Estimates of Heterosis and Combining Ability for Resistance of Maize to Colletotrichum graminicola

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ABSTRACT

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Various heterosis constants for resistance in maize to leaf blight and stalk rot caused by *Colletotrichum graminicola* were estimated from 45 F_1 diallel crosses and their ten parental inbreds. Leaf blight reactions, disease severity, and lesion lengths were evaluated on seedlings (five- to six-leaf stage) in the greenhouse and on adult plants in the field 2 wk after mid-silk. Stalk rot reactions, number of internodes discolored 75% or more, and total number of internodes discolored were evaluated in the field following artificial inoculation. Seedling blight reactions in the greenhouse were significantly correlated with leaf blight reactions of adult plants in the field, but leaf blight was not correlated with stalk rot. All constants, parental inbreds (V_i), overall heterosis (h_{ij}), the average heterosis ($\bar{h}$), the parent heterosis (h_i), general (g.c.a.) and specific combining ability (s.c.a.), and mean squares (m.s.) were significant for all disease evaluations except $\bar{h}$ effects for stalk rot reactions (number of internodes discolored 75% or more) and s.c.a. effects for lesion length from adult plants. Overall heterosis effects accounted for 29 to 43% of the disease severity of the entry sum of square (s.s.). Certain susceptible inbreds contributed more heterosis for resistance in single crosses than resistant inbreds. However, crosses between resistant inbreds were more resistant to *C. graminicola* for both leaf blight and stalk rot than were those involving intermediately resistant or susceptible inbreds. Of inbreds used in the study, Pa91 and T111 were the most resistant to leaf blight. The significant g.c.a. effects for resistance were usually found from resistant inbreds. Based on predominant additive gene effects and partial dominance for resistance, we believe that combinations of inbreds resistant to leaf blight with inbreds resistant to stalk rot may be used to produce hybrid corn resistant to both leaf blight and stalk rot.

Additional key words: *Zea mays* L., anthracnose, disease resistance, heterotic effects, genetic constants, combining ability.

The maize anthracnose caused by *Colletotrichum graminicola* (Ces.) Wiles. has been known primarily as a leaf spot disease in the United States. Recently, this disease has been observed more frequently throughout a wide range of maize-growing areas and it often causes not only a severe leaf spot but a stalk rot resulting in premature plant kill and in lodging (7, 13, 15). Severe infection on the upper portion of the maize stalk, including the tassel, has been observed in Central Illinois for several years (5). The increase in importance of maize anthracnose has prompted studies on the distribution, pathogenicity, and survival of *C. graminicola* and on the reactions of maize to this fungus (11, 12, 14).

In this paper we report the effects of heterosis and combining ability on resistance to maize anthracnose.

MATERIALS AND METHODS

An isolate of *C. graminicola* was obtained from maize leaves infected in the field and cultured on oatmeal agar at room temperature. Leaf blight inoculum was prepared by blending sporulating cultures with distilled water in a Waring Blendor and filtering the resulting suspension through cheesecloth. The conidial concentration was estimated with a hemocytometer and adjusted to 3.5×10^5/ml. Stalk rot inoculum was prepared by washing conidia from the culture surface and adjusting the suspension to 2×10^5 conidia/ml.

Forty-five F_1 diallel crosses and their ten parental inbreds were tested. Ten inbreds representing a range in susceptibility to *C. graminicola* were crossed in all possible combinations. Inbreds used were Pa91, T111, C123, Oh07B, Mo17, Va26, R177, H95, B73, and Mo940.

Three pots were planted with ten kernels per pot for each entry, and seedlings were thinned to five plants per pot at the two- to three-leaf stage. Seedlings at the four- to five-leaf stage were sprayed with the spore suspension until runoff. They then were placed in moisture chambers for 16 hr. A randomized complete block design with three replications was used to arrange pots in the greenhouse benches.

Plants were rated for disease reaction 14 days after inoculation using the Horsfall-Barratt grading scale (3). The readings were converted with Elanco Conversion tables (Eli Lilly and Co., Indianapolis, IN 46206) into percent leaf area infected. Also, the length of clearly expressed lesions on the fifth leaf of five plants per pot were measured.

