Relationships of Environmental and Cultural Factors with Severity of Gray Leaf Spot in Maize

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ABSTRACT

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Gray leaf spot of maize caused by *Cercospora zeae-maydis* is a major foliar disease in the United States and other parts of the world. Efficient management of gray leaf spot is hindered by a lack of quantitative information regarding environmental and cultural influences on disease severity. We collected environmental, cultural, and disease severity data in southern Iowa at 13 locations in 1998 and 11 locations in 1999. The independent variables that we considered included temperature, relative humidity, leaf wetness, percent maize residue cover, distance to nearest maize residue, planting date, and previous crop. A time-duration value (TDV) variable was created to represent cumulative hours of favorable temperature ($22 \leq T \leq 30^\circ\text{C}$) and relative humidity ($\geq 95\%$). Disease severity was assessed at 2-week intervals on three to eight maize genotypes differing in gray leaf spot resistance and maturity at each location. Environmental, cultural, and disease data were summarized for four different periods during the growing season and analyzed by stepwise multiple linear regression in order to determine which variables significantly contributed to gray leaf spot severity at the dough or dent growth stages of maize. In 1998, genotype resistance, planting date, distance to nearest maize residue, wetness duration, and TDV had significant effects on disease severity. R^2 values were similar among the four periods. The best-fitting model for the 1998 data had an R^2 of 0.65. With 1998 and 1999 data combined, results were similar except that percent maize residue cover was significant rather than distance to nearest maize residue. The best-fitting model had an R^2 of 0.55. The 2-year model utilizing only the weather variables from emergence to 2 weeks before silking had an R^2 value of 0.43. Strong linear relationships existed between gray leaf spot severity and genotype resistance, maize surface residue, planting date, and TDV. These results can serve as a foundation for the development of a prediction model for gray leaf spot severity on maize.

Additional keywords: corn

Gray leaf spot, caused by the fungus *Cercospora zeae-maydis* Tehon & E. Y. Daniels, is an important disease of maize (*Zea mays* L.) in the United States (15,35), parts of South and Central America (4,15,35), and South and Central Africa (35). In the United States, gray leaf spot originally was damaging only in the south-eastern states (15,31), but now causes losses throughout the eastern half of the country and as far west as Nebraska. The maize-growing area in the United States

affected by gray leaf spot grew from 7.2 to 14.9 million ha during the 1980s and 1990s (31). In Iowa, gray leaf spot became prevalent in the southern half of the state throughout the 1990s, and the disease now can be found statewide. Gray leaf spot can be a significant problem in the production of both maize seed and grain and can cause major reductions in yield. For example, control of the disease with fungicides has resulted in yield increases as high as 7,129 kg/ha in Virginia (32) and 3,869 kg/ha in Iowa (13), reflecting yield losses of 69 and 44%, respectively, due to gray leaf spot. Critical factors that determine the extent of yield loss in gray leaf spot epidemics include the growth stage at which gray leaf spot infects the maize plant, genotype susceptibility, the presence of sufficient hours of favorable weather conditions, and the amount of initial inoculum in the field as affected by tillage practices and crop rotation (17).

Widespread adoption of minimum tillage practices combined with maize monoculture are believed to be responsible for the increased prevalence and severity of gray leaf spot throughout maize-cropping regions (15,35). The pathogen survives

well in maize residue on the soil surface (8,23,24) and gray leaf spot severity increases as the percent of soil surface covered with maize residue increases (9). Residue in neighboring fields also can serve as a potential source of inoculum (10,35). Another cultural practice that influences severity of gray leaf spot is planting date. Later-planted maize generally has greater gray leaf spot severity and higher yield losses than earlier-planted maize (17,29). This is because initial infection by *C. zeae-maydis* takes place at an earlier plant growth stage on late-planted maize, enabling the fungus to undergo a greater number of secondary cycles during the grain-fill period (29,35).

