

## DIALLEL ANALYSIS OF MAIZE RESISTANCE TO *Phaeosphaeria maydis*

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**ABSTRACT:** In breeding programs directed towards genetic resistance against diseases, the estimation of genetic parameters that control resistance allows the introduction of resistance into susceptible germplasm to be clearly focused. The purposes of this study were to estimate heterosis effects, and the general (GCA) and specific (SCA) combining abilities by using two rating methods for resistance to *Phaeosphaeria maydis* in a diallel analysis of 36 F<sub>1</sub> maize hybrids and their nine inbred lines. Trials were conducted in three environments. Disease severity was evaluated in the whole plant (PI) and in the leaf positioned just below the point of insertion of the main ear (AFA). The trials followed a randomized block design with plots represented by a 5 m long rows. Differences among combining ability estimates for different environments and in both evaluation methods showed significant effects ( $P < 0.01$ ) for environment (E), GCA, and GCA  $\times$  E. The SCA, and SCA  $\times$  E effects were not significant for any of the disease severity variables. The GCA effects were more important than SCA for this set of inbred lines, suggesting that additive genetic effects are the most important sources of variation for this trait. Heterosis effects for resistance were estimated, and it was possible to identify specific hybrid combinations between lines which have high potential for genetic control of this pathogen. Results for both disease severity variables were practically identical, even though the PI method was more convenient to use.

**Key words:** *Zea mays* L., genetic resistance, heterotic effects, general and specific combining ability

## ANÁLISE DIALÉLICA DA RESISTÊNCIA A *Phaeosphaeria maydis* EM MILHO

**RESUMO:** Em programas de melhoramento visando resistência genética a doenças, a estimativa de parâmetros genéticos que governam a resistência permite direcionar a introdução de resistência em germoplasmas. O objetivo deste trabalho foi estimar os efeitos heteróticos, a capacidade geral (CGC) e específica (CEC) de combinação, utilizando-se de dois métodos de avaliação da resistência, à *Phaeosphaeria maydis* através da análise dialélica de 36 híbridos F<sub>1</sub> e de suas nove linhagens genitoras, em experimentos conduzidos em três ambientes. Foi utilizado um delineamento experimental em blocos casualizados com três repetições e a parcela experimental foi representada por uma fileira de 5 m. As diferenças entre as estimativas da capacidade de combinação, em diferentes ambientes e para os dois métodos de avaliação, apresentaram efeitos significativos ( $P < 0.01$ ) para ambientes (E), CGC e CGC  $\times$  E. O efeito de CEC e a interação CEC  $\times$  E não foi significativa para os dois métodos de avaliação. Os efeitos de CGC foram mais importantes que CEC nesse conjunto de linhagens, sugerindo que efeitos genéticos aditivos são mais importantes como fonte de variação para resistência a esta doença. Efeitos heteróticos para resistência foram estimados, sendo possível identificar combinações híbridas específicas entre linhagens com alto potencial para o controle genético deste patógeno. Resultados para os dois métodos de avaliação foram praticamente idênticos, embora o método PI seja de maior praticidade de uso.

**Palavras-chave:** *Zea mays* L., genética da resistência, efeito heterótico, capacidade geral e específica de combinação

### INTRODUCTION

*Phaeosphaeria* leaf spot, caused by the fungus *Phaeosphaeria maydis* (Henn.) Rane, Payak & Renfro (*Sphaerulina maydis* = *Leptosphaeria zae-maydis* Saccas), anamorphous stage - *Phyllosticta* sp., is considered the most important maize disease in Brazil, because of both its widespread distribution and the damages it causes to susceptible cultivars. In Brazil, *P. maydis* has

been considered of great importance in recent years in tropical areas with altitudes above 600 m, favorable conditions are prevalent in the states of São Paulo, Minas Gerais and Goiás (Silva, 1997).

Earlier on, *P. maydis* had not been causing great damage to the crop because it occurred more frequently at the end of the cropping cycle. Currently, it has been observed in plants at phenological stage 7 according to Hanway's scale (1966).

