Diallel Analysis of Resistance of Eight Maize Inbred Lines to *Sphacelotheca reiliana*

I. V. Whythe and H. O. Gevers

Senior agricultural researcher and assistant director, Summer Grain Sub-Centre, c/o University of Natal, P.O. Box 375, Pietermaritzburg, Natal, Republic of South Africa.

Accepted for publication 20 February 1987.

ABSTRACT

Whythe, I. V., and Gevers, H. O. 1988. Diallel analysis of resistance of eight maize inbred lines to *Sphacelotheca reiliana*. Phytopathology 78:65-68.

A diallel set of hybrids (excluding reciprocals) involving eight maize inbred lines was used to analyze the genetic basis of resistance to *Sphacelotheca reiliana*. Inoculum was applied at planting, and the incidence of disease, yield, and plant height measured. Correlations among these three characters were highly significant. The most resistant crosses involved Mo17 or U267Y as a parent. Estimates of combining ability indicated that general combining ability effects were an important source of genetic variance for ear and tassel smut resistance. The V_r, W_r graphic analysis indicated that resistance to *S. reiliana* was additive and partially dominant. The relative position on the regression line of Mo17 and U267Y to the other inbreds suggested that these lines had the most dominant genes. Recurrent selection is therefore suggested for the development of maize resistant to *S. reiliana*.

Additional key words: ear and tassel smut, susceptibility, variances.

Ear and tassel smut (also known as head smut), which is caused by the fungus *Sphacelotheca reiliana* (Kühn) Clint., is a soilborne disease of both maize and sorghum in the drier parts of the world. The incidence of the disease is dependent on the moisture, temperature, and pH of the soil and the time of planting (1,6,10). The disease is manifested by the production of sori or anomalous shootlike growths on the reproductive parts of the plant that result in a loss of yield. It is also associated with stunting and excessive tillering of the plant (7).

Differences in resistance to *S. reiliana* have been observed among inbred lines of maize (2,4,12,13,16), tropical populations (3), and varieties (10). It has been proposed that there are both additive and dominant gene effects for the expression of resistance to *S. reiliana* (16). The present study determined the general and specific combining ability of eight maize inbred lines and investigated the genetic effects of resistance to ear and tassel smut.

MATERIALS AND METHODS

Eight maize inbred lines were selected on their performance in an inoculated observation trial during the 1981–1982 season. The inbreds showed either resistance (U267Y, F2834T, Mo17, and I137TN), intermediate (D0940Y-1), or susceptible (G119Y, M162W, and B1138T) reactions to *S. reiliana* (I. V. Whythe, *unpublished*). A diallel set of 28 F_1 hybrids, excluding reciprocals, was made from these eight inbred lines.

In 1984, the eight parents and 28 single crosses were planted at Ukulinga Research Farm, Pietermaritzburg, in a 6×6 triple lattice design with three replications. Each plot contained three rows of 20 plants at a population of 40,000 plants per hectare. All plots were inoculated with a spore-soil mixture as described by Whythe and Gevers (16) with inoculum collected from smutted plants in 1982. The same entries were also planted on the same date in an adjacent field but without inoculation.

The number of plants with smut on the tassels or ears was counted for each plot. The weight of grain from the middle row of each plot was recorded at harvest, and the yield was adjusted to 12.5% moisture. Plant height of 10 plants from the middle row of each plot from two replications was measured, and the mean was calculated for each plot. The variance of the percentage of smutted plants of each plot suggested that a square root (arcsin) transformation of the original data was required to achieve normality (14).

Analyses of variance were performed for smut incidence, yield, and plant height. General combining ability (GCA) and specific combining ability (SCA) effects of the parents for smut incidence were estimated according to Griffing's method 2, model I, as appropriate for fixed effects and selected parents (5).

Graphic analysis (V_r, W_r) was used to determine the genetic dominance effects and relations within the parental inbred lines. V_r is the variance of all the offspring of each parent in each array (complete row or column), and W_r is the covariance between these offspring and their nonrecurrent parents (8,9). The slope of the regression line V_r, W_r was tested for deviation from unity by Student's *t*-test (11). Two-way analyses of variance on the $W_r + V_r$ and $W_r - V_r$ values calculated for each of the parents were used to test the underlying assumptions of the additive-dominance model.