Relative humidity (RH) and temperature are key influences on gray leaf spot development (1,2,33). Previous studies have identified the optimum temperature and RH ranges for growth of and subsequent infection by *C. zeae-maydis*, but specific infection periods during the growing season have not been defined. Thorson and Martinson (33) showed that $\text{RH} \geq 95\%$ is optimal for germ tube elongation and formation of appressoria. They also found that the number of appressoria formed was correlated with number of hours spent at $\geq 95\%$ RH. As a result, prolonged periods of high RH resulted in high levels of the disease (29,33). A temperature of 22 to 30°C is optimal for germination and growth of the fungus (1,2). The role of leaf wetness in gray leaf spot development is not fully understood. One study in Kentucky indicated a correlation between frequent, prolonged leaf wetness during July to September and high gray leaf spot severity (29). The authors concluded that wetness may encourage spore germination and spore survival, as has been shown by Beckman and Payne (1). In the greenhouse, long periods of wetness or free water favored germination (1,3), germ tube growth, and formation of mycelium on the leaf surface (1,33); however, intermittent shorter periods of wetness favored infection and resulted in more disease (1). Conidia and germlings of *C. zeae-maydis* can survive periods of unfavorable temperatures or humidity and can resume the infection process once suitable conditions return (33).

Management practices for gray leaf spot include a combination of partially resistant hybrids, crop rotation, residue management, early planting, and foliar fungicide

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applications (5,21,35). The implementation of each tactic is subject to considerable constraints. For example, tillage buries infested residue but is not a long-term solution because of the problem of soil erosion. Moreover, the gray leaf spot situation is exacerbated by the reluctance of farmers to adopt crop rotation schemes that reduce monoculture because of a lack of marketing opportunities for other crops. The use of partially resistant cultivars is another good disease control method, but flexibility in genotype selection does not exist in seed production and many commonly used inbred seed parents are susceptible to the disease. In grain production, farmers often prefer to plant a high-yielding hybrid (even though it may be susceptible) and risk yield loss to disease because gray leaf spot may not occur. Furthermore, even the best partially resistant hybrids that are available can suffer significant yield loss (11).

Foliar fungicide use for gray leaf spot control has increased because of the limitations of other management practices. Fungicides have been shown to be profitable primarily in maize seed production operations (19). At least one application of propiconazole (i.e., Tilt fungicide, Syngenta Crop Protection, Greensboro, NC) or azoxystrobin (Quadris, Syngenta) per season is common for maize grown for seed in the United States and the price of application usually is recovered due to high crop value. It also has been shown that fungicide use can be profitable in grain production (18,21,34), but this practice can be economically risky because of the unpredictability of gray leaf spot severity. Current fungicide application decisions are based on crop growth stage, cropping history, tillage practices, cultivar susceptibility, general weather conditions, and disease incidence or severity threshold, but these

criteria are qualitative (5,34). If disease severity could be predicted quantitatively, a grower's risk could be managed more efficiently.

Disease-warning models have been developed and implemented for other economically important *Cercospora* leaf spot diseases. For example, advisories for fungicide applications for the control of peanut leaf spot in Virginia, Alabama, and North Carolina (7,12,25) and *Cercospora* leaf spot of sugar beet (36) have been successfully implemented. These advisories have used weather indices based on accumulated hours during which conditions are favorable for components of the infection cycle of the pathogen.

The objective of this research was to establish the basis for a gray leaf spot warning model by describing the quantitative relationships among environmental factors, agronomic factors, and gray leaf spot severity using an empirical modeling approach.

MATERIALS AND METHODS

Environmental and agronomic data were collected from 13 locations in 1998 and 11 locations in 1999 in southern Iowa (Fig. 1). The locations were chosen based on cropping history, previous history of gray leaf spot, and the willingness of growers to participate in the study. Locations included commercial seed production fields, hybrid strip trials, and research plots. The latitude and longitude of each location were measured using a hand-held battery-operated global positioning unit (Magellan GPS 4000; Magellan Systems Corporation, San Dimas, CA). Data were collected throughout the growing season from mid-May to late September, when the maize had reached the dent stage (R5) (28). Data loggers were placed at all the locations and were visited every 2 weeks to download

environmental data and collect agronomic data. Each data logger was a self-contained unit that measured environmental variables and stored the data.

Environmental factors. Three environmental variables were measured at each location: air temperature, leaf wetness, and RH. In both years, on-site rainfall data was only available at one location (Crawfordsville). Rainfall data for the remaining sites was obtained from the nearest weather stations.

