A Temperature and Leaf Wetness Duration-Based Model for Prediction of Gray Leaf Spot of Perennial Ryegrass Turf

W. Uddin, K. Serlemitsos, and G. Viji

Department of Plant Pathology, The Pennsylvania State University, University Park 16802.
Accepted for publication 14 November 2002.

ABSTRACT

Uddin, W., Serlemitsos, K., and Viji, G. 2003. A temperature and leaf wetness duration-based model for prediction of gray leaf spot of perennial ryegrass turf. *Phytopathology* 93:336-343.

Gray leaf spot is a serious disease of perennial ryegrass (*Lolium perenne*), causing severe epidemics in golf course fairways. The effects of temperature and leaf wetness duration on the development of gray leaf spot of perennial ryegrass turf were evaluated in controlled environment chambers. Six-week-old Legacy II ryegrass plants were inoculated with an aqueous conidial suspension of *Pyricularia grisea* (approximately 8×10^4 conidia per ml of water) and subjected to four different temperatures (20, 24, 28, and 32°C) and 12 leaf wetness durations (3 to 36 h at 3-h intervals). Three days after inoculation, gray leaf spot developed on plants at all temperatures and leaf wetness durations. Disease incidence (percent leaf blades symptomatic) and severity (index 0 to 10; 0 = leaf blades asymptomatic, 10 = >90% leaf area necrotic) were assessed 7 days after inoculation. There were significant effects ($\alpha = 0.0001$) of temperature and leaf wetness duration on disease incidence and severity, and

there were significant interactions ($\alpha = 0.0001$) between them. Among the four temperatures tested, 28°C was most favorable to gray leaf spot development. Disease incidence and severity increased with increased leaf wetness duration at all temperatures. A shorter leaf wetness duration was required for disease development under warmer temperatures. Analysis of variance with orthogonal polynomial contrasts and regression analyses were used to determine the functional relationships among temperature and leaf wetness duration and gray leaf spot incidence and severity. Significant effects were included in a regression model that described the relationship. The polynomial model included linear, quadratic, and cubic terms for temperature and leaf wetness duration effects. The adjusted coefficients of determination for the fitted model for disease incidence and severity were 0.84 and 0.87, respectively. The predictive model may be used as part of an integrated gray leaf spot forecasting system for perennial ryegrass turf.

Additional keywords: disease management, turfgrass.

Gray leaf spot, caused by *Pyricularia grisea* (Cooke) Sacc., is a serious disease of perennial ryegrass (*Lolium perenne* L.) turf. Despite its susceptibility to the fungus, the grass is widely used in the golf course industry due to its desirable upright and bunch growth habit, rapid germination and fill-in, color, and its tolerance to close mowing and soil compaction (18). Additionally, cold weather tolerance has led to the use of perennial ryegrass for overseeding dormant Bermudagrass tees and fairways during the winter. Severe outbreaks of the disease have occurred in golf course fairways in various regions of the United States in recent years, resulting in extensive loss of turf. Gray leaf spot has long been associated with St. Augustinegrass (*Stenotaphrum secundatum* Walt.) in the southern United States (17,27,34). Epidemics of gray leaf spot on Italian ryegrass (*L. multiflorum* Lam.) (1,4) and tall fescue (*Festuca arundinacea* Schreb.) (31) have also been reported during the past three decades. The disease was first diagnosed on perennial ryegrass turf in golf courses in 1986 (8), and a serious outbreak of the disease was first report in Pennsylvania in 1991 (15). Since then, severe gray leaf spot epidemics have been reported from several states in the Middle Atlantic region (8,30), Midwest (12,35), New England states (24), and western United States (32).

The influence of temperature and leaf wetness duration on the development of plant disease epidemics has been well defined for a number of pathosystems, and such information has been effectively used for developing predictive models (2,3,5,9,13,14,16,

