1.53d	1.20cd
6 x 7	1.28c	4.33f	0.75fghij	0.15f	0.44d	0.16d
Overall mean	2.14	17.67	1.64	0.43	4.91	2.86

[(1)]Means followed by the same letter do not differ at 5% probability by Duncan's test. [(2)]ID: infection degree; NLF: number of lesions per leaflet; LMD: lesion mean diameter; NLC: number of lesions per square centimeter; PLFA: percentage of lesioned foliar area; DI: disease index.

Cultivars Cristalina, Davis and Uberaba carry genes of resistance to frogeye leaf spot. Almost no infection spots were observed in these cultivars. Possibly, these cultivars possess resistance genes in highly favorable combinations that optimize the expression of resistance. In Cristalina, the combination of genes for resistance to the fungus is such that in the production of hybrids no other genetic combination provided a superior resistance expression.

The mean squares for general (GCA) and specific combining abilities (SCA) were highly significant for all characters indicating that the crosses were heterogeneous (Table 4). The significance of GCA and SCA indicates the existence of additive and non-additive genetic variability among the evaluated genotypes, respectively.

According to Ramalho et al. (1993), GCA is of great importance to the breeders that work with autogamous species because it depends on the additive variance. In breeding programs, selections are performed on segregating generations and in advanced generations, several pure lines with additive gene effect are obtained.

The partial circulant diallel cross, proposed by Kempthorne & Curnow (1961), allows for the prediction of hybrid combinations based on their GCA, ignoring the effect of SCA. This is only valid when the magnitude of the additive variance is relatively superior to the non-additive variance. In the present work, although either the GCA and the SCA have been significant for all the evaluated characters, there is indication of the superiority of GCA due to the greater magnitude of the mean squares for GCA relating to the mean squares for SCA (Table 4). Thus, on the basis of the reasoning of the partial circulant diallel method, there is indication of efficiency for genetic progress in the advanced segregant generations, due to the additive effect of the genes in these populations. Oliveira Júnior et al. (1999) concluded that GCA effect is a good predictor for the performance of segregant field beans F_3 populations, working with an unbalanced diallel and a circulant diallel. The same authors based this fact on the principles of the quantitative genetics, once the phenotypic value of F_1 is strongly determined by the heterotic effect conditioned by the dominance deviations, which are not transferred to posterior generations. As the heritable genetic factors are of additive nature, it is acceptable that the prediction is more efficient when the information of the hybrid is based solely on the effect of the general combining ability.

When the estimates of GCA are low, positive or negative, they indicate that the values of the GCA of the parents, which are obtained from their hybrids with the other parents, do not differ from the overall mean of the diallel crosses; and when the estimates of GCA are high, positive or negative, they indicate that the parents in question are superior or inferior to the other parents included in the diallel, in relation to the average behavior of the crosses (Oliveira Júnior et al., 1999; Cruz & Regazzi, 2001). These GCA estimates (g_i) constitute an indication of the genes that are predominantly additive in their effects. The ancestors with bigger estimates are indicated for the constitution of new populations, aiming at the attainment of higher genetic progress. Therefore, for the case of disease resistance evaluation, the interest concentrates on genotypes with lower severity

Table 4. Partitioning of treatment effect into general (GCA) and specific combining abilities (SCA) for the evaluated characters. Viçosa, 2001[(1)].

Source of variation	df	Mean square					
		ID	NLF	LMD	NLC	PLFA	DI
GCA	6	75.74**	16,990.70**	112.72**	9.00**	1,917.13**	673.55**
SCA	21	8.81**	584.61**	8.17**	1.48**	416.86**	206.96**
Error	308	0.48	271.76	0.77	0.19	45.73	15.82

[(1)]ID: infection degree; NLF: number of lesions per leaflet; LMD: lesion mean diameter; NLC: number of lesions per square centimeter; PLFA: percentage of lesioned foliar area; DI: disease index. **Significant at 1% probability level by the F test.

of the disease, or either, genotypes that contribute to diminish the expression of the character and, consequently, shows negative estimates of g_i (Cruz & Regazzi, 2001).

Negative values of g_i indicate the contribution for the resistance to *C. sojina* in soybean, which were observed for resistant parents: Cristalina, Davis and Uberaba (Table 5). Positive estimates were observed on susceptible and intermediate resistant parents (Bossier, Lincoln, Kent and Paraná). The estimates of g_i differed sufficiently among parents and show evidence of the presence of genes of large additive effects. Cultivars Cristalina, Davis and Uberaba are the ones that possess greater potential to increase the resistance to *C. sojina* in soybean, while Bossier, Kent, Lincoln and Paraná cultivars presented genetic contribution towards susceptibility. Bossier cultivar presented the most unfavorable general combining ability estimate, and therefore, is the parent which presents the smallest capacity to contribute with resistance alleles to the genic pool under study.