RESULTS

Artificial inoculation assured that all plants were infected, whereas the control trial gave a comparison to show the effects of the disease on yield and plant height (Table 1). The drop in yield and loss of vigor were demonstrated when the data from the inoculated and control trials of the susceptible inbreds G119Y, B1138T, and M162W were compared. In the inoculated trial the correlation coefficients (r) between yield and smut incidence ($r = -0.74$) and between plant height and smut incidence ($r = -0.49$) were highly significant. The correlations between plant height and yield from the inoculated ($r = 0.80$) and control ($r = 0.84$) were also highly significant, which is to be expected because of the greater number of hybrids in relation to inbreds in the trials. Significant differences among inbreds and hybrids were found for disease reaction (Table 1). The inbreds U267Y and Mo17 had little or no infection, and this was reflected in their crosses. Similarly, inbreds F2834T and I137TN showed resistance in their crosses except when crossed to the highly susceptible inbred G119Y. The inbred D0940Y-1 was less susceptible than G119Y, B1138T, and M162W.

The means of the smut incidence data (arcsin transformed) of the crosses were plotted against the midparent values and the regression line fitted (Fig. 1). The slope of the regression line ($b = 0.84$) indicated that additive gene action was important in reaction to this disease (17).

GCA and SCA effects for disease reaction were highly significant (Table 2). However, mean squares for GCA were much greater than those for SCA, indicating a preponderance of additive gene effects for reaction to the disease in this material.

The resistant inbred Mo17 had the highest negative GCA effect for disease incidence of all the inbreds, whereas G119Y, the most susceptible inbred, had the highest positive CGA effect (Table 3). Although U267Y and Mo17 had high negative GCA effects, they attained their high average performance by entirely different means. The relatively low SCA variance for Mo17 indicates that it transmits its high resistance to all its hybrid progenies, whereas the higher SCA variance for U267Y indicates that there are specific combinations of U267Y with certain inbreds (e.g., U267Y × B1138T) that are more resistant and other combinations that are more susceptible (e.g., U267Y × F2834T) than would be expected.

The low SCA variance for F2834T indicates that hybrids with this line have performed as would be expected on the basis of their GCA. The high SCA variance for some lines (e.g., G119Y) indicates that some combinations were less susceptible (e.g., B1138T×G119Y), and others were more susceptible (e.g., D0940Y-1 × G119Y) than expected (Table 3).

The low estimate of GCA variance for D0940Y-1 indicates that this line is intermediate in its general combining ability for reaction to ear and tassel smut infection. The estimate of the SCA variance for this inbred line is much greater than its GCA variance. This suggests that, in this case, epistasis and dominance effects are more important than additive gene effects. For all the other inbred lines,

TABLE 1. Mean incidence percentage, yield, and plant height for eight maize inbreds lines and their 28 single crosses from inoculated and control trials

	Inoculated			Control		
Inbred/hybrid	Incidence (%)	Yield (t/ha)	Height (cm)	Incidence (%)	Yield (t/ha)	Height (cm)
U267Y	0.00	1.94	129.50	0.00	1.66	125.00
Mo17	1.13	2.19	140.50	0.00	1.97	142.00
F2834T	1.71	1.84	126.25	1.15	1.32	127.25
I137TN	7.38	2.67	108.00	0.00	1.22	96.50
D0940Y-1	19.77	0.23	128.75	0.00	0.23	137.25
M162W	76.13	0.68	110.00	6.25	1.85	129.25
B1138T	91.26	0.17	101.00	9.44	0.85	115.50
G119Y	99.36	0.00	78.75	21.32	1.06	96.00
U267Y × Mo17	1.11	4.41	182.75	0.00	3.89	184.25
U267Y × F2834T	3.36	4.45	169.50	0.60	4.37	168.00
U267Y × I137TN	4.44	5.28	200.25	1.11	5.08	179.00
U267Y × D0940Y-1	5.60	4.17	194.75	0.56	4.21	187.25
U267Y × M162W	38.82	3.68	172.00	1.20	4.96	186.00
U267Y × B1138T	10.18	4.07	185.00	0.00	3.89	178.50
U267Y × G119Y	44.63	1.71	165.00	5.09	3.08	163.75
Mo17 × F2834T	0.56	3.62	188.00	0.00	3.43	175.75
Mo17 × I137TN	1.11	4.88	196.50	0.00	4.27	184.75
Mo17 × D0940Y-1	15.56	4.13	200.00	2.22	3.70	184.00
Mo17 × M162W	16.28	4.02	179.00	2.22	3.30	169.25
Mo17 × B1138T	18.89	3.86	179.50	3.36	3.81	173.00
Mo17 × G119Y	37.50	2.74	165.00	12.30	3.07	174.25
F2834T × I137TN	6.14	4.29	168.00	0.56	4.02	156.25
F2834T × D0940Y-1	12.36	3.61	178.50	0.56	3.72	177.00
F2834T × M162W	25.56	3.80	172.75	3.89	3.92	179.50
F2834T × B1138T	23.34	3.79	167.75	1.67	3.81	167.00
F2834T × G119Y	59.23	1.86	139.75	7.78	3.12	139.25
I137TN × D0940Y-1	25.18	4.69	194.50	1.67	5.18	190.75
I137TN × M162W	11.86	3.80	190.50	2.84	4.10	176.50
I137TN × B1138T	42.78	2.33	162.50	6.67	4.08	151.50
I137TN × G119Y	73.33	1.53	162.50	19.77	2.86	170.50
D0940Y-1 × M162W	40.55	2.88	172.50	8.33	3.48	173.50
D0940Y-1 × B1138T	67.96	1.68	176.25	8.51	3.33	176.50
D0940Y-1 × G119Y	93.83	0.09	151.25	20.68	2.62	163.00
M162W × B1138T	59.77	1.46	169.25	6.67	3.15	176.25
M162W × G119Y	85.00	0.54	138.25	26.33	2.76	167.75
B1138T × G119Y	77.22	0.95	140.00	27.63	3.27	163.75