The first of Koch's postulates with the fungus *P. maydis* was established by Rane et al. (1965). Later, Fantin & Balmer (1997) managed to reproduce the symptoms. Paccola-Meirelles et al. (1998) performed the isolation of fungi from lesions described as being from *P. maydis*. However, there is a controversy about the identification of the etiological agent of this disease. Later on, Paccola-Meirelles et al. (2001) did not detect the presence of the fungus, by cytological analysis, at the initial stages of the disease. The isolation of the bacterium *Pantoea ananas* (*Erwinia ananas*), from lesions supposedly caused by *Phaeosphaeria* leaf spot, suggest its participation in the initial stage of the disease, and indicates that the fungus is not the primary pathogen of this disease, as originally proposed.

Maize has great genetic diversity for resistance to pathogens, which makes the use of resistant cultivars the most economic and efficient form of disease control (Balmer & Pereira, 1987; Silva, 2001). It has been reported that resistance to *P. maydis* is a quantitative trait, and the additive gene action has greater importance for character inheritance, while the dominant gene action has a less important expression (Carson et al., 1996; Pegoraro et al., 2000; Carson, 2001).

The application of concepts of heterosis, general and specific combining abilities (GCA and SCA, respectively) has been utilized for grain-producing crop breeding; GCA is relatively more important than SCA for non-selected endogamic lines, while the opposite is true for previously-selected lines (Sprague & Tatum, 1942; Hallauer & Miranda Filho, 1988; Nass et al., 2000). These concepts are useful both for the characterization of lines in crosses and for establishing heterotic standards between maize populations (Hallauer & Miranda Filho, 1988; Beck et al., 1990; Crossa et al., 1990; Han et al., 1991; Vasal et al., 1992), and in maize disease genetic resistance studies (Nelson & Scott, 1973; Lim & White, 1978; Callaway et al., 1990). To provide support for the development of varieties and hybrids resistant to *P. maydis*, the present work aimed at evaluating the heterotic

effects, the interaction of those effects with the environment, and the combination ability of a group of endogamous maize lines, adapted to the conditions of South and Central regions of Brazil, on the resistance to *P. maydis*, in order to select superior hybrid combinations with a high degree of resistance to this pathogen.

## MATERIAL AND METHODS

The nine lines utilized in this work were obtained by at least seven successive self-fertilizations (Table 1). DAS41 and DAS21 are early lines, with semi-flint, orangish kernels, from the Suwan DMR population, and are considered, respectively, resistant and susceptible to *P. maydis*. The Suwan DMR population was developed in Thailand from a selection of tropical flint materials from the Caribbean and from Tuxpeño dent materials, and was released as Thai Composite 1 after several recurring selection cycles. Two sources of resistance to *Peronosclerospora sorghi* from the Philippines (DMR 1 and DMR 5) were incorporated into this material, resulting in the CMS 05 population, which is being utilized by Centro Nacional de Pesquisa de Milho e Sorgo (CNPMS) of Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). DAS42 and DAS56, susceptible to *P. maydis*, are early lines, with flint, orangish kernels, originated from the Suwan-3 population. This population was obtained by means of recurring selection from the Suwan-1 population.

Lines DAS86, DAS72, and DAS2 are resistant to moderately resistant to this pathogen, early, with semiflint, orangish kernels, from the same restricted-genetic-base synthetic, group of lines obtained from the Amarillo Dentado population and from endogamous lines obtained from a tropical flint population of the Caribbean. Both populations are widely utilized in public and private breeding programs in Asia. The resistant line DAS95 is early, with flint, orangish kernels, originating from a synthetic group of lines from flint tropical

Table 1 - Lines evaluated for reactions to *Phaeosphaeria* leaf spot and their sources.