A SPECWARE datalogger (Spectrum Technologies, Inc., Plainfield, IL) was placed at each location to record instantaneous air temperature ($^{\circ}\text{C}$) and leaf wetness (0-to-15 scale) at 30-min intervals. The flat sensor grid of the datalogger was painted by a proprietary process using three coats of a latex-based paint (Bob Olson, Savannah, GA; 16). The latex paint has been shown to increase the sensitivity of the sensor to dew and mimics emissivity of leaves better than an unpainted grid (16). The datalogger was mounted on a steel pole in a grassy area immediately adjacent to each field at a height of 1.4 m, with the wetness grid at a 45° angle facing north. The 45° angle was chosen because it best represents the natural orientation angle of the maize leaves.

The dataloggers measured leaf wetness indirectly; therefore, it was necessary to calibrate sensor measurements to the wetness observed on the maize leaves. The wetness dataloggers were calibrated on two mornings and two nights between July and September in both years (1998 and 1999) by placing two to four dataloggers at the edge of a maize field near Ames, IA. The sensors were deployed as described previously. Dew onset was recorded in the evenings (night calibration) and dew dry off in the mornings (morning calibration). Ten plants were randomly selected from the center of the field. Leaves that were at the height of the datalogger and facing the same direction and angle as the datalogger were observed carefully every 10 to 15 min. The time was noted at the first sign of dew on the upper leaf surface in at least 50% of the plants. In the morning calibration, the maize leaves were observed at the same intervals and the time when all the visible dew had dried off the leaf surface in at least 50% of the plants checked was recorded. Data from the dataloggers were compared to the visual observations to determine logger readings that corresponded to dew onset and dew dry off. On the basis of these results, any sensor reading greater than zero was recorded as a wet period.

RH was measured by placing a HOBO datalogger (Model RH Stowaway, Spectrum Technologies) in 1998, or Model H8 Pro Series (Onset Computer Corporation, Bourne, MA) in 1999, inside a radiation shield (Spectrum Technologies) attached on the opposite side of the pole from the

Fig. 1. Research plot locations established in Iowa for the assessment of effects of environmental and cultural factors on gray leaf spot severity in maize. Stars indicate the 1998 locations and triangles indicate the 1999 locations.

temperature-wetness datalogger at the same height. The HOBO measured RH at 15-min intervals. Daily rainfall amounts were accumulated for appropriate intervals during the growing season for each location.

Cultural factors. Tillage practices, cropping history, planting dates, and hybrids or inbreds varied among locations. The crop (soybean or maize) that had been planted in the field the previous year was noted. In 1998, planting dates ranged from 23 April to 24 June, and in 1999, from 27 April to 27 May. At each location, single plots of three to eight maize genotypes (hybrids or inbreds) varying in gray leaf spot resistance and maturity ratings were planted by the cooperating grower. Both hybrids and inbreds were rated on the same resistance scale. The genotypes were each given a gray leaf spot resistance rating (a scale of 1 to 9, with 1 being most susceptible and 9 being most resistant) based on information provided by the seed suppliers. In this study, the gray leaf spot ratings ranged from 2 to 7 and maturities ranged from 98 to 119 days comparative relative maturity. Plot size ranged from 2 rows by 5 m to 12 rows by several hundred meters. Row spacing was 0.76 m at all locations. Plant populations varied from 64,000 to 79,000/ha. The same hybrids or inbreds were not planted in every location, but some genotypes were planted in several locations. Standard weed control and fertility practices were followed.

At each field, maize residue cover was measured in May, using the line transect method (20). The residue measurements represented surface residue at the time of planting. A 16-m measuring tape was strung diagonally across the rows of corn. Presence or absence of any maize residue at least 0.25 cm in width was recorded at 50 consecutive points separated by 0.3-m intervals. The total number of points at which residue was found was the residue count for each transect. Three transects were sampled in each field, and the average residue count then was determined. The percentage of soil surface covered with residue was calculated by multiplying the average residue count by two. For fields that had no maize residue on the surface (usually because the previous crop was soybean), the distance to the nearest source of surface maize residue was estimated visually, accurate to the nearest 10 m.

Disease assessment. Gray leaf spot severity was assessed visually approximately every 14 days at the same time that environmental data were downloaded from the dataloggers. Before taking any disease severity ratings in the field, a computerized disease assessment program, CornPro version 2.0 (F. W. Nutter, Iowa State University, Ames; 22), was used as a training tool for disease assessment.