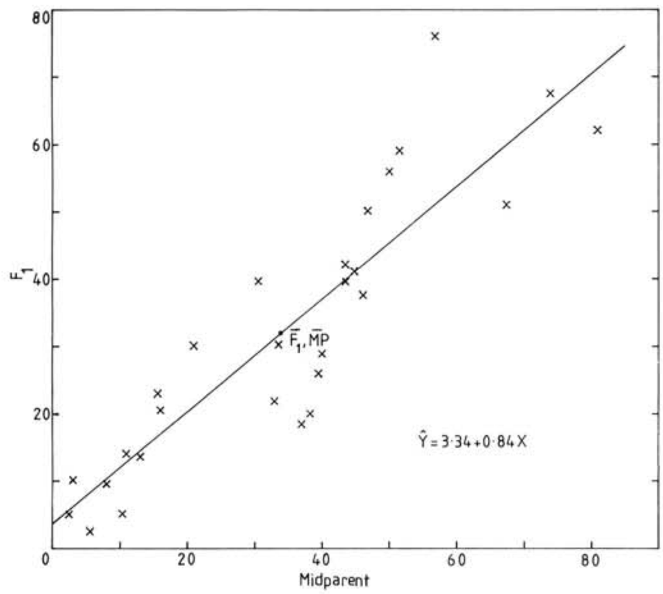

Fig. 1. Regression of the hybrid on midparent value for the incidence of ear and tassel smut (arcsin transformed data) of 28 crosses from a diallel of eight maize inbred lines.

TABLE 2. Mean squares from analysis of variance of combining ability for incidence of *Sphacelotheca reiliana* in an eight maize line diallel, after Griffing (5)

Source of variation	df	Mean squares	*F*
Entries	35	554.16	72.55**
GCA	7	2536.70	332.11**
SCA	28	58.53	7.66**
Error	70	7.64	

[a]** = Significant at 0.01 level.

TABLE 3. Estimates of specific combining ability (SCA) and general combining ability (GCA) effects and their variances for disease incidence of *Sphacelotheca reiliana* for eight maize inbreds

	SCA effects							
Inbred	U267Y	Mo17	F2834T	I137TN	D0940Y-1	M162W	B1138T	G119Y
U267Y	−1.35	4.09	5.82	1.06	−5.20	11.64	−12.14	−2.59
Mo17		4.62	−1.53	−3.14	−4.86	−2.66	−4.48	−6.38
F2834T			−1.61	2.24	−1.31	0.32	−5.00	2.67
I137TN				−0.21	4.10	−13.97	2.89	7.23
D0940Y-1					−9.84	−4.69	7.90	14.03
M162W						8.61	−5.45	−2.42
B1138T							14.11	−11.94
G119Y								−0.29
GCA effects	−15.65	−16.14	−12.49	−8.42	1.67	9.84	13.70	27.49
GCA variance	243.81	259.39	154.89	69.78	1.68	95.71	186.58	754.59
SCA variance	55.03	13.70	6.16	41.73	52.04	59.53	66.21	68.98

the GCA variance was much greater than the corresponding SCA variance.