| Line  | Source                            | Reaction to <i>P. maydis</i> |
|-------|-----------------------------------|------------------------------|
| DAS95 | Tropical Flint Synthetic          | Resistant                    |
| DAS41 | Suwan DMR                         | Resistant                    |
| DAS86 | Amarillo Dentado/ Caribbean Flint | Resistant                    |
| DAS72 | Amarillo Dentado/ Caribbean Flint | Moderately Resistant         |
| DAS2  | Amarillo Dentado/ Caribbean Flint | Moderately Resistant         |
| DAS56 | Suwan 3                           | Moderately Resistant         |
| DAS21 | Suwan DMR/ Caribbean Flint        | Moderately Susceptible       |
| DAS42 | Suwan 3                           | Susceptible                  |
| DAS93 | BSSS *                            | Susceptible                  |

\* BSSS is an abbreviation for Iowa Stiff Stalk Synthetic.

materials with an orangish coloration. Finally, line DAS93 is super-early, with dent, yellowish kernels, originated from temperate materials derived from the BSSS synthetic (Iowa Stiff Stalk Synthetic) and formed from 16 lines, with at least seven of them derived from the Reid Yellow Dent population. This synthetic is widely utilized in breeding programs in the United States, Europe and Argentina.

Multiplication of the endogamous lines and the obtainment of  $F_1$  generations were performed during the 1997/98 cropping season, in Cravinhos - SP. The thirty six simple hybrids were obtained from diallelic crosses between the nine lines.

Evaluations were performed during the 1999/2000 cropping season in three locations: Cravinhos, Northeast São Paulo State (21°20'25''S, 47°43'46''W; altitude 820 m), Iraí de Minas, Minas Gerais State (18°59'02''S, 47°27'41''W; altitude 980 m) and Taquarituba, Southwestern São Paulo State (23°31'59''S, 49°14'40''W; altitude 730 m). The cultural practices adopted in the trials were the same as those adopted by growers of the specific regions.

Thirty days prior to planting, a border hybrid susceptible to *Phaeosphaeria maydis* was planted and inoculated with pycnidiospores from Cravinhos, Taquarituba, and Iraí de Minas. The pycnidiospores were obtained by washing infected leaves with distilled water; the leaves had been previously placed inside plastic bags, with the interior moistened with water, and left in the shade for 48 hours. Inoculation consisted in spraying 5 mL of the spore suspension into the whorl of each plant, adjusted to a concentration of  $1 \times 10^3$  pycnidiospores mL<sup>-1</sup> distilled water, which had been added of one droplet of mineral oil at viscosity 80 per 1000 mL. Inoculations were performed 30 and 45 days after planting, corresponding, respectively, to growth stages 3 and 5, according to the methodology described by Hanway (1966). The experimental area was irrigated one hour before inoculation, in the afternoon. Calibration of the inoculum was performed with a hemocytometer.

Resistance to *Phaeosphaeria* leaf spot was evaluated in all plants all trials by scoring the severity of the disease in the entire plant (PI) and in the leaf located below the insertion point of the main ear (AFA), at phenological stage 7, according to Fancelli & Silveira Neto (1997). The evaluation of the disease in the entire plant was performed by attributing nine severity ratings with the use of a diagrammatic scale, in which 1=0%, 2=0 to 1%, 3=1 to 2.5%, 4=2.5 to 5%, 5=5 to 10%, 6=10 to 25%, 7=25 to 50%, 8=50 to 75%, 9= >75% of affected leaf area in the plant. The severity of the disease in the leaf positioned below the main ear was evaluated with the diagrammatic scale containing the values: 0; 0.1%; 0.3%; 0.7%; 2%; 5%; 12%; 27% and >50% of affected leaf area.

For ANOVA purpose, data expressed as severity ratings and percentages were transformed to square root and arcsine of square root, respectively. The experimental design consisted of randomized blocks with three replicates in each environment. Plots were represented by 5 m-long rows, spaced at 0.80 m, with 25 plants per plot; plants were spaced 20 cm, with a population stand of 62,500 plants ha<sup>-1</sup>. Within each replicate, the usable plots containing lines were surrounded by a resistant line border, while the usable plots containing hybrids were surrounded by a simple resistant hybrid border. The ANOVA for reactions to *Phaeosphaeria* leaf spot were performed according to the Gardner & Eberhart (1966) method and to method 4, model I, by Griffing (1956).