Ten plants from each genotype were selected arbitrarily from the middle of each

plot and disease severity was visually assessed as the percentage of the ear leaf that was diseased due to gray leaf spot. Standard diagrams were used as reference (22,30). Prior to ear leaf emergence, presence or absence of gray leaf spot lesions was noted on whole plants. The growth stage (28) of each hybrid or inbred was also noted at every assessment date during the season.

Data organization and analysis. Weather data were summarized by calculating the cumulative hours of conditions favorable for infection, similar to criteria used in other models for *Cercospora* diseases (7,12,25,36). Thus, the following variables were derived from the weather measurements: cumulative hours of leaf wetness (LW), hours with RH $\geq$ 95% (RH), and hours with temperature in the range of 22 to 30°C (TEMP). An index, termed the time-duration value (TDV), analogous to the TDV in the peanut early leaf spot model (7), was derived from RH and temperature. TDV was defined as the number of hours of conditions favorable for infection (in which both RH $\geq$ 95% and 22 $\leq$ T $\leq$ 30°C occur simultaneously). These variables were summed for the following periods during the growing season: (i) from growth stage V1 to R5, (ii) from growth stage V10 to R5, (iii) from growth stage V10 to R4, and (iv) from growth stage V1 to V10. In maize, growth stage R1 is the silking stage, R2 is blister stage, R3 is milk stage, R4 is dough, and R5 is dent (28). These periods were chosen because they were believed to be relevant to gray leaf spot development during the grain-fill period and also to timing of fungicide applications.

Stepwise multiple linear regression (PROC REG, SAS System for Windows; SAS Institute, Cary, NC) was used to identify the mathematical relationships among the dependent variable, gray leaf spot severity at the R4 or R5 stage, and the several independent variables (derived weather variables, rainfall, agronomic and cultural factors, and disease severity at silking). A default significance level of $P = 0.15$ was used as the basis for the addition of a variable as well as for the retention of an added variable.

Disease severity at dough or dent (R4 or R5) stage was chosen as the dependent variable because disease severity assessment at this stage is optimum for yield loss estimation (13). Several different combinations of variables were analyzed for their importance in the model. Combinations were tested that included temperature and relative humidity separately or combined (as TDV), that included or did not include a preliminary disease assessment, and that included different residue-related variables (percent residue cover and distance to nearest maize residue). For each combination, a stepwise multiple linear regression was run in SAS separately for each period

during which variables were summed, in order to compare coefficients of determination and significant variables among the four periods. Ten independent variables were analyzed for their importance in gray leaf spot severity at the dough or dent stage (Table 1). There were 80 observations each in combinations 1 to 6 (1998 data only), and combinations 7 and 8 had 180 observations (1998 and 1999 data). A linear regression was performed between the observed and the predicted gray leaf spot severity values for 1998 for each combination, as well as between the observed and predicted severity values for 1998 and 1999 combined.

RESULTS

Disease variability among locations.

Gray leaf spot severity on the same hybrid varied considerably among locations due to weather and cultural factors (Figs. 2 and 3). Only the locations with hybrids in common are shown in Figures 2 and 3, demonstrating the range of gray leaf spot severities among locations with the same hybrids. In 1998, Pioneer hybrid 34T14, a susceptible hybrid with a resistance rating of 2, had gray leaf spot severities ranging from 2 to 23%, and the moderately resistant Pioneer hybrid 33G26 had severities ranging from 0.5 to 4.5% (Fig. 2A). Disease severities generally were higher in eastern than in western Iowa. Similarly, the numbers of hours of RH over 95% and TDVs also tended to be higher in eastern Iowa (Fig. 2B). In 1999, the results were similar to those of 1998, with the susceptible hybrids developing the most disease in eastern Iowa (Fig. 3A); the locations with high disease severity on the susceptible hybrids (Keota in Keokuk County and West Branch in Cedar County) had correspondingly greater numbers of hours of RH $>$ 95% and TDVs (Fig. 3B). Specific inbreds were not planted at multiple locations each year; they tended to have lower disease resistance ratings and therefore higher disease severity than the hybrids (*data not shown*).

Wetness sensor calibration. It was determined that the smallest error in wetness measurements occurred if sensor readings of greater than zero were regarded as wet. Using this criterion, each sensor responded early (0.17 to 0.83 h) to dew onset and to dew dry-off (0.25 to 1.25 h). Therefore, wetness periods were likely underestimated by <1 h/day.