According to Cruz & Regazzi (2001), SCA effect can be interpreted as the deviation of the hybrid relating to what would be expected based on the GCA of its parents. Thus, the low absolute values for SCA indicate that the F_1 hybrids, derived from crosses between the studied parents, behaved as expected, while high absolute values of $\hat{s}_{ij}$ demonstrate that the behavior of a particular crossing is relatively better or worse than the expected value on the basis of the GCA of the parents. The estimates of s_{ij} show the importance of the genes with non-additive effects. In the present study, hybrids of lower SCA estimates are distinguished by having Cristalina, Davis or Uberaba cultivar as one of their parents (Table 6).

The magnitude of the values of the SCA of each parent ($\hat{s}_{ii}$) is an indication of the genetic divergence of the cultivar in question, regarding the average of the other parents tested in the diallel. The greater the absolute value of $\hat{s}_{ii}$ the greater is the effect of heterosis inherent to the cultivar, which has been manifested in all F_1 populations from this cross (Cruz & Regazzi, 2001).

The largest values for $\hat{s}_{ii}$ (absolute values) were presented by Paraná, Cristalina and Davis parents, evidencing their genetic divergence in relation to the average of the other parents involved in the diallel, as well as the biggest effect of heterosis revealed in the F_1 of the crossing between them. The positive signals of $\hat{s}_{ii}$, as found for the resistant parents Cristalina, Davis and Uberaba, indicate existence of unidirectional dominance deviations (Silva et al., 2000) and, consequently, of negative manifestation of heterosis in the hybrid combinations, involving divergent ancestors (Table 6). Negative values of $\hat{s}_{ii}$ were observed for Bossier, Kent and Paraná parents, revealing positive heterosis in their hybrids, which in this case is disadvantageous, because it leads to increased disease symptoms.

Table 5. Estimates of general combining ability effect (g_i) of seven soybean varieties for the evaluated characters. Viçosa, 2001[1].

Effect	ID	NLF	LMD	NLC	PLFA	DI
$\hat{g}_1$	0.9457	11.2010	1.1561	0.2687	5.2676	2.8729
$\hat{g}_2$	-1.0209	-15.5489	-1.3809	-0.3768	-4.3570	-2.5365
$\hat{g}_3$	-0.8801	-13.1415	-1.0291	-0.3028	-4.1702	-2.4539
$\hat{g}_4$	0.4615	7.6640	0.4986	0.2005	1.0434	0.5008
$\hat{g}_5$	0.8606	14.2751	1.0913	0.2414	4.9009	3.2777
$\hat{g}_6$	0.3041	5.8862	0.3135	0.2028	1.2723	0.6421
$\hat{g}_7$	-0.6709	-10.3360	-0.6495	-0.2339	-3.9571	-2.3032

[1]ID: infection degree; NLF: number of lesions per leaflet; LMD: lesion mean diameter; NLC: number of lesions per square centimeter; PLFA: percentage of lesioned foliar area; DI: disease index.

Table 6. Estimates of the specific combining ability effects ($\hat{s}_{ii}$), for characters evaluated in the assay of soybean reaction to *Cercospora sojina*, involving seven ancestors and their 21 hybrid combinations, in a diallel cross. Viçosa, 2001[(1)].