## RESULTS AND DISCUSSION

Heterosis and combination ability estimates in crosses between lines allow not only to determine the contribution of each line toward resistance, but also to identify hybrid combinations of agronomic interest. The average disease severity in the entire plant (PI) and for leaf area affected in the leaf, located below the insertion point of the 1<sup>st</sup> ear (AFA), for the Taquarituba, Cravinhos and Iraí de Minas environments, ranged from 1.27 to 7.90 for PI (Table 2) and from 0.12 to 50.00% for AFA (Table 3). The greatest mean disease severity values were observed in the Iraí de Minas environment for both evaluation methods, followed by Cravinhos and Taquarituba, which presented smaller severity value means.

The hybrid combinations with the greatest level of resistance were obtained from crosses of line DAS95 with lines DAS41, DAS86, DAS72, and DAS2 in the three locations: Taquarituba, Cravinhos and Iraí de Minas (Tables 2 and 3). Considering the mean for the three locations and for the two evaluation methods, the studies involving endogamous lines DAS95, DAS41, and DAS86 evidenced the smallest severity values (data not shown). However, hybrids DAS42 × DAS93 and DAS21 × DAS93 were the most susceptible. The presence of total heterosis for resistance was found in both crosses between resistant lines and between susceptible lines. (Tables 2 and 3).

The diallelic analysis by the Gardner & Eberhart (1966) method revealed variation between lines for resistance evaluated by the two methods (Table 4). The mean squares for total heterosis, mean heterosis, line heterosis and specific heterosis were not significant for both evaluation methods. Severity evaluated for the entire plant (PI) should be used as evaluation method, because of the little differences between methods, as well as to the absence of a G × E interaction, because it presented smaller coefficient of variation values in the analysis of variance, and because it is more practical to be used. The utilization of a single variable reduces the amount of work involved in data collection.

The Suwan DMR population has been developed in Thailand from a selection of tropical flint materials from the Caribbean and from Tuxpeño dent materials, which was released as Thai Composite 1. This population has demonstrated to be a good source for the extraction of lines resistant to *Phaeosphaeria* leaf spot, has wide genetic variability for resistance to the disease, good GCA for agronomic characters and productivity, and has great adaptation ability to tropical and subtropical environments. The lines obtained from the Amarillo Dentado/Caribbean Flint materials also presented good level of resistance, good agronomic characters and were adapted to tropical environments.

By the Griffing method, the combination ability determination in different environments produced highly significant values ( $P < 0.01$ ) for the A.F.A method, but were non-significant by the PI evaluation method for environments (E), and showed highly significant effects ( $P < 0.01$ ) for GCA and GCA  $\times$  E evaluated through both methods. For SCA and SCA  $\times$  E the effects were non-significant

for both evaluation methods (Table 5). The significances of mean square effects for GCA  $\times$  E suggest that it is necessary to select parental lines to obtain hybrids in specific environments. Choosing parents based on the mean for the GCA effects can be done if there is interest in simple hybrids adapted to all environments. The GCA  $\times$  E interaction, however, indicated that the greatest GCA values were not the same for all environments.

Studies aimed at resistance to diseases and grain productivity have shown that GCA and SCA can interact with the environment (Rojas & Sprague, 1952; Matzinger et al., 1959; Parodas & Hayes, 1971; Nelson & Scott, 1973). In tropical regions, these interactions are particularly interesting, since there is expressive variation between locations, even when they are not far apart from each other. In temperate regions, under variations in altitude, greater variations in day length and temperature can be observed than in tropical regions, which makes the work of the breeder more intense and more challenging (Miranda Filho, 1985; Paterniani, 1990).