22,23,26,28,29,36). In recent years, the effects of temperature and leaf wetness duration on the development of certain diseases of turfgrasses such as Rhizoctonia blight (brown patch) (10,25), anthracnose (7), and Pythium foliar blight (21) have also been well defined. Of these diseases, the effects of environmental factors on Rhizoctonia blight have been studied most extensively. Schumann et al. (25) and Fidanza et al. (10) proposed predictive models for Rhizoctonia blight that were based on intricate field monitoring systems under complex field conditions, for which interpretation required consideration of various environmental and cultural conditions. Recently, a temperature and leaf wetness duration-based model for prediction of Rhizoctonia blight of perennial ryegrass has been developed based on a controlled environment chamber study (11). Such conditions with well-defined environmental parameters provide a basis for understanding the effects of temperature and leaf wetness duration on disease development. In this model, analysis of variance (ANOVA) with orthogonal polynomial contrast and regression analyses were used to predict disease incidence. The polynomial model included linear and quadratic terms for temperature and leaf wetness durations, and an excellent fit of data was achieved with a coefficient of determination of 0.93. Such information is not available for developing a predictive model for gray leaf spot of perennial ryegrass turf. A study on gray leaf spot of forage Italian ryegrass in the early 1980s (20) indicated 26°C to be the most favorable temperature for gray leaf spot development, and a cubic polynomial model was described for the temperature effects on disease severity. Disease severity reportedly increased with increasing leaf wetness duration up to 24 h; however, the interactions between temperature and leaf wetness duration were not determined. In tall fescue turf, a slightly higher temperature (28°C) was the most favorable to gray leaf

Corresponding author: W. Uddin; E-mail address: wxu2@psu.edu

Publication no. P-2003-0114-02R
© 2003 The American Phytopathological Society

spot development, and an increase in disease incidence was associated with an increase in temperature (31). Additionally, there were significant interactions between temperature and leaf wetness duration. In perennial ryegrass turf, gray leaf spot severity was higher at 29°C than at 22°C; however, the effect of leaf wetness on disease severity was not determined (15).

In order to improve disease control, development of a predictive model as part of a forecasting system is necessary; therefore, fungicide applications can be timed more accurately. Determination of a quantitative relationship between the environmental conditions such as temperature and leaf wetness duration and gray leaf spot incidence and severity is critical in the development of such a model. Therefore, this study was undertaken to determine the effects of temperature and leaf wetness duration on development of gray leaf spot on perennial ryegrass turf.

MATERIALS AND METHODS

Maintenance of plants and preparation of inoculum. Legacy II perennial ryegrass plants were grown in 4-cm diameter, 20-cm plastic Cone-tainers (Stuewe & Sons, Corvallis, OR) that were filled to 1 cm below the rim with granular calcine clay medium (Turface MVP, Allied Industrial Material Corp., Buffalo Grove, IL). Two weeks after seeding, plants were fertilized with water-soluble 20-20-20 N-P-K fertilizer (1.3 g/liter of water) once a week to field capacity of the growing medium. Fertilization continued weekly during the course of the study. A mononidial isolate of *P. grisea*, collected from a perennial ryegrass fairway in Willow Hollow Golf Course, Leesport, PA, was used in this study. The fungus was maintained on nitrocellulose filter paper disks at -20°C (33). Prior to inoculation, the filter paper disks were removed from storage, placed on potato dextrose agar plates, and incubated at 26°C under fluorescent light (72 $\mu\text{E m}^{-2} \text{s}^{-1}$) at 12 h day/night cycles for 7 days. Agar blocks (approximately 2 × 2 mm) containing actively growing mycelia of *P. grisea* were then transferred to oatmeal agar plates and incubated at the same conditions as indicated earlier. Sterilized distilled water (approximately 10 ml) was dispensed into each culture plate, and the conidia of *P. grisea* were harvested by scraping the surface of the plates with a sterilized needle. The conidial suspension was filtered through four layers of cheesecloth, and an aqueous suspension (approximately 8×10^4 conidia per ml of water with 0.1% Tween 20) was prepared for inoculation of the ryegrass plants.

Effects of temperature and leaf wetness duration. Treatments included four different temperatures (20, 24, 28, and 32°C) and 12 leaf wetness durations (3, 6, 9, 12, 15, 18, 21, 24, 27, 30, 33, and 36 h). Each run of temperature-leaf wetness duration combination was repeated twice. The experimental layout was a split-plot design with main-plot arranged in a randomized complete block. The main-plot factor was represented by temperature and four replications of temperature (four runs) in time served as blocks (6). The sub-plot factor was represented by leaf wetness duration and there were 11 subsamples (Cone-tainers) within each temperature-leaf wetness duration treatment combination. Four dew chambers (Percival E-54U DL; Percival Scientific, Inc., Perry, IA), each assigned to a temperature treatment, were used in each run of the experiment. During the four runs of experiments, dew chambers were assigned to each temperature treatment in a way that each chamber received all four temperature treatments. The experimental layout for the temperature-leaf wetness duration effects was similar to that described by Gross et al. (11).