During 1976, a set of parents and all possible F_1 crosses,

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excluding reciprocal crosses, were evaluated for leaf blight and for stalk rot reactions. Evaluations to the two phases of the disease were done in separate fields. Each set was in a randomized complete block with three replications at the Agronomy South Farm, Urbana. Each plot (row) within a block contained 12 hills spaced about 40 cm apart with two plants per hill. Plots were spaced approximatly 90 cm apart. Plants were thinned to one plant per hill at the five- to six-leaf stage. Plants were inoculated by spraying spore suspensions with a hand sprayer at the seven- to nine-leaf stage and again 2 wk later. Ten plants in each plot, excluding end plants, were rated with the Horsfall-Barratt grading scale for leaf blight reactions approximately 2 wk after mid-silk. Also, the length of clearly expressed lesions on the ear-leaf of 10 plants per plot was measured.

Stalk rot inoculations were made approximately 2 wk after full-silk stage by injecting 2 ml of inoculum into the first elongated internode above the brace roots. Inoculations were made with a 50-ml Vaco Pistol-Grip Rubber Plunger Syringe (Ideal Instruments, Inc., Chicago, IL 60612) fitted with 2.3-mm-diameter (11-gauge) stainless steel needles. Needles were cut to 7- to 9-cm long, hammered shut at the tip, and the tips ground to a sharp point. Small holes were drilled in both sides of the needles about 1 cm from the tips.

Ratings for stalk rot reaction were made 26 days after inoculation. Stalks were split lengthwise and rated on the basis of number of internodes with discoloration of 75% or more (Rating I) and total number of internodes with discoloration (Rating II).

Analyses of variances for disease reactions were made by use of statistical genetic Models II and III of Gardner and Eberhart (1). The Model II analysis is based on fitting genetic constants in the following model:

$$Y_{ij} = \mu_v + (V_i + V_j)/2 + \gamma\bar{h} + \gamma (h_i + h_j) + \gamma s_{ij}$$

In this model:

Y_{ij} = the observed value of the cross between parents i and j;

μ_v = the mean of all parental varieties;

V_i and V_j = the variety effects when parental cultivars are included in the analysis;

$\bar{h}$ = the average heterosis contributed by the particular set of cultivars used in crosses;

h_i = the average heterosis contributed by variety i in its crosses measured as a deviation from h ($\xi_i h_i = 0$);

S_{ij} = the specific heterosis that occurs when variety i is mated to variety j [same as specific combining ability effects (s.c.a.)–variation not accounted for by average performance of the parent as defined for Griffing's Model I, Method 4(2)];

$$\gamma = \begin{bmatrix} 0 \text{ where } i = j \\ 1 \text{ where } i \neq j \end{bmatrix}$$

$\bar{h} + h_i + h_j + S_{ij} = h_{ij}$ is the overall heterosis due to differences in gene frequences in parental varieties i and j and to dominance in crosses.

In the Model III analysis, variation due to crosses fits to the following model:

$$Y_{ij} = \mu_c + g_i + g_j = s_{ij}$$

in which:

μ_c = the mean of all crosses in the diallel set;

g_i and g_j = general combining ability effects (g.c.a.)–variation accounted for by average performance of the parent, which is the same as that defined in Griffing's Model I, Method 4(2).

A complete Analysis II is given with the addition of the g.c.a. mean squares from Analysis III to provide additional genetic information about the parental inbreds used in this study.