Table 2 - Reactions of nine endogamous lines and 36 crosses in relation to *Phaeosphaeria maydis*, in three locations, evaluated by a severity scale of the disease in the entire plant.

|               | Line  |       |       |       |      |       |       |       |       |
|---------------|-------|-------|-------|-------|------|-------|-------|-------|-------|
| Taquarituba   | DAS95 | DAS41 | DAS86 | DAS72 | DAS2 | DAS56 | DAS21 | DAS42 | DAS93 |
| DAS95         | 1.45  | 1.27  | 1.99  | 1.83  | 3.03 | 3.28  | 3.58  | 3.20  | 3.72  |
| DAS41         |       | 1.91  | 3.03  | 2.78  | 4.78 | 3.92  | 4.50  | 5.69  | 5.93  |
| DAS86         |       |       | 2.83  | 3.57  | 3.82 | 3.73  | 4.70  | 5.52  | 4.45  |
| DAS72         |       |       |       | 3.80  | 3.48 | 3.77  | 4.82  | 4.88  | 5.17  |
| DAS2          |       |       |       |       | 4.72 | 4.93  | 5.88  | 5.85  | 5.93  |
| DAS56         |       |       |       |       |      | 4.58  | 5.50  | 6.08  | 5.57  |
| DAS21         |       |       |       |       |      |       | 6.08  | 6.53  | 6.95  |
| DAS42         |       |       |       |       |      |       |       | 6.78  | 6.62  |
| DAS93         |       |       |       |       |      |       |       |       | 7.47  |
| Cravinhos     |       |       |       |       |      |       |       |       |       |
| DAS95         | 1.72  | 1.78  | 1.77  | 1.83  | 2.75 | 3.22  | 3.28  | 3.30  | 3.58  |
| DAS41         |       | 2.25  | 3.05  | 3.07  | 5.35 | 4.77  | 5.62  | 6.08  | 4.87  |
| DAS86         |       |       | 2.93  | 4.05  | 4.03 | 4.05  | 4.80  | 5.83  | 4.70  |
| DAS72         |       |       |       | 4.30  | 3.73 | 4.28  | 4.68  | 5.20  | 4.65  |
| DAS2          |       |       |       |       | 5.03 | 5.68  | 6.22  | 5.98  | 5.53  |
| DAS56         |       |       |       |       |      | 5.97  | 5.63  | 6.17  | 6.45  |
| DAS21         |       |       |       |       |      |       | 6.23  | 6.52  | 6.35  |
| DAS42         |       |       |       |       |      |       |       | 6.62  | 6.50  |
| DAS93         |       |       |       |       |      |       |       |       | 6.97  |
| Iraí de Minas |       |       |       |       |      |       |       |       |       |
| DAS95         | 1.48  | 2.02  | 2.00  | 1.98  | 3.08 | 3.55  | 3.85  | 3.70  | 5.42  |
| DAS41         |       | 3.48  | 3.37  | 3.52  | 5.40 | 6.07  | 5.93  | 6.68  | 6.82  |
| DAS86         |       |       | 3.10  | 5.12  | 4.47 | 5.05  | 4.72  | 6.43  | 6.77  |
| DAS72         |       |       |       | 5.45  | 4.10 | 4.88  | 5.77  | 6.52  | 6.47  |
| DAS2          |       |       |       |       | 6.48 | 6.32  | 6.43  | 6.98  | 6.92  |
| DAS56         |       |       |       |       |      | 6.88  | 6.00  | 6.85  | 7.07  |
| DAS21         |       |       |       |       |      |       | 6.50  | 6.90  | 7.12  |
| DAS42         |       |       |       |       |      |       |       | 7.23  | 6.93  |
| DAS93         |       |       |       |       |      |       |       |       | 7.90  |

Table 3 - Reactions of nine endogamous lines and 36 crosses in relation to *Phaeosphaeria maydis*, in three locations, evaluated by percentage of affected leaf area.