The regression of W_r on V_r (Fig. 2) was significant ($t_{(6)} = 5.7$, $P = 0.001$) and the value of the regression coefficient, b, did not depart significantly from unity (S.E. = 0.16). This indicates the presence of dominance, but there is no indication of nonallelic interaction. As the intercept of the regression line passes through the W_r axis above the origin ($a = 242.57$), this suggests that dominance is partial. The inbred line Mo17 appeared to have the most dominant genes, whereas D0940Y-1 had the most recessive genes (Fig. 2).

Analyses of variance of $W_r + V_r$ and $W_r - V_r$ were performed, and the mean squares between arrays for $W_r - V_r$ was highly significant when tested against that within arrays, which is evidence of nonallelic interaction ($F = 4.88$, $P = 0.01$) (8). Similarly, in the analysis of variance of $W_r + V_r$, the mean squares between arrays was significantly greater than that within arrays ($F = 4.46$, $P = 0.01$), which confirms the presence of dominance indicated in the combining ability analyses. The order of dominance of the parents as determined by $W_r + V_r$ is also shown graphically in Figure 2. Mo17 and U267Y carried the most dominant genes and were the most resistant, whereas D0940Y-1 carried the least dominant genes. The correlation of 0.35 between $W_r + V_r$ and $\bar{y}_r$ suggests that dominance is not the only factor involved in the expression of resistance.

DISCUSSION

The effects of ear and tassel smut on yield and plant height have been quantified and show the potential loss of yield that may arise with the use of susceptible breeding material. Baier and Krüger (1) also showed the importance of this disease in terms of yield loss when conditions favor the development of the fungus, while Halisky (7) reported its stunting effect. The highly significant correlations between yield and incidence and plant height and incidence confirm these earlier observations.

The resistance associated with the inbred line Mo17 was also demonstrated by Bockholt et al (2) and Stromberg et al (15). They also reported that the inbred line WF9, which features in a recovered form in the pedigree of the resistant inbred line U267Y (viz., Mex 155^3.WF9R), was resistant. Similarly, Krüger (10) reported the susceptibility of the inbred line K64, the original version of the line involved in the derivation of M162W. However, the inbred line B1138T, which was used as the backcross donor in the development of M162W (viz., $K64R^2$.B1138T), was probably the main source of susceptibility in this line.

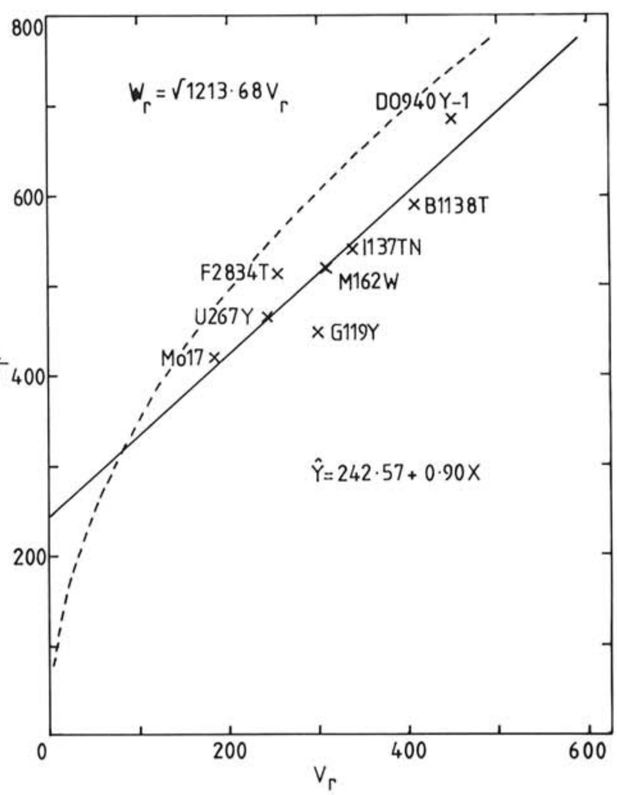

Fig. 2. Variance–covariance graph of eight maize inbred lines for incidence of *Sphacelotheca reiliana*. V_r is the variance of all the offspring of each parent in each array (complete row or column); W_r is the covariance between these offspring and their nonrecurrent parents.