Plants were inoculated with the aqueous suspension of *P. grisea* conidia by spraying the plants with an atomizer until the leaves were completely wet. Noninoculated plants sprayed with sterilized distilled water served as the control. Continuous fogging was provided by a built-in misting system in the chambers in order to maintain continuous leaf surface wetness. Temperature and rela-

tive humidity in each chamber were monitored by a data logger (WatchDog 450; Spectrum Technologies, Inc., Plainfield, IL). A temperature of ± 0.5 to 0.8°C was maintained in each chamber, and the relative humidity was maintained at 96 to 100%. The plants were exposed to continuous fluorescent and incandescent light (77 to 85 $\mu\text{E m}^{-2} \text{s}^{-1}$) during a 12 h day/night cycle. Every 3 h after inoculation, the Cone-tainers assigned to each leaf wetness duration treatment were removed from the dew chambers and air dried with a hair-dryer (Conair Corp., East Windsor, NJ) set at warm temperature and medium air emission for approximately 2 min. Following the drying of plants that were exposed to each leaf wetness duration treatment, the Cone-tainers were immediately placed in controlled environment chambers (Convion PGR15; Controlled Environment Limited, Winnipeg, Manitoba, Canada) set at 20, 24, 28, or 32°C and continuous fluorescent light (73 to 82 $\mu\text{E m}^{-2} \text{s}^{-1}$). As described previously, each of the four controlled environment chambers was randomly assigned to a temperature treatment in each run of the experiment, and each chamber received a temperature treatment once during the four runs. Relative humidity in each controlled environment chamber was maintained at 64 to 70%. Seven days after inoculation, disease incidence (percent leaf blades symptomatic) and severity (index 0 to 10; 0 = plants asymptomatic; 10 = >90% leaf area necrotic) were assessed. Additionally, a set of plants (11 Cone-tainers in each chamber), designated as 0 h leaf wetness duration, was also included in the experiment to determine the development of gray leaf spot when free moisture is removed from the leaf surface immediately after inoculation.

Statistical analysis and model development. ANOVA and multiple regression procedures were performed to determine the relationship between the environmental factors (independent variable x) and gray leaf spot incidence and severity (dependent variable y). Analysis of the residual plots for normality and error variance indicated that transformation of the disease incidence and severity data was not necessary. The linear model describing the experimental design for ANOVA was as follows:

$$Y_{ijkl} = \mu + r_i + T_j + a_{(ij)} + W_k + TW_{jk} + b_{(ijk)} + e_{(ijkl)} \quad (1)$$

where $i = 1, 2, 3, 4$; $k = 1, 2, 3, \dots, 12$; $j = 1, 2, 3, 4$; $l = 1, 2, \dots, 11$; y_{ijkl} is the $ijkl$ th response for the individual subunit; μ is the overall mean; r_i is the i th replication effect (random); T_j is the j th temperature effect (fixed); W_k is the k th wetness effect (fixed); $a_{(ij)}$ is the i th whole-plot and j th temperature effect (effect); TW_{jk} is the interaction effect of i th temperature and k th wetness (fixed); $b_{(ijk)}$ is the sub-plot random effect; and $e_{(ijkl)}$ is the l th unit random effect in $ijkl$ th sub-plot. Thus, a mixed model was fitted using SAS ANOVA.

Regression models were developed for the 48 treatment means using SAS PROC REG procedure to formulate the surface response based on the significant orthogonal polynomial contrasts. The 95% confidence intervals about predicted means of response surface were derived from the polynomial regression. Sums of squares temperature (T), hours of leaf wetness duration (W), and their interactions ($T \times W$) were partitioned into orthogonal polynomial contrast coefficients using SAS S-PLUS POLY procedure. All statistical procedures were conducted using the Statistical Analysis System software (version 8.2, SAS Institute, Cary, NC).