| Taquitubá     | Line  |       |       |       |       |       |       |       |       |
|---------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|               | DAS95 | DAS41 | DAS86 | DAS72 | DAS2  | DAS56 | DAS21 | DAS42 | DAS93 |
| DAS95         | 0.49  | 0.12  | 1.01  | 1.11  | 0.90  | 3.22  | 6.02  | 2.08  | 4.92  |
| DAS41         |       | 0.65  | 1.18  | 2.38  | 8.03  | 4.85  | 5.49  | 18.99 | 25.27 |
| DAS86         |       |       | 2.26  | 3.19  | 6.56  | 6.34  | 8.25  | 14.97 | 7.65  |
| DAS72         |       |       |       | 3.73  | 3.77  | 3.89  | 10.80 | 9.27  | 9.82  |
| DAS2          |       |       |       |       | 4.99  | 6.87  | 17.55 | 18.07 | 15.75 |
| DAS56         |       |       |       |       |       | 5.15  | 18.28 | 20.60 | 19.35 |
| DAS21         |       |       |       |       |       |       | 24.90 | 35.40 | 40.07 |
| DAS42         |       |       |       |       |       |       |       | 38.83 | 34.72 |
| DAS93         |       |       |       |       |       |       |       |       | 48.47 |
| Cravinhos     |       |       |       |       |       |       |       |       |       |
| DAS95         | 0.89  | 0.54  | 0.872 | 1.12  | 2.48  | 2.33  | 3.25  | 3.26  | 4.21  |
| DAS41         |       | 1.15  | 2.27  | 1.59  | 18.90 | 5.24  | 17.80 | 23.28 | 21.92 |
| DAS86         |       |       | 3.22  | 5.43  | 5.61  | 7.09  | 11.05 | 15.33 | 11.30 |
| DAS72         |       |       |       | 5.00  | 5.27  | 5.74  | 9.70  | 14.86 | 8.33  |
| DAS2          |       |       |       |       | 7.17  | 22.19 | 27.45 | 26.50 | 22.53 |
| DAS56         |       |       |       |       |       | 23.90 | 16.88 | 20.36 | 28.48 |
| DAS21         |       |       |       |       |       |       | 26.93 | 30.53 | 40.72 |
| DAS42         |       |       |       |       |       |       |       | 42.62 | 29.18 |
| DAS93         |       |       |       |       |       |       |       |       | 41.95 |
| Iraí de Minas |       |       |       |       |       |       |       |       |       |
| DAS95         | 0.46  | 0.95  | 1.09  | 0.79  | 3.48  | 4.20  | 5.63  | 5.49  | 10.55 |
| DAS41         |       | 5.85  | 6.82  | 5.25  | 12.78 | 10.01 | 18.25 | 31.25 | 30.97 |
| DAS86         |       |       | 5.72  | 9.67  | 9.57  | 8.32  | 14.96 | 35.18 | 29.91 |
| DAS72         |       |       |       | 19.42 | 4.72  | 11.13 | 22.16 | 27.22 | 23.20 |
| DAS2          |       |       |       |       | 35.87 | 26.82 | 30.88 | 43.10 | 32.13 |
| DAS56         |       |       |       |       |       | 38.63 | 24.05 | 38.25 | 41.83 |
| DAS21         |       |       |       |       |       |       | 34.58 | 35.45 | 41.18 |
| DAS42         |       |       |       |       |       |       |       | 47.26 | 34.68 |
| DAS93         |       |       |       |       |       |       |       |       | 50.00 |

Table 4 - Joint variance analysis by the Gardner & Eberhart method for severity of the disease in the entire plant (PI) and percentage of affected leaf area (AFA) by *P. maydis* for nine endogamous lines and 36 diallelic crosses evaluated in three locations.

| Source of Variation       | D.F. | Mean square |            |
|---------------------------|------|-------------|------------|
|                           |      | PI          | % A. F. A. |
| Environments (E)          | 2    | 0.169 ns    | 0.083 **   |
| Genotypes (corrected) (G) | 44   | 0.150 **    | 0.034 **   |
| Lines                     | 8    | 0.758 **    | 0.171 **   |
| Heterosis                 | 36   | 0.014 ns    | 0.004 ns   |
| Mean Heterosis            | 1    | 0.003 ns    | 0.013 ns   |
| Line Heterosis            | 8    | 0.023 ns    | 0.005 ns   |
| Specific Heterosis        | 27   | 0.012 ns    | 0.003 ns   |
| GCA                       | 8    | 37.682 **   | 1.107 **   |
| G×E Interaction           | 88   | 0.003 ns    | 0.001 n.s  |
| Error                     | 270  | 0.108       | 0.013      |
| MS(GCA)/MS(SCA)           |      | 3260.900    | 368.895    |
| CV %                      |      | 15.272      | 31.138     |

n.s.,\*, \*\* -Significance levels by F test: non-significant and significant at  $P < 0.05$  and  $P < 0.01$ , respectively.