Regression analysis. Coefficients of determination differed by 2 to 13% among the four periods for given combinations of independent variables (Table 1). Genotype maturity was not significant in any of the analyses and is therefore absent from Tables 1 and 2. When disease severity at silking was included as an independent variable (combinations 2, 3, and 7), it was almost always significant for all four periods but it improved the R^2 values only

slightly (i.e., combination 1 versus 2, and combination 4 versus 3). The replacement of RH and TEMP with TDV (combination 3 versus 1) also did not have much effect on the R^2 values.

In most of the combinations of variables tested, genotype resistance, planting date, distance to nearest source of maize residue, LW, rainfall, and TDV (RH and TEMP both favorable) were significant (Table 1). Regression coefficients for planting date, amount of surface residue, TDV, duration of favorable RH, and disease severity at silking were positive, whereas coefficients for gray leaf spot resistance ratings, distance to nearest maize residue, and duration of surface wetness were negative. The regression coefficients for rainfall amount were not consistently significant. When significant, regression coefficients for early-season rainfall were positive, whereas those for late-season rainfall were negative.

The two residue-related variables were negatively correlated (i.e., distance to nearest maize residue had a value greater than zero only when the percentage surface

residue in the field was equal to zero). In the combinations based on the 1998 data (combinations 1 to 6), distance to nearest maize residue was significant in the model but percent maize residue cover was not. When distance was excluded from the analysis, percent residue cover was significant but the R^2 decreased a few points (combination 5), and when percent residue cover was excluded, model results were identical to those for combination 1, which included both variables. When 1998 and 1999 data were analyzed together, percent residue cover was significant and distance was not (Table 1). High distance values sometimes resulted in negative values for predicted disease severity.

Linear regression of observed versus predicted disease severities resulted in slope coefficients <1 and positive intercept values for each combination of variables (Table 2). Coefficients of determination ranged from 0.08 to 0.55. For the prediction equations from the 1998 data, the R^2 values for the regression between observed and predicted values were generally higher using the model that incorporated envi-

ronmental variables for V1 to V10. When both years of data contributed to the prediction equation, the R^2 values were similar among the four periods, but were slightly lower for the V1-to-V10 period.

DISCUSSION

The stepwise multiple regression models explained up to 65% of the variation in disease severity and also identified the variables that had significant effects on disease. Cultural factors such as genotype resistance, planting date, and crop residue-related variables had consistent linear relationships with disease severity. Additionally, there were consistent linear effects of weather variables such as cumulative hours of high RH and favorable temperature. Similar coefficients of determination were obtained for models based on accumulation of weather variables over the different periods of the growing season. It would be advantageous to use V1 to V10 accumulation of environmental variables for disease prediction because this period would allow the earliest disease prediction to be made. However, regression models including

Table 1. Regression term coefficients and coefficients of determination for linear multiple regression equations describing gray leaf spot severity in Iowa and involving eight different combinations of independent weather and cultural variables, measured during four different maize growth periods in 1998 and 1999