Genotype/ treatment	Effect (s_{ij})	Character					
		ID	NLF	LMD	NLC	PLFA	DI
1. Bossier	$\hat{s}_{11}$	-0.8183	-6.4884	-0.9676	-0.0330	-0.1031	-1.6496
2. Cristalina	$\hat{s}_{22}$	0.8766	13.4282	1.1250	0.3259	3.8086	2.2174
3. Davis	$\hat{s}_{33}$	0.6285	8.7801	0.5046	0.1823	3.4368	2.5031
4. Kent	$\hat{s}_{44}$	-0.7632	-16.9143	-0.3843	-0.3767	-4.1617	-2.5730
5. Lincoln	$\hat{s}_{55}$	0.0220	-11.2199	-0.3194	-0.1094	-5.5530	-4.4684
6. Paraná	$\hat{s}_{66}$	-1.0400	-21.1088	-0.5972	-0.5107	-6.5351	-3.8506
7. Uberaba	$\hat{s}_{77}$	0.4099	6.7523	0.4120	0.1970	3.2135	1.8159
1 x 2	$\hat{s}_{12}$	-1.0234	-12.4884	-1.1620	-0.3045	-5.8041	-3.1844
1 x 3	$\hat{s}_{13}$	-1.0474	-13.7292	-1.1805	-0.3030	-5.8157	-3.2303
1 x 4	$\hat{s}_{14}$	0.8275	32.5486	0.7083	0.3616	6.6231	6.3616
1 x 5	$\hat{s}_{15}$	-0.0715	13.3542	0.6157	0.0725	10.6504	7.9031
1 x 6	$\hat{s}_{16}$	0.7016	6.4097	-0.1065	0.5667	0.2471	-1.3805
1 x 7	$\hat{s}_{17}$	-1.0234	-13.1181	-0.8102	-0.3259	-5.6947	-3.1701
2 x 3	$\hat{s}_{23}$	0.7359	11.0208	0.7731	0.2519	3.6219	2.1348
2 x 4	$\hat{s}_{24}$	-0.6058	-9.7847	-0.7546	-0.2515	-1.5918	-0.8199
2 x 5	$\hat{s}_{25}$	-0.9548	-15.8958	-1.0139	-0.2803	-5.4339	-3.5892
2 x 6	$\hat{s}_{26}$	-0.4484	-8.0069	-0.5694	-0.2537	-1.8207	-0.9611
2 x 7	$\hat{s}_{27}$	0.5433	8.2986	0.4768	0.1862	3.4113	1.9850
3 x 4	$\hat{s}_{34}$	-0.1715	2.5579	-0.1065	0.1185	-0.8459	-0.5125
3 x 5	$\hat{s}_{35}$	-0.9706	-17.7199	-0.7824	-0.3381	-5.5454	-3.6385
3 x 6	$\hat{s}_{36}$	-0.1891	-5.4977	0.2454	-0.2029	-1.5104	-0.7613
3 x 7	$\hat{s}_{37}$	0.3859	5.8079	0.0417	0.1090	3.2220	1.9016
4 x 5	$\hat{s}_{45}$	0.5544	-0.6921	0.2731	0.1269	1.6080	-0.0774
4 x 6	$\hat{s}_{46}$	1.0442	13.3634	0.5509	0.5188	3.7953	0.8765
4 x 7	$\hat{s}_{47}$	-0.1224	-4.1643	0.0972	-0.1210	-1.2652	-0.6823
5 x 6	$\hat{s}_{56}$	1.4868	44.8356	1.6250	0.6357	14.1430	10.9663
5 x 7	$\hat{s}_{57}$	-0.0882	-1.4421	-0.0787	0.0021	-4.3161	-2.6275
6 x 7	$\hat{s}_{67}$	-0.5150	-8.8866	-0.5509	-0.2431	-1.7842	-1.0386

[(1)]ID: infection degree; NLF: number of lesions per leaflet; LMD: lesion mean diameter; NLC: number of lesions per square centimeter; PLFA: percentage of lesioned foliar area; DI: disease index.

Conclusions

1. The additive, dominant and epistatic genic effects are important in the expression of resistance related characters.

2. The contribution of Cristalina, Davis and Uberaba parents for heterosis on their hybrids is in the direction of reducing the disease symptoms.

3. Cristalina, Davis and Uberaba cultivars are preferably indicated as parents in programs of soybean improvement seeking genotypes carrying resistance to *Cercospora sojina*.

References

AKEM, C. N.; DASHIELL, K. E. Effect of planting date on severity of frogeye leaf spot and grain yield of soybeans. **Crop Protection**, Oxford, v. 13, p. 607-610, 1994.

BARBIERI, R. L.; CARVALHO, F. I. F.; BARBOSA NETO, J. F.; CAETANO, V. R.; MARCHIORO, V. R.; AZEVEDO, R.; LONRECETTI, C. Análise dialélica para tolerância ao vírus-do-nanismo-amarelo-da-cevada em cultivares brasileiras de trigo. **Pesquisa Agropecuária Brasileira**, Brasília, v. 36, n. 1, p. 131-135, jan. 2001.

CORDEIRO, A. C. C. **Herança da resistência da soja (*Glycine max* (L.) Merrill), à *Cercospora sojina* Hara,**

isolado de São Gotardo, Minas Gerais. 1986. 61 f. Dissertação (Mestrado em Genética e Melhoramento de Plantas) - Universidade Federal de Viçosa, Viçosa, MG, 1986.

CORDEIRO, A. C. C.; SEDIYAMA, T.; GOMES, J. L. L.; SEDIYAMA, C. S.; REIS, M. S. Herança da resistência da soja à *Cercospora sojina* Hara, isolado de São Gotardo, Minas Gerais. **Pesquisa Agropecuária Brasileira**, Brasília, v. 27, n. 7, p. 1035-1042, jul. 1992.