It must be emphasized that the estimates of SCA and GCA effects reported here are only relative to one another and specific to the selected group of inbred lines involved in this study. Therefore, the large values of GCA variance for Mo17 and G119Y may have arisen because these lines are much more resistant (Mo17) or susceptible (G119Y) than the other lines with which they were tested. The high values of GCA variance compared with SCA variance indicate the greater relative importance of genes with additive effects. However, there is some evidence for the presence of epistasis and dominance effects, as shown by the greater SCA variance than the GCA variance for D0940Y-1.

The graphic analysis (V_r, W_r) indicated that resistance to ear and tassel smut was additive and partially dominant. The evidence from the analyses of variance of nonallelic interactions precluded further detailed analysis of this data. However, the behavior of the inbred line D0940Y-1 in both the combining ability analysis of Griffing (5) and the graphic analysis of Hayman (8) suggests that epistasis and dominance effects may in some cases be more important than additive gene effects.

The high GCA and SCA variances for U267Y suggest that the resistance associated with this line would be best used in the production of specific hybrids and synthetics. Mo17, which has a higher GCA variance and a lower SCA variance than U267Y, and F2834T, which has a low SCA variance, would probably be most useful in a resistant synthetic. The results from the graphic analyses agree with those from the combining ability analyses in that genes with additive effects, and to a lesser extent those with dominance effects, are the main factors involved in the response to *S. reiliana* of these eight maize inbred lines. This investigation generally confirms that useful sources of resistance to this disease are available in elite local breeding material for the development of new resistant inbred lines and populations. The overall importance of additive gene action suggests that recurrent selection would be an effective procedure to develop material with resistance to ear and tassel smut.

LITERATURE CITED

1. Baier, W., and Krüger, W. 1962. *Sphacelotheca reiliana* on maize. II. Field studies on the effect of soil conditions. S. Afr. J. Agric. Sci. 5:183-190.
2. Bockholt, A. J., Frederiksen, R. A., Foster, J. H., and McClung, A. M. 1980. Reaction of corn cultivars to head smut. Tex. Agric. Exp. Stn. Misc. Publ. MP-1455. 18 pp.
3. Fuentes, S. 1963. Resistance to head smut in Mexican races of corn. (Abstr.) Phytopathology 53:24.
4. Gevers, H. O. 1975. Ecology of smut in the high rainfall area. Proc. 1st S. Afr. Maize Breeding Symp. Potchefstroom. Tech. Commun. Dep. Agric. Tech. Serv. Repub. S. Afr. 132:95-97.
5. Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. 9:463-493.
6. Halisky, P. M. 1962. Prevalence and pathogenicity of *Sphacelotheca reiliana* causing head smut of field corn in California. Phytopathology 52:199-202.
7. Halisky, P. M. 1963. Head smut of sorghum, Sudangrass and corn caused by *Sphacelotheca reiliana* (Kühn) Clinton. Hilgardia 34:287-304.
8. Hayman, B. I. 1954. The theory and analysis of diallel crosses. Genetics 39:789-809.
9. Jinks, J. L. 1954. The analysis of continuous variation in a diallel cross of *Nicotiana rustica* varieties. I. The analysis of F_1 data. Genetics 39:767-788.
10. Krüger, W. 1962. *Sphacelotheca reiliana* on maize. I. Infection and control studies. S. Afr. J. Agric. Sci. 5:43-56.
11. Mather, K., and Jinks, J. L. 1977. Introduction to Biometrical Genetics. Chapman & Hall, London. 231 pp.

12. Simpson, W. R., and Fenwick, H. S. 1968. Chemical control of corn head smut. Plant Dis. Rep. 52:726-727.
13. Simpson, W. R., and Fenwick, H. S. 1971. Suppression of corn head smut with carboxin seed treatments. Plant Dis. Rep. 55:501-503.
14. Snedecor, G. W. 1956. Statistical Methods. Iowa State University Press, Ames. 535 pp.
15. Stromberg, E. L., Stienstra, W., Kommedahl, T., Matyac, C. A., Windels, C. E., and Geadelmann, J. L. 1984. Smut expression and resistance of corn to *Sphacelotheca reiliana* in Minnesota. Plant Dis. 68:880-884.
16. Whythe, I. V., and Gevers, H. O. 1983. Tassel smut in maize: A brief review of inoculation techniques. Proc. 5th S. Afr. Maize Breeding Symp. Potchefstroom. Tech. Commun. Dep. Agric. Repub. S. Afr. 182:53-55.
17. Widstrom, N. W. 1976. Graphic interpretation of regressions of F_1 on midparent and the application to anomalous data. J. Hered. 67:54-58.