The GCA effects were more important than SCA, as judged from their mean square values. Therefore, the genetic additive effects are, for the most part, responsible for the source of variation for resistance to this disease, in this set of lines, for both evaluation methodologies or for both characters (PI and AFA) (Table 5). Consequently, emphasis should be placed on the mean performance of the line in hybrid combinations during selection, for the breeding program to advance toward resistance to *Phaeosphaeria* leaf spot. Even though not significant in the analysis of variance, SCA presented some prominent combinations, such as the DAS95 × DAS41 cross, with a  $(s_{ij}) = -0.206$  and mean for the three locations = 1.69, for the PI character. Significant specific combinations were also found, however at a lower significance level. SCA was significant, at a lower significance level, but it is important with respect to the expression of resistance, even if this is true for only some of the crosses. Its effects, whether positive or negative, should be consistent in the environments, given the non-significance of the SCA × E term.

The means for the GCA estimate, for the three locations and for the nine lines evaluated by the two methods, are presented in Table 6. The orientations of the genetic effects for resistance to the disease were negative in several cases because resistant plants presented lower severity values. Approximately half of the parental lines, evaluated by the two methods, had negative GCA effects, indicating that, on average, these parents contributed to increased resistance of the crosses. Greater negative GCA effects were observed on line DAS95 and greater positive GCA effects were observed on lines DAS93 and DAS42, for both evaluation methods. Highly significant and negative GCA effects were found on lines DAS95, DAS41, DAS86, and DAS72, for both evaluation methods and for crosses between resistant lines. Positive GCA values indicate that it is pointless to utilize parents in crosses.

Table 5 - Mean squares by the Griffing method IV, of the general combination (GCA) and specific combination abilities (SCA), and interactions with locations, for severity in the entire plant (PI), and percentage of leaf area affected (AFA) by *Phaeosphaeria maydis* for nine endogamous lines and 36 diallelic crosses evaluated in three locations.

| Source of Variation | D.F. | Mean square |            |
|---------------------|------|-------------|------------|
|                     |      | PI          | A. F. A. % |
| Environments (E)    | 2    | 0.169 ns    | 0.083 **   |
| GCA                 | 8    | 37.682 **   | 1.107 **   |
| SCA                 | 27   | 0.012 ns    | 0.003 ns   |
| GCA × E             | 8    | 75.556 **   | 2.277 **   |
| SCA × E             | 27   | 0.035 ns    | 0.011 ns   |
| G×E Interaction     | 88   | 0.002 ns    | 0.001 ns   |
| Combined error      | 270  | 0.108       | 0.013      |
| CV %                |      | 15.272      | 31.138     |

ns,\*, \*\* -Significance levels by F test: non-significant, significant at  $P < 0.05$  and  $P < 0.01$ , respectively.

Line DAS95 shows potential for utilization in breeding programs, since an increase in resistance was observed in all crosses with other lines. Line DAS41, on the other hand, can be utilized in specific crosses for the synthesis of hybrids resistant to *Phaeosphaeria* leaf spot.

The highest negative and positive SCA values for severity in the entire plant (PI) were observed for crosses DAS95 × DAS41 and DAS86 × DAS72, respectively (Table 7). For the AFA evaluation, the highest negative and positive SCA effect was observed for crosses of lines DAS95 × DAS42 and DAS41 × DAS93, respectively; this highlights the magnitude of the SCA effects in hybrid combinations for resistance to this disease, which are combinations that can be successfully utilized for its genetic control.