Period, combination ^b	R ²	C ^c	Independent variables ^a								
			RESIS	PLANT	RESID	DIST	RAIN	LW	RH	TDV	DIS at R1
V1 to R5											
1	0.62	-200.99	-3.11	2.01	NS	-0.77	1.39	-0.06	NS	...	...
2	0.64	-162.35	-2.57	1.75	NS	-0.58	NS	-0.05	NS	...	3.59
3	0.65	-183.14	-2.44	1.72	NS	-0.66	NS	-0.06	...	0.03	3.33
4	0.64	-221.65	-2.91	1.96	NS	-0.85	1.35	-0.07	...	0.04	...
5	0.49	-121.25	-3.26	1.31	0.27	...	-1.52	-0.03	NS	...	...
7	0.55	-101.14	-4.54	0.34	0.44	0.04	-2.07	-0.02	...	0.13	2.46
8	0.48	-104.37	-5.11	0.44	0.53	0.04	-1.96	-0.02	...	0.11	...
V10 to R5											
1	0.61	-179.76	-3.02	1.66	NS	-0.48	NS	-0.11	0.07	...	...
2	0.64	-160.82	-2.32	1.52	NS	-0.43	NS	-0.10	0.06	...	3.57
3	0.62	-153.20	-1.99	1.49	NS	-0.49	NS	-0.10	...	0.05	4.92
4	0.59	-203.16	-2.91	1.87	NS	-0.71	2.31	-0.11	...	0.06	...
5	0.58	-125.56	-3.22	1.18	NS	...	-5.36	-0.08	0.11	...	...
7	0.51	-76.13	-4.76	0.57	0.27	NS	-2.80	NS	...	0.08	2.37
8	0.45	-97.08	-5.31	0.68	0.40	NS	-1.86	NS	...	0.08	...
V10 to R4											
1	0.62	-113.55	-3.04	1.27	NS	-0.43	-2.08	-0.13	0.07	...	...
2	0.62	-78.34	-2.18	1.04	NS	-0.44	NS	-0.10	NS	...	4.29
3	0.63	-110.73	-2.06	1.23	NS	-0.48	NS	-0.12	...	0.04	4.28
4	0.63	-104.23	-2.89	1.21	NS	-0.45	3.83	-0.13	...	0.10	...
5	0.50	-145.74	-2.82	1.23	0.30	...	NS	-0.09	0.05	...	...
7	0.50	-89.74	-4.97	0.76	0.35	NS	-4.22	-0.04	...	0.11	1.94
8	0.46	-91.27	-5.35	0.78	0.42	NS	-4.63	-0.04	...	0.11	...
V1 to V10											
1	0.60	-212.02	-3.39	1.99	NS	-0.71	1.75	-0.10	NS	...	...
2	0.60	-212.02	-3.39	1.99	NS	-0.71	1.75	-0.10	NS	...	NS
3	0.62	-195.31	-3.52	1.81	NS	-0.81	NS	-0.12	...	0.07	NS
4	0.62	-195.31	-3.52	1.81	NS	-0.81	NS	-0.12	...	0.07	...
5	0.45	-148.89	-3.26	1.26	0.32	...	NS	-0.04	NS	...	...
7	0.48	-100.42	-4.90	0.86	0.37	NS	1.67	-0.03	...	NS	2.18
8	0.43	-109.14	-5.36	0.94	0.47	NS	1.43	-0.03	...	NS	...

^a RESIS = gray leaf spot resistance rating, PLANT = planting date, RESID = % maize residue cover, DIST = distance to nearest maize surface residue, RAIN = rainfall (inches), LW = hours of leaf wetness >0, RH = hours of relative humidity ≥95%, TDV = hours when RH ≥ 95% and 22 ≤ T ≤ 30°C, DIS at R1 = gray leaf spot severity at R1 growth stage, ... = variable not used in combination, NS = not significant. Variables MAT (maturity of genotype) and TEMP (temperature) are not shown because they were not significant in any of the combinations.

^b Combinations 1 through 6 used only 1998 data; combinations 7 and 8 used both 1998 and 1999 data. Combination 6 results were identical to combination 1 results; therefore, combination 6 is not shown.

^c Regression constant (intercept).

environmental data collected through the grain-filling period tended to have slightly higher coefficients of determination than the V1 to V10 models.

As expected, disease severity at the dough or dent stages was positively related to later planting dates, increasing amounts of surface residue, TDV, increased durations of favorable RH, and higher disease severity at silking. Conversely, gray leaf spot resistance, distance to nearest maize residue, and duration of surface wetness were negatively related to final disease severity. These results are as expected for a foliar disease, except for the effect of surface wetness. The uncertain relationship between gray leaf spot severity and leaf wetness duration has been noted in other studies conducted on *C. zea-maydis* (1,27,33). Thorson and Martinson (33) showed that increased wetness duration stimulated germination and favored the development of mycelium on the leaf surface but discouraged the formation of appressoria by *C. zea-maydis* germplings. Lapaire and Dunkle (14) found that conidia of *C. zea-maydis* undergo secondary sporulation on the surface of water droplets on the leaf, increasing the number of conidia on the leaf surface. Conidia submerged in water droplets did not produce secondary conidia. For *C. beticola* on sugar beet, the germ tube was found to grow toward stomata only in the absence of free water; therefore, it has been suggested that the tropism may occur in response to a water-vapor gradient (26). The same may hold true for *C. zea-maydis* on maize. Therefore, leaf wetness may have complicated and counteracting effects on different pre-infection events on the leaf surface. Calculation of cumulative hours of wetness may not capture the subtleties of these effects.