TABLE 1. Analyses of variance for disease reaction to *Colletotrichum graminicola* in the diallel crosses of maize inbreds

Source	d.f.	Mean squares: Seedling reaction: Disease severity (%)[a]	Seedling reaction: Lesion length (mm)[b]	Adult plant reaction: Disease severity (%)	Adult plant reaction: Lesion legnth (mm)[c]	Stalk rot reaction: I[d]	Stalk rot reaction: II[e]
Entries	54	1,686.1*[f]	18.44*	1,456.6*	11.50*	2.28*	3.74*
Parents (V_i)	9	7,151.3*	76.48*	4,937.6*	46.58*	8.93*	14.40*
Heterosis ($\bar{h}_{ij}$)	45	593.0*	6.83*	760.4*	4.48*	0.95*	1.60*
Average (h)	1	381.7*	21.47*	15,095.8*	97.64*	0.35	10.40*
Parents (h_i)	9	606.5*	6.11*	1,127.8*	4.17*	1.53*	2.32*
g.c.a. (g_i)	9	5,254.3*	53.46*	3,541.1*	28.02*	7.83*	9.36*
s.c.a. (s_{ij})	35	595.6*	6.59*	236.4*	1.90	0.82*	1.17*
Error	108	153.3	0.62	132.3	1.74	0.39	0.46

[a]Data are Horsfall and Barratt's scale of 1-12 (Phytopathology 35:655) converted to percentage of disease severity.
[b]The length of clearly expressed lesion on the fifth leaf of seedlings.
[c]The length of clearly expressed lesion on the ear-leaf.
[d]Number of internodes 75% or more discolored.
[e]Total number of internodes discolored.
[f]Asterisks following mean squares indicate statistically significant difference, $P = 0.05$.

RESULTS

Mean squares (m.s.) for parent (V_i) and overall heterosis (h_{ij}) were significant for all disease evaluations (Table 1). The average m.s. for heterosis ($\bar{h}$) were significant for all disease ratings except stalk rot reactions evaluated with Rating I. The heterosis (h_i) m.s. of the parents were significant for all disease evaluations. Variances of the effects of both general combining ability (g.c.a.) and specific combining ability (s.c.a.) were significant for all disease evaluations except s.c.a. for lesion length in adult plants. Although variances of the effects of both g.c.a. and s.c.a. were significant for disease reactions, the m.s. for the g.c.a. effect were much greater than the m.s. of the s.c.a. effect.

The relative importance of those heterotic effects can be compared most effectively by determining the proportion of the sum of square (s.s.) of the entry (Table 1) that are accounted for by h_{ij} and the proportion of the s.s. of h_{ij} that are accounted for by the s.s. of each $\bar{h}$, h_i, and s.c.a. effect. Percentage of the entry s.s. accounted for by h_{ij} ranged from 29 to 43 for all disease evaluations (Table 2). Leaf blight severity in the field had the highest, and that in the greenhouse the lowest, percentage of the s.s. of entry accounted for by h_{ij}. Disease reactions varied greatly in the percentage of the s.s. of h_{ij} accounted for by $\bar{h}$ or s.c.a. s.s. The h_i accounted for 18% (seedling blight severity) to 32% (stalk rot Rating I) of the h_{ij} s.s. The percentages of h_{ij} s.s. accounted for by the $\bar{h}$ for seedling reactions (both blight severity and lesion length) were less than 10%, whereas $\bar{h}$ accounted for over 40% of the h_{ij} s.s. for the adult plant reactions (both blight severity and lesion length). Less than 14% of the h_{ij} s.s. were accounted for by the $\bar{h}$ for both stalk rot Ratings I and II. Specific combining ability effects accounted for at least 26% of the h_{ij} s.s. for all disease evaluations. The proportion of h_{ij} s.s. accounted for by s.c.a. effects were more than 70% for seedling reactions but less than 33% for adult plant reactions. The h_{ij} s.s. of seedling reactions also accounted for a relatively low percentage of the entry s.s. The s.c.a. accounted for more than 50% of the h_{ij} s.s. for both stalk rot ratings.

TABLE 2. Percentage of entry sum of squares (s.s.) accounted for by the heterosis sum of squares; percentage of heterosis sum of squares accounted for by sums of squares of average heterosis, parent heterosis, and specific combining ability (s.c.a.)