RESULTS

Effects of temperature and leaf wetness duration. Gray leaf spot developed on perennial ryegrass plants 3 days after inoculation, and disease incidence and severity were assessed 7 days after inoculation. Gray leaf spot developed at all temperature regimes and leaf wetness durations tested, except in 0 h leaf wetness

duration treatments, in which plants were air dried immediately after spraying with aqueous suspension of *P. grisea* conidia. Further, there was no development of gray leaf spot in the non-inoculated control plants. There were significant effects ($P = 0.0001$) of temperature and leaf wetness duration on disease severity and incidence. Additionally, there were significant interactions between the temperature and leaf wetness durations (Tables 1 and 2).

Disease incidence and severity. Disease incidence increased with an increase in temperature from 20 to 32°C at 3 to 6 h leaf wetness durations; however, at 9 h or greater leaf wetness durations, the disease incidence was lower at 32°C than at 28°C (Fig. 1). The number of symptomatic blades was lowest at 20°C at 3 h leaf wetness (2%) and increased to 11, 44, and 52% at 24, 28, and 32°C, respectively. Increase in disease incidence followed a similar trend at 6 h leaf wetness; however, at 9 h it increased from 20°C (12%) to 28°C (83%) and remained at a similar level at 32°C. Disease severity also increased with increased leaf wetness durations at each temperature tested (Fig. 1). However, the increase in disease incidence varied with temperature treatments. At 20°C, disease incidence was relatively low at leaf wetness durations of 3 to 9 h (2 to 12%), but there were notable increases at leaf wetness durations of 12 to 18 h (21 to 42%), reaching a maximum of 57% at 36 h. The increase in disease incidence followed a similar trend at 24, 28, and 32°C; however, it did not increase further at leaf wetness durations greater than 21 h. The effects of temperature and leaf wetness duration on disease severity followed a similar pattern. Only some specks developed on a small number (2%) of leaf blades at 3 h leaf wetness duration. Although there was an increase in disease severity from 20°C (severity index 0.05) to 32°C (severity index 3) at 3 h, the differences were less than that between 20 and 32°C for disease incidence. At 20°C, disease severity was relatively low at leaf wetness durations of 3 to 12 h (0.05 to 0.9), and there were no further notable increases at greater leaf wetness durations

(1.3 at 15 h to 2.7 at 36 h). Overall, gray leaf spot was most severe at 28°C when exposed to leaf wetness durations of 24 h or greater.

The polynomial model. The data for the 0 h leaf wetness duration treatment were not included in the analyses because there was no disease development on plants that were air dried immediately after inoculation. ANOVA indicated that there were significant linear ($P \leq 0.05$) and highly significant cubic ($P \leq 0.001$) relationships between temperature (T) and disease incidence (Y) across the leaf wetness duration; however, the quadratic relationship was not significant (Table 1). There were also highly significant linear ($P \leq 0.001$), quadratic, and cubic relationships between leaf wetness duration (W) and disease incidence (Y) across the temperature. The T -linear $\times$ W -linear, T -linear $\times$ W -cubic, T -linear $\times$ W -quartic, and T -quadratic $\times$ W -quadratic terms were highly significant ($P \leq 0.001$). Additionally, the T -linear $\times$ W -quintic, T -quadratic $\times$ W -linear, T -cubic $\times$ W -quadratic, T -cubic $\times$ W -cubic, and T -cubic $\times$ W -quadratic terms were significant ($P \leq 0.05$). The influence of temperature and leaf wetness duration on disease severity was similar to that of disease incidence (Table 2). There were highly significant ($P \leq 0.001$) linear and cubic relationships between temperature (T) and disease severity (Y) across the leaf wetness duration; however, the quadratic relationship was not significant. There were highly significant linear ($P \leq 0.001$), quadratic, and cubic relationships between leaf wetness duration (W) and disease severity (Y) across the temperatures. Additionally, there was significantly higher order terms (fifth and sixth) in the interactions between temperature and leaf wetness duration (Table 2). The interaction terms T -linear $\times$ W -linear, T -linear $\times$ W -quadratic, T -linear $\times$ W -cubic, T -quadratic $\times$ W -quadratic, T -cubic $\times$ W -linear, T -cubic $\times$ W -quadratic, and T -cubic $\times$ W -cubic were highly significant ($P \leq 0.001$). Additionally, the T -linear $\times$ W -quartic, T -quadratic $\times$ W -linear, and T -cubic $\times$ W -quintic terms were significant ($P \leq 0.05$). The influence of temperature and leaf wetness duration on incidence and severity