The inconsistency of the rainfall effect might be explained by the fact that rainfall is an indirect measure of wetness and was already represented by the wetness variable in the model. Also, rainfall was not measured on location, so its accuracy may be variable. Our results regarding rainfall support those of Ringer and Grybauskus (27), who found that rainfall amount early in the season was positively related with levels of gray leaf spot. Total rainfall observed throughout the full growing season was not consistently related with gray leaf spot severity. Our conclusions about the effects of rainfall would be strengthened by accurate on-site measurement of rainfall at each location.

Hours of favorable temperature were not significant in any of the models and hours of RH $\geq 95\%$ did not tend to have a significant effect on disease severity. However, when these variables were replaced with TDV (i.e., hours when both RH and TEMP are simultaneously favorable), this variable was almost always significant in the regression models. Replacing hours of favor-

able relative humidity and hours of favorable temperature with TDV improved the R^2 of the regression models, but did not change the significance of other variables. Although this temperature range (22 to

30°C) previously was identified as optimal for *C. zea-maydis* development (1,2), it might be of value to explore other ways of summarizing temperature data and re-assessing the relationship between gray leaf

Fig. 2. A, Gray leaf spot severity at growth stage R2/R3 in 1998 on three Pioneer hybrids at five Iowa locations and **B**, associated cumulative hours (from emergence to R5) of relative humidity (RH) $\geq 95\%$ and time-duration values (TDV, hours with simultaneous RH $\geq 95\%$ and temperatures between 22 and 30°C). Numbers in parentheses are gray leaf spot resistance ratings (1 = most susceptible to 9 = most resistant). Locations are arranged from west to east, with county names in parentheses.

Fig. 3. A, Gray leaf spot severity at growth stage R2/R3 in 1999 on three Pioneer hybrids at five Iowa locations and **B**, associated cumulative hours (from emergence to R5) of relative humidity (RH) $\geq 95\%$ and time-duration values (TDV, hours with simultaneous RH $\geq 95\%$ and temperatures between 22 and 30°C). Numbers in parentheses are gray leaf spot resistance ratings (1 = most susceptible to 9 = most resistant). Locations are arranged from west to east, with county names in parentheses.

spot severity and temperature. Our results suggest that RH was a more limiting factor than temperature, and that simultaneously favorable RH and temperature are required for infection.

Maize surface residue was an important factor related to disease severity, as demonstrated by the significant effects of percent maize surface residue and distance to nearest maize residue. The former variable applied primarily to fields where maize was the previous crop, and the latter applied to fields where soybean was the previous crop. These two variables were inversely related and only one could be greater than zero for any given observation. In the 1998 models, distance was the significant residue-related variable. In models based on both years of data, residue cover was the significant residue-related variable. With both years of data, there were more observations with positive values for percent residue cover, and the effect of percent residue cover was no longer

overshadowed by the effect of distance in the model. When distance to nearest residue was included in the models, some of the predicted values for disease severity were negative. The large negative coefficient for the distance variable had a disproportionate effect on disease severity estimates for fields that were far from a neighboring inoculum source. If distance were to be used in a predictive model, it should be given a maximum value based on dispersal gradients for *C. zea-maydis* (10).

Genotype resistance and planting date clearly were important factors in gray leaf spot development. The effect of genotype resistance was evident in the various locations (Figs. 2 and 3) and in the regression analysis. Planting date was a significant variable in nearly every regression equation. Late-planted maize may tend to develop more severe gray leaf spot because the plants experience initial infection at an earlier growth stage and, therefore, there is

a greater opportunity for multiple infection cycles before the plants reach physiological maturity. This result is consistent with previous studies (17,29). Rupe et al. (29) found that initial gray leaf spot symptoms occurred at an earlier growth stage and reached higher final disease severities with later planting. However, in a recent study (6), researchers reported a higher area under the disease progress curve and rate of disease development in an earlier versus a later planting date.

In both 1998 and 1999, the susceptible hybrids in the eastern part of the state developed much greater disease severities than those planted in the western part of the state. This difference was related to the weather conditions in eastern and western Iowa. West Branch (Cedar County) and Anamosa (Jones County), both in eastern Iowa, had the highest number of hours of favorable RH in 1998 and hence also had the highest levels of disease. Disease development appeared to be less sensitive to temperature than to RH, a result consistent with those of Rupe et al. (29). It has been observed that high temperature and low rainfall are not as limiting on gray leaf spot severity as are microclimatic factors such as RH (3). However, the relationships between RH, TDV, and gray leaf spot severity are confounded with other variables that differed among locations.