Plant reactions	Heterosis s.s. as % of entry s.s.	Percentage of heterosis s.s. accounted for by: Average	Parent	s.c.a.
Seedling reactions				
Disease severity (%)[a]	29.3	1.4	20.4	78.1
Lesion length (mm)[b]	30.8	7.0	17.9	75.1
Adult plant reactions				
Disease severity (%)	43.5	44.1	29.7	26.2
Lesion length (mm)[c]	32.5	48.4	18.6	33.0[f]
Stalk rot reactions				
I[d]	34.7	1.0[f]	32.3	66.9
II[e]	35.8	14.4	29.0	56.6

[a]Data are Horsfall and Barratt's scale of 1-12 (Phytopathology 35:655) converted to percentage of disease severity.
[b]The length of clearly expressed lesion on the fifth leaf of seedlings.
[c]The length of clearly expressed lesion on the ear-leaf.
[d]Number of internodes 75% or more discolored.
[e]Total number of internodes discolored.
[f]Mean square not statistically significant, $P = 0.05$.

Means of disease evaluations for parental inbred, g.c.a. and h_i effects are presented in Table 3. The direction of the genetic effects for disease resistance was negative (−) because the resistant plants had lower disease severities, smaller lesions, and lower stalk rot ratings.

For most disease evaluations, ranking of inbreds based on parental means were similar to rankings based on g.c.a. effects (Table 3). However, the inbred R177 ranked ninth in leaf blight severity obtained from adult plants and fifth in g.c.a. effects. Lesion length on adult plants of inbred R177 ranked ninth and third for g.c.a. effects. Inbred R177 had a spotty yellow appearance at senescence, which probably resulted in overestimates of the leaf blight severity. The overestimates for leaf blight reactions of R177 in the field apparently contributed to the higher negative h_i heterosis in associated crosses. In seedling reactions, both blight severity and lesion length on inbred R177 were lower and smaller. Inbred R177 ranked third in both blight severity and lesion length as a parental inbred. The g.c.a. effects for both blight severity and lesion length were negative and ranked third among parental inbreds. Inbred T111 had the lowest means for both blight severity and lesion length at the seedling stage in the greenhouse. The g.c.a. effects were also significantly negative. In the field, Pa91 inbred had the lowest means for both blight severity and lesion length, and g.c.a. effects were significantly negative. Both T111 and Pa91 inbreds ranked either first or second as parental inbreds for leaf blight resistance in the greenhouse and in the field.

Inbred R177 had the lowest mean in stalk rot reaction. Also, g.c.a. effects were highly negative when evaluated by both stalk rot rating methods. Inbred Va26 ranked fourth in ratings with Rating I and first in negative g.c.a. effects. However, with Rating II it ranked eighth as parental inbred and sixth in positive g.c.a. effects. Inbred T111 ranked second with the Rating I and fifth with Rating II. It ranked third in negative g.c.a. effects for both Rating I and Rating II of stalk rot. Inbred Pa91 ranked sixth and eighth in Ratings I and II. General combining ability effects were all positive.

Average heterosis ($\bar{h}$) was significantly negative for leaf blight reactions from both seedlings and adult plants. However, it was positive for stalk rot reactions obtained by both Ratings I and II. The mean of all parents from Rating I was not significantly different from mean of all crosses. A similar result was obtained with the Rating II. However, from all the data for leaf blight reactions, the means of all crosses were significantly lower for blight severity and smaller for lesion lengths than parental means. Individual cross means and heterosis (h_{ij}) effects for all disease reactions are presented in Table 4.

Most crosses of resistant (R) × susceptible (S) and S × S had a large negative h_{ij} effect for both leaf blight severity and lesion length. Resistant inbreds, Pa911, T111, and R177, or susceptible inbreds, C123, Oh07B, Va26, and Mo940, were always associated as one of parents in these crosses. The highly significant negative h_{ij} effects in the

TABLE 3. Parental means ($\bar{x}$), general combining ability (g_i) effects, and average parental heterosis (h_i) effects for disease reactions in the diallel crosses of maize inbreds to *Colletotrichum graminicola*