CRUZ, C. D. **Programa Genes**: aplicativo computacional em genética e estatística: versão Windows. Viçosa, MG: Editora UFV, 2001. 648 p.

CRUZ, C. D.; REGAZZI, A. J. **Modelos biométricos aplicados ao melhoramento genético**. 2. ed. rev. Viçosa, MG: Editora UFV, 2001. 390 p.

GARDNER, C. O.; EBERHART, S. A. Analysis and interpretation of the variety cross diallel and related populations. **Biometrics**, Washington, v. 22, p. 439-452, 1966.

GRIFFING, B. Concept of general and specific combining ability in relation to diallel crossing systems. **Australian Journal of Biological Science**, Collingwood, v. 9, p. 463-493, 1956.

HAYMAN, B. I. The theory and analysis of diallel crosses. **Genetics**, Bethesda, v. 39, p. 789-809, 1954.

JINKS, J. L.; HAYMAN, B. I. The analysis of diallel crosses. **Maize Genetics Cooperation Newsletter**, Columbia, v. 27, p. 48-54, 1953.

JINKS, J. L.; PERKINS, J. M. Predicting the range of inbred lines. **Heredity**, Oxford, v. 28, n. 3, p. 399-403, 1972.

KEMPTHORNE, O.; CURNOW, R. N. The partial diallel cross. **Biometrics**, Washington, v. 17, p. 229-250, 1961.

KUREK, J. A.; CARVALHO, F. I. F.; ASSMANN, I. C.; CRUZ, J. P. Capacidade combinatória como critério de eficiência na seleção de genitores em feijoeiro. **Pesquisa Agropecuária Brasileira**, Brasília, v. 36, n. 4, p. 645-651, abr. 2001.

MARTINS FILHO, S. **Análise dialélica da resistência da soja (*Glycine max* (L.) Merrill) à *Cercospora sojina* Hara**. 1991. 59 f. Dissertação (Mestrado em Genética e Melhoramento de Plantas) - Universidade Federal de Viçosa, Viçosa, MG, 1991.

MARTINS FILHO, S. **Mancha olho-de-rã da soja**: análise genética e identificação de marcadores moleculares. 1999. 82 f. Tese (Doutorado em Genética e Melhoramento de Plantas) - Universidade Federal de Viçosa, Viçosa, MG, 1999.

MIRANDA, J. E. C. de; COSTA, C. P. da; CRUZ, C. D. Análise dialélica em pimentão - I: capacidade combinatória. **Revista Brasileira de Genética**, Ribeirão Preto, v. 7, p. 431-440, 1988.

OLIVEIRA JÚNIOR, A.; MIRANDA, G. V.; CRUZ, C. D. Predição de populações F_3 a partir de dialelos desbalanceados. **Pesquisa Agropecuária Brasileira**, Brasília, v. 34, n. 5, p. 781-787, maio 1999.

RAMALHO, M. A. P.; SANTOS, J. P. dos; ZIMMERMANN, M. J. de O. **Aplicações ao melhoramento do feijoeiro**. Goiânia: Ed. da UFG, 1993. 271 p.

ROJAS, B. A.; SPRAGUE, G. F. **A comparison of variance components in corn yields trials - III**: general and specific combining ability and their interaction with location and years. **Agronomy Journal**, Madison, v. 44, n. 9, p. 462-466, 1952.

SILVA, S. A. G.; MORAIS, O. P. de; RAVA, C. A.; COSTA, J. G. C. Método generalizado de análise de dialelos desbalanceados. **Pesquisa Agropecuária Brasileira**, Brasília, v. 35, n. 10, p. 1999-2005, out. 2000.

SINCLAIR, J. B.; BACKMAN, P. A. (Ed.). Frogeye leaf spot. In: COMPENDIUM of soybean diseases. 3rd ed. St. Paul: American Phytopathology Society, 1989, p. 19-21.

VEIGA, P. ***Cercospora sojina* Hara**: obtenção de inóculo, inoculação e avaliação da resistência em soja (*Glycine max* (L.) Merrill). 1973. 32 f. Dissertação (Mestrado em Genética e Melhoramento de Plantas) - Escola Superior de Agricultura Luiz de Queiroz, Piracicaba, 1973.

YORINORI, J. T. **Potential for integrated disease management in soybean**. In: WORLD SOYBEAN RESEARCH CONFERENCE, 5., 1994, Chiang Mai. **Proceedings**… Bangkok: Kasetsart University Press, 1997. p. 233-238.

YORINORI, J. T.; KLINGELFUSS, L. H. Novas raças de *Cercospora sojina* em soja. **Fitopatologia Brasileira**, Brasília, v. 24, n. 4, p. 509-512, 1999.