When the disease rating at silking (R1) was included in the regression analysis, it was almost always significant and improved the coefficients of determination slightly. If this variable were included in a predictive model, it would delay the disease prediction by 2 weeks compared with a model based only on V1-to-V10 data. A disease rating taken at stage V10 might be valuable in predicting subsequent disease severity, but ear-leaf disease ratings are not possible at that time, and we did not assess this variable.

This research has shown linear relationships between gray leaf spot severity and genotype resistance, maize surface residue, planting date, and hours of favorable RH and temperature. These relationships can be exploited to develop a predictive model for gray leaf spot severity. However, it may be possible that better predictions might result from a nonlinear modeling approach; in addition, coefficients of determination for models based on 2 years were lower than those based only on 1998 data, because some year-to-year variability was not captured by the independent variables. Additional years of data collection should improve model fit and contribute to the development of a more robust predictive model.

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Table 2. Slope, intercept, and regression term coefficients for simple linear regression of observed (independent) and predicted (dependent) gray leaf spot severity for models based on eight combinations of agronomic and weather variables assessed during four different periods within the growing season during 1998 and 1999 in Iowa^a

Period, prediction equation ^b	Slope	Intercept	R ²
V1 to R5			
1 DIST + RAIN + LW	0.35	7.81	0.36
2 DIST + LW + DIS-R1	0.57	9.95	0.48
3 DIST + LW + TDV + DIS-R1	0.58	2.44	0.55
4 DIST + RAIN + LW + TDV	0.38	6.51	0.42
5 RESID + RAIN + LW	0.32	6.28	0.37
6 DIST + RAIN + LW	0.35	7.81	0.36
7 RESID + DIST + RAIN + LW + TDV + DIS-R1	0.53	12.17	0.53
8 RESID + DIST + RAIN + LW + TDV	0.46	7.40	0.47
V10 to R5			
1 DIST + LW + RH	0.33	3.67	0.33
2 DIST + LW + RH + DIS-R1	0.55	9.10	0.43
3 DIST + LW + TDV + DIS-R1	0.62	2.98	0.46
4 DIST + RAIN + LW + TDV	0.33	9.81	0.32
5 RAIN + LW + RH	0.34	4.34	0.37
6 DIST + LW + RH	0.33	3.67	0.33
7 RESID + RAIN + TDV + DIS-R1	0.50	10.80	0.50
8 RESID + RAIN + TDV	0.45	13.17	0.45
V10 to R4			
1 DIST + RAIN + LW + RH	0.34	7.15	0.34
2 DIST + LW + DIS-R1	0.57	8.06	0.42
3 DIST + LW + TDV + DIS-R1	0.59	8.63	0.45
4 DIST + RAIN + LW + TDV	0.14	45.2	0.08
5 RESID + LW + RH	0.31	7.61	0.36
6 DIST + RAIN + LW + RH	0.34	7.15	0.34
7 RESID + RAIN + LW + TDV + DIS-R1	0.49	10.26	0.49
8 RESID + RAIN + LW + TDV	0.45	10.06	0.46
V1 to V10			
1 DIST + RAIN + LW	0.40	6.75	0.48
2 DIST + RAIN + LW	0.40	7.07	0.49
3 DIST + LW + TDV	0.41	5.98	0.50
4 DIST + LW + TDV	0.41	5.67	0.49
5 LW	0.33	6.90	0.44
6 DIST + RAIN + LW	0.40	6.75	0.48
7 RAIN + LW + DIS-R1	0.47	8.93	0.48
8 RAIN + LW	0.42	10.89	0.43

^a All combinations had gray leaf spot resistance rating, (RESIS) and planting date (PLANT) because the two variables were significant. In addition, the remaining variables that were significant in each combination are listed in the table.

^b Prediction equation of significant variables. DIST = distance to nearest maize surface residue, RAIN = rainfall (inches), LW = hours of leaf wetness >0, DIS-R1 = gray leaf spot severity at R1 growth stage, TDV = hours when relative humidity (RH) ≥ 95% and 22 ≤ T ≤ 30°C, RESID = % maize residue cover.

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