	Parent and disease reaction										
	Pa91	T111	C123	Oh07B	Mo17	Va26	R177	H95	B73	Mo940	X[a]
Seedling: disease severity (%)[b]											
$\bar{x}$	9.4	6.3	84.3	81.2	45.8	15.6	12.5	31.2	25.0	54.2	36.5
g_i	−12.7*[c]	−22.7*	12.7*	11.0*	6.7	−12.5*	−12.5*	6.6	−1.1	24.7*	32.6
h_i	0.8	−7.6*	−11.2*	−11.4*	2.0	−2.0	−0.4	9.3*	4.6	15.9*	−3.9
Lesion length (mm)[d]											
$\bar{x}$	2.3	1.0	10.3	11.0	4.8	3.0	3.3	6.7	4.7	6.3	5.2
g_i	−1.2*	−2.2*	1.7*	1.1*	0.9*	−1.4*	−1.3*	0.4	−0.2	2.2*	4.3
h_i	0.3	−0.1	−0.8*	−1.3*	1.1*	−0.3	−0.3	−0.3	0.1	1.7*	−0.9
Adult plant: disease severity (%)											
$\bar{x}$	9.4	25.0	60.4	54.2	12.5	45.8	89.1	31.2	39.6	93.7	46.1
g_i	−12.5*	−12.8*	9.4*	5.4	4.2	−6.0	−5.3	−9.7*	0.7	26.7*	21.3
h_i	5.8	−2.3	2.2	1.4	21.0*	−5.9	−26.8*	−2.3	4.0	2.9	−24.8
Lesion length (mm)[e]											
$\bar{x}$	2.7	4.2	7.7	5.7	4.7	5.0	8.0	5.7	6.3	12.7	6.2
g_i	−1.4*	−1.2*	0.9*	0.5	0.2	−0.4	−0.4	0.7	0.2	2.2*	4.2
h_i	0.4	−0.2	0.2	0.8*	1.0*	0.2	−1.2*	−0.4	0.2	0.9*	−2.0
Stalk rot: Method I rating[f]											
$\bar{x}$	2.3	1.0	3.1	2.8	0.4	1.5	0.4	1.2	1.9	2.3	1.7
g_i	0.60	−0.01	0.02	0.20	−0.80*	−0.90*	−0.70*	0.30	0.20	0.90*	1.80
h_i	0.30	0.30	−0.70*	−0.30	−0.20	−0.60*	−0.10	0.50*	0.10	0.60*	0.12
Method II rating[g]											
$\bar{x}$	4.9	3.3	4.7	4.5	2.2	4.9	1.4	3.0	6.7	3.1	3.9
g_i	0.1	−0.1	0.3	0.1	−1.0*	0.7	−1.0*	−0.2	0.5*	0.8*	4.5
h_i	−0.4*	0.1	−0.1	−0.3	−0.1	0.2	0.2	0.2	−0.9*	1.1*	0.6

[a]Parent $\bar{x}$ = mean of all parents; g_i $\bar{X}$ = mean of all crosses; h_i $\bar{X} = \bar{h}$.
[b]Data are Horsfall and Barratt's scale of 1-12 (Phytopathology 35:655) converted to percentage of disease severity.
[c]Significantly different from zero, $P = 0.05$.
[d]The length of clearly expressed lesion on the fifth leaf of seedling.
[e]The length of clearly expressed lesion on the ear-leaf.
[f]Number of internodes 75% or more discolored.
[g]Total number of internodes discolored.

TABLE 4. Means ($\bar{x}$) and overall heterosis (h_{ij}) values for disease reaction of forty-five crosses among ten maize inbreds infected with Colletotrichum graminicola