TABLE 1. Analysis of variance for incidence of gray leaf spot of perennial ryegrass at 48 combinations of temperature and leaf wetness duration

Source of variation	df	Mean square	F^a
Temperature (T)	3	354,434.08	217.747*
T -linear (T -ln)	1	901,523.15	19.051**
T -quadratic (T -qd)	1	907.29	0.557
T -cubic (T -cb)	1	160,871.82	98.832*
Error (a)	9	1,627.73	
Leaf wetness duration (W)	11	47,321.30	184.264*
W -linear (W -ln)	1	406,817.77	1,584.108*
W -quadratic (W -qd)	1	98,898.95	385.103*
W -cubic (W -cb)	1	11,343.26	44.168*
W -quartic (W -qr)	1	563.00	2.192
W -quintic (W -qn)	1	2,335.26	9.092**
Lack of fit	6	95.83	0.373
$T \times W$	33	1,865.80	7.265*
T -ln $\times$ W -ln	1	28,491.91	110.945*
T -ln $\times$ W -qd	1	345.09	1.343
T -ln $\times$ W -cb	1	5,481.29	21.342*
T -ln $\times$ W -qr	1	8,630.00	33.604*
T -ln $\times$ W -qn	1	1,034.81	4.030**
T -qd $\times$ W -ln	1	1,859.71	7.243**
T -qd $\times$ W -qd	1	3,705.28	14.427*
T -qd $\times$ W -cb	1	14.62	0.058
T -qd $\times$ W -qr	1	656.60	2.558
T -qd $\times$ W -qn	1	727.87	2.835
T -cb $\times$ W -ln	1	399.28	1.554
T -cb $\times$ W -qd	1	1,177.31	4.583**
T -cb $\times$ W -cb	1	2,507.25	9.762**
T -cb $\times$ W -qr	1	1,479.73	5.763**
T -cb $\times$ W -qn	1	392.40	1.526
Lack of fit	18	259.22	1.009
Error (b)	132	256.81	
Sampling error	1,920	118.76	

^a * and ** indicate significant at 0.001 and 0.05, respectively.

of gray leaf spot can be described by the following polynomial regression model:

$$Y_{is} = b_0 + b_1T + b_2T^2 + b_3T^3 + b_4W + b_5W^2 + b_6TW \quad (2)$$

where Y_{is} is the disease incidence or disease severity index, T is the temperature, and W is the leaf wetness duration in hours. The letters $b_0, b_1, \dots, b_{15}$ are the estimates of the regression coefficients (Tables 3 and 4). The r^2 values for disease incidence and severity were 0.84 and 0.87, respectively. The predicted disease incidence as a function of leaf wetness duration generally increased with time. The predicted disease incidence as a function of temperature generally increased with leaf wetness duration. The predicted disease severity as a function of temperature and leaf wetness duration showed a similar trend. The response surface of the polynomial model for disease incidence and severity are presented in Figure 2.

Additionally, multiple regression analysis indicated that disease severity was positively correlated with disease incidence across the temperatures and leaf wetness duration treatments. The relationship was best described by a quadratic model, $y = 0.25 - 0.002x + 0.0009x^2$; $r^2 = 0.90$, where y = disease severity and x = disease incidence (Fig. 3).

DISCUSSION

To our knowledge, this is the first study to demonstrate the interaction of temperature and leaf wetness duration on the development of gray leaf spot of perennial ryegrass. This is a late summer disease that is highly destructive to ryegrass in golf course fairways. The presence of free moisture in the turf canopy for prolonged periods is common in golf courses as a result of irrigation practices employed during the summer. Additionally, extended periods of leaf surface moisture are common in the morn-

ing hours due to accumulation of dew in the turf canopy. Grasses in shaded areas remain wet for prolonged periods because the drying time in such areas is relatively longer. In order to effectively manage the disease by proper timing of fungicide applications, it is crucial that the effects of temperature and leaf wetness duration on gray leaf spot development is quantitatively described; therefore a predictive model can be developed as part of a disease forecasting system.