The absence, or small magnitude, of non-additive genetic effects for resistance to a number of diseases has been reported by several authors (Hughes & Hooker, 1971; Lim & Hooker, 1976; Kappelman Jr. & Thompson, 1981). The smaller expression of the non-additive genetic effects for the characters under evaluation should be attributed to the absence of deleterious genes that cause endogamic depression, even though these effects, on the average, have smaller importance than additive effects; however, in specific hybrid combinations, they can be of paramount importance (Hallauer & Miranda Filho, 1988). Results herein presented concerning the genetic control of resistance to the disease as additivity or dominance, are restricted to this group of materials and serve as a reference for projects dealing with fixed groups of lines.

Table 6 - Mean estimates of general combination ability (gi) for the scale of severity of the disease in the entire plant (PI) transformed to square root, and percentage of leaf area affected (AFA) transformed to arcsine of the square root of percentage, of reactions to *Phaeosphaeria maydis*, according to the Gardner and Ebehart method, analysis II, associated to method 2 by Griffing (1956) model I, for nine lines in three locations.

| Endogamous lines         | General combination ability (g <sub>i</sub> ) |            |
|--------------------------|---|------------|
|                          | Severity of the disease (PI) (Rating)         | A .F .A. % |
| DAS95                    | -0.553  | -0.227     |
| DAS41                    | -0.104  | -0.055     |
| DAS86                    | -0.150  | -0.081     |
| DAS72                    | -0.160  | -0.098     |
| DAS2                     | 0.077   | 0.025      |
| DAS56                    | 0.104   | 0.017      |
| DAS21                    | 0.206   | 0.109      |
| DAS42                    | 0.292   | 0.155      |
| DAS93                    | 0.288   | 0.156      |
| Standard deviation (g)   | 0.097   | 0.046      |
| Standard deviation (g-g) | 0.146   | 0.069      |

Table 7 - Mean estimates of specific combination ability ( $s_{ij}$ ) for severity of the disease in the entire plant (PI), (above diagonal), and percentage of affected leaf area (AFA), (below diagonal), by *P. maydis*, according to the Gardner and Eberhart method, analysis II, associated to method 2 by Griffing (1956) model I, for 36 diallelic crosses in three locations.

|       | DAS95               | DAS41               | DAS86  | DAS72  | DAS2   | DAS56  | DAS21  | DAS42  | DAS93  |
|-------|---------------------|---------------------|--------|--------|--------|--------|--------|--------|--------|
| DAS95 | -                   | -0.206 <sup>a</sup> | -0.069 | -0.072 | 0.039  | 0.123  | 0.080  | -0.052 | 0.158  |
| DAS41 | -0.004 <sup>b</sup> | -                   | -0.128 | -0.127 | 0.144  | 0.053  | 0.051  | 0.136  | 0.077  |
| DAS86 | 0.053               | -0.045              | -      | 0.207  | -0.059 | -0.047 | -0.036 | 0.135  | -0.002 |
| DAS72 | 0.070               | -0.032              | 0.067  | -      | -0.132 | -0.027 | 0.052  | 0.060  | 0.039  |
| DAS2  | -0.007              | 0.041               | -0.029 | -0.068 | -      | 0.035  | 0.046  | -0.023 | -0.049 |
| DAS56 | 0.033               | -0.060              | -0.021 | -0.015 | 0.033  | -      | -0.076 | -0.030 | -0.029 |
| DAS21 | -0.017              | -0.038              | -0.043 | 0.014  | 0.035  | -0.023 | -      | -0.075 | -0.042 |
| DAS42 | -0.097              | 0.059               | 0.049  | 0.006  | 0.030  | 0.008  | 0.001  | -      | -0.151 |
| DAS93 | -0.031              | 0.079               | -0.031 | -0.042 | -0.035 | 0.045  | 0.071  | -0.056 | -      |

<sup>a</sup>Standard deviation. ( $s_{ij}$ ) = 0.083 ; ( $s_{ij}-s_{ik}$ )=0.154 ; ( $s_{ij}-s_{kl}$ )=0.115

<sup>b</sup>Standard deviation. ( $s_{ij}$ ) = 0.039 ; ( $s_{ij}-s_{ik}$ )=0.073 ; ( $s_{ij}-s_{kl}$ )=0.054

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