	Disease reaction											
	Seeding				Adult plant				Stalk rot			
	Severity (%)[a]		Lesion length (mm)[b]		Severity (%)		Lesion length (mm)[c]		Method I rating[d]		MethodII rating[e]	
Crosses	$\bar{x}$	h_{ij}	$\bar{x}$	h_{ij}	$\bar{x}$	h_{ij}	$\bar{x}$	h_{ij}	$\bar{x}$	h_{ij}	$\bar{x}$	h_{ij}
Pa91 × T111	9.4	1.6	1.7	0.0	6.2	−10.9	2.7	−0.7	3.1	1.5	5.3	1.2
C123	21.9	−25.0	2.7	−3.7	15.6	−19.3	4.2	−0.7	1.7	−1.0	3.6	−1.3
Oho7B	37.5	−7.8	5.0	−1.2	10.9	−20.8	3.3	−1.0	2.8	0.2	4.5	−0.2
Mo17	18.7	−8.9	5.3	1.7	4.7	−6.2	2.0	−0.8	1.9	0.5	3.7	0.1
Va26	6.3	−6.2	1.0	−1.7	5.5	−22.1	2.7	−1.7	2.1	0.2	5.5	0.6
R177	10.9	−0.0	2.2	−0.7	3.1	−46.1	2.0	−1.7	1.3	−0.0	3.9	0.7
H95	7.8	−12.5	2.8	−1.7	3.1	−17.2	1.5	−3.3	2.0	0.2	3.3	−0.6
B75	25.0	7.8	5.2	1.7	4.7	−19.8	2.7	−2.7	3.3	1.2	6.8	0.9
Mo940	54.2	22.4	3.7	−0.7	37.5	−14.1	6.3	−1.8	2.7	0.4	5.0	0.9
T111 × C123	15.6	−29.7	3.8	−1.8	9.4	−33.3	2.7	−3.2	1.5	−0.5	4.1	0.0
Oho7B	21.9	−21.9	4.7	−0.8	12.8	−27.1	3.7	−1.2	2.1	0.2	3.8	−0.1
Mo17	7.0	−18.2	1.3	−1.6	9.4	−9.4	3.3	−1.1	0.8	0.0	4.3	1.5
Va26	4.7	−6.2	1.0	−1.0	10.9	−24.5	3.7	−0.9	1.2	0.0	5.4	1.3
R177	4.7	−4.7	1.7	−0.5	6.2	−50.8	2.7	−3.4	0.9	0.2	3.7	1.3

(Continued)

TABLE 4. (continued)

	Disease reaction											
	Seeding				Adult Plant				Stalk rot			
	Severity (%)[a]		Lesion length (mm)[b]		Severity (%)		Lesion length (mm)[c]		Method I rating[d]		Method II rating[e]	
Crosses	x	h_{ij}	x	h_{ij}	x	h_{ij}	x	h_{ij}	x	h_{ij}	x	h_{ij}
H95	4.7	−14.0	1.3	−2.5	6.2	−21.9	2.7	−2.2	2.1	1.0	3.9	0.8
B73	6.3	−9.3	1.2	−1.7	6.2	−26.0	2.3	−2.9	2.2	0.8	4.7	−0.4
Mo940	36.5	6.2	4.3	0.7	21.9	−37.5	4.7	−3.7	2.3	0.7	4.6	1.3
C123 × Oho7B	52.1	−30.7	6.3	−3.8	31.2	−26.0	5.3	−1.3	2.9	−0.0	5.1	0.5
Mo17	45.8	−19.2	6.7	−0.9	33.3	−3.1	5.0	−1.1	0.6	−1.2	4.2	0.8
Va26	33.3	−16.7	4.3	−2.3	12.5	−40.6	4.0	−2.3	0.2	−2.0	5.6	0.8
R177	54.2	5.7	5.7	−1.2	21.9	−52.9	5.3	−2.5	1.1	−0.6	4.2	1.1
H95	75.0	17.2	8.0	−0.5	18.7	−27.1	4.2	−2.5	2.9	0.8	4.9	1.1
B73	54.2	−0.5	6.3	−1.2	36.5	−13.5	5.3	−1.7	1.7	−0.7	5.6	−0.1
Mo940	42.8	−26.5	8.7	0.3	87.5	10.4	9.3	−0.8	3.7	1.0	6.2	2.3
Oho7B × Mo17	52.1	−11.5	2.0	−0.4	45.8	12.5	6.3	1.2	0.9	−0.7	3.1	−0.2
Va26	18.8	−29.6	3.3	−3.2	18.7	−31.2	4.0	1.3	1.0	−1.2	5.1	0.4
R177	12.0	−34.4	2.8	−3.8	12.5	−59.1	4.0	−2.8	1.7	0.1	3.8	0.8
H95	54.2	−2.1	6.7	−1.7	9.4	−33.3	3.3	−2.3	2.6	0.5	4.5	0.7
B73	60.4	7.3	5.5	−1.8	31.2	−15.6	6.0	0.0	1.6	−0.7	4.9	−0.7
Mo940	71.9	4.2	6.0	−2.2	62.5	−11.5	6.7	−2.5	2.5	−0.0	6.2	2.4
Mo17 × Va26	37.5	6.8	4.7	0.7	19.5	−9.6	4.0	−0.8	0.8	−0.2	3.9	0.4
R177	25.0	−4.2	2.7	−1.4	20.3	−30.5	4.3	−2.0	0.3	−0.1	2.3	0.5
H95	45.8	7.3	4.0	−1.7	19.5	−2.3	3.8	−1.3	1.4	0.6	3.7	1.1
B73	25.0	−10.4	4.2	−0.6	20.3	−5.7	4.7	−0.8	1.4	0.2	3.4	−1.0
Mo940	89.0	39.0	10.0	4.4	52.1	−1.0	6.3	−2.3	2.0	0.6	4.2	1.5
Va26 × R177	12.5	−1.5	1.5	−1.7	17.2	−50.3	4.0	−2.5	1.0	0.1	3.8	0.7
H95	14.0	−9.4	2.0	−2.8	15.6	−22.9	4.0	−1.3	1.5	0.2	5.1	1.1
B73	6.3	−14.0	1.5	−2.3	18.7	−23.9	4.3	−1.3	0.9	−0.8	5.4	−0.4
Mo940	60.4	25.5	8.3	3.7	25.0	−44.8	4.7	−4.2	1.9	0.0	6.4	2.4
R177 × H95	15.6	−6.7	3.3	−1.7	9.4	−50.8	3.7	−3.2	1.1	0.3	3.9	1.7
B73	25.0	6.2	4.3	0.3	18.7	−45.6	4.0	−3.2	1.5	0.4	3.8	−0.3
Mo940	33.3	−0.0	4.3	−0.5	39.6	−51.8	5.3	−5.0	1.4	0.0	3.2	1.0
H95 × B73	54.2	26.1	5.7	−0.0	7.0	−28.4	3.5	−2.5	1.7	0.2	4.4	−0.5
Mo940	75.0	32.3	8.3	1.8	25.0	−37.5	5.7	−3.5	3.1	1.3	5.2	2.2
B73 × Mo940	28.17	−11.4	3.2	−2.3	54.2	−12.5	7.3	−2.2	3.6	1.5	5.7	0.8
L S D ($P=0.05$) for heterosis values:		22.6		1.4		21.0		2.4		1.1		1.2

[a]Data are Horsfall and Barratt's scale of 1-12 (Phytopathology 35:655) converted to percentage of disease severity.
[b]The length of clearly expressed lesion on the fifth leaf of seedlings.
[c]The length of clearly expressed lesion on the ear-leaf.
[d]Number of internodes 75% or more discolored.
[e]Total number of internodes discolored.

crosses associated with R177 inbred as one of parents for adult plant reactions probably resulted from an overestimate of leaf blight severity due to early senescence in the field.

For stalk rot reactions, crosses of C123 × Mo17, C123 × Va26, and Oh07B × Va26 had significant negative h_{ij} effects with Rating I; however, Pa91 × C123 was the only cross that had significant negative h_{ij} effects with Rating II. In our crosses, inbred Mo17 was the only resistant parent and Va26 was intermediately resistant by Rating I. None of the crosses associated with resistant R177 inbred exhibited significant negative h_{ij} effects. The s.c.a. effects from crosses of C123 × Mo940 (s.c.a. = −27.2*) and B73 × Mo940 (s.c.a. = −28.0*) were negative and significant for the seedling leaf blight severity. Negative s.c.a. effects were found from various crosses for all the disease reactions, but they were not significant.

Correlation coefficients (r) between leaf blight severity and lesion length from both seedlings in the greenhouse ($r = 0.88$) and adult plants in the field ($r = 0.94$) were highly significant (Table 5) indicating disease severity depends upon lesion length. Leaf blight severity and lesion length in seedlings were significantly correlated with those reactions in adult plants. The correlation between the two

TABLE 5. Correlations among disease reactions of maize to Colletotrichum graminicola by use of means of forty-five crosses among ten inbreds

	Disease reaction					
	Seedling		Adult plant		Stalk rot	
	Severity (%)[a]	Lesion length (mm)[b]	Severity (%)	Lesion length (mm)[c]	Rating I[d]	Rating II[e]
Seedling						
Severity (%)		0.88**[f]	0.57*[g]	0.62*	0.28	0.23
Lesion length (mm)			0.56*	0.56*	0.32	0.22
Adult plant						
Severity (%)				0.94**	0.29	0.28
Lesion length (mm)					0.26	0.29
Stalk rot						
Rating I						0.52*
Rating II						

[a]Data are Horsfall and Barratt's scale of 1-12 (Phytopathology 35:655) converted to percentage of disease severity.
[b]The length of clearly expressed lesion on the fifth leaf of seedlings.
[c]The length of clearly expressed lesion on the ear-leaf.
[d]Number of internodes 75% or more discolored.
[e]Total number of internodes discolored.
[f]Significant at the 0.01 probability level.
[g]Statistically significant, $P = 0.05$.

stalk rot ratings was also significant. However, these r values are relatively low, ranging from 0.52 to 0.62. Leaf blight reactions from both seedlings and adult plants were not correlated with the stalk rot reactions obtained by either Ratings I or II.

DISCUSSION

The estimation of genetic constants and their associated m.s. from Analytical Methods II and III of Gardner and Eberhart (1) provided useful information on the heterotic effects on resistance in maize to *C. graminicola.* The partitioning of the heterosis sum of squares into various types of heterosis constants from Analysis II was particularly useful, whereas the g.c.a. effects estimated from Analysis III provided additional information.

The significant h_{ij} effects for both leaf blight and stalk rot reactions indicated that partial dominance for resistance or susceptibility was at some loci. Crosses with significant negative h_{ij} effects for resistance always had susceptible inbreds as one of the parents. Significant positive h_{ij} effects for susceptibility were found in some crosses of S × S. Heterosis accounted for most of the variation in leaf blight reactions of adult plants, indicating that expression of heterosis for resistance was greater in adult plants than in seedlings.

The significant m.s. for g.c.a., h_i, and s.c.a. effects suggested that both additive and nonadditive genetic effects were important in anthracnose resistance. However, greater m.s. for g.c.a. effects indicated that additive effects were more important than nonadditive effects. Highly significant negative g.c.a. effects were found from resistant inbreds T111 and Pa91 for leaf blight and Mo17 and R177 for stalk rot resistance, and crosses between resistant inbreds were the most resistant to *C. graminicola.* This was true even though contributions of heterotic effects for resistance were smaller in single crosses of resistant than in single crosses of susceptible inbreds. Evidence of predominantly additive genetic effects and partial dominance for resistance to both leaf blight and stalk rot suggested that combination of two resistant inbreds would produce a resistant single cross.

No significant negative s.c.a. effects were found from any crosses for both leaf blight and stalk rot resistance, except for resistance to leaf blight in some crosses of S × S. The importance of additive genetic variation and the absence or relatively small magnitude of the nonadditive genetic effects for resistance to numerous diseases has been reported (4, 6, 8, 9, 10). The insignificant correlations of leaf blight with stalk rot reactions indicated that each reaction was influenced by a separate genetic system. The significant correlations of seedling leaf blight with those of adult plants were lower than would be expected under favorable environmental conditions, probably because dry weather early in the season resulted in slow development of leaf blight. This could have influenced the disease reactions. Although the correlation between stalk rot reactions evaluated by Ratings I and II was significant, only 27% ($R = 0.52$) of the variation in Rating II was ascribed to the effect of Rating I. These correlations are specific for the set of crosses used in this study and are not necessarily typical of other populations.

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