In this study, we propose a polynomial model (equation 2) for predicting gray leaf spot based on temperature and leaf wetness durations. ANOVA and multiple regression analysis indicate that the polynomial model can be applied in the prediction of disease incidence and severity, because the effects of these two environmental factors on incidence and severity followed a similar trend. The largest contributor to the response surface for gray leaf spot incidence was T -linear and W -linear and the interactions between them. Additionally, the cubic term for temperature effect was highly significant. Similarly, the largest contributor to the response surface for gray leaf spot severity was T -linear and W -linear. However, the largest interaction term in the response surface for severity was T -linear and W -quadratic. The highly significant cubic terms for temperature effects and higher order interaction terms for gray leaf spot severity and incidence may have contributed to the highly pronounced sigmoid-shaped curve where there was a slight drop at the points between 20 and 24°C (Fig. 2). Although some higher order terms for leaf wetness duration effects and the interactions between temperature and leaf wetness durations were significant, we did not include those terms in our model because no biological mechanisms beyond the cubic terms are likely in gray leaf spot pathosystem. The observed data showed that disease incidence and severity increased from 20 to 24°C, and the drop was unlikely at the temperatures between 20 and 24°C during the infection process. Despite the slight drop in the predicted values of disease incidence and

TABLE 2. Analysis of variance for severity of gray leaf spot of perennial ryegrass at 48 combinations of temperature and leaf wetness duration

Source of variation	df	Mean square	F^a
Temperature (T)	3	4,432.31	159.205*
T -linear (T -ln)	1	10,963.90	393.818*
T -quadratic (T -qd)	1	1.74	0.061
T -cubic (T -cb)	1	2,331.28	83.736*
Error (a)	9	27.85	
Leaf wetness duration (W)	11	314.77	157.335*
W -linear (W -ln)	1	2,590.36	1295.150*
W -quadratic (W -qd)	1	719.71	359.850*
W -cubic (W -cb)	1	94.34	47.150*
W -quartic (W -qr)	1	0.41	0.200
W -quintic (W -qn)	1	20.33	10.150**
W -hexadic (W -hx)	1	23.04	11.500*
Lack of fit	5	2.76	1.330
$T \times W$	33	19.66	9.811*
T -ln $\times$ W -ln	1	26.83	13.400*
T -ln $\times$ W -qd	1	201.35	100.650*
T -ln $\times$ W -cb	1	51.10	25.550*
T -ln $\times$ W -qr	1	13.42	6.700**
T -ln $\times$ W -qn	1	2.10	1.050
T -qd $\times$ W -ln	1	18.51	9.250**
T -qd $\times$ W -qd	1	30.22	15.100*
T -qd $\times$ W -cb	1	0.11	0.050
T -qd $\times$ W -qr	1	6.90	3.450
T -qd $\times$ W -qn	1	4.87	2.400
T -cb $\times$ W -ln	1	98.25	49.100*
T -cb $\times$ W -qd	1	86.71	43.350*
T -cb $\times$ W -cb	1	41.28	20.600*
T -cb $\times$ W -qr	1	0.01	0.005
T -cb $\times$ W -qn	1	13.48	6.750**
Lack of fit	18	2.92	1.465
Error (b)	132	2.00	
Sampling error	1,440	0.92	

^a * and ** indicate significant at 0.001 and 0.05, respectively.

Fig. 1. The observed mean and predicted values of gray leaf spot incidence and severity on *Lolium perenne* at various leaf wetness durations for each of four temperatures. Mean incidence and severity values for each treatment represents four replicates and 11 subsamples (Cone-tainers). Predicted values were derived from the polynomial regression (equation 2).

severity at the temperatures between 20 and 24°C, we propose that the cubic terms are important components in this model as indicators for an overall trend which reflects the decreased disease incidence and severity at 32°C compared with 28°C at all leaf wetness duration treatments, except for 3 and 6 h. The polynomial model adopted to describe the functional relationship between gray leaf spot incidence and severity and temperature and leaf wetness duration were similar to the models developed to predict other diseases of turfgrass such as brown patch of perennial ryegrass turf (11) and anthracnose of annual bluegrass (7). However, linear and quadratic terms were the major contributors in these models, whereas linear and cubic terms were the important contributors of temperature and leaf wetness duration effects in the predictive model for gray leaf spot of perennial ryegrass turf. Our model provided information similar to that generated for predicting diseases of field crops such as Septoria blotch of wheat (16), Alternaria leaf blight of muskmelon (9), anthracnose of watermelon (19), and white rust of spinach (28). The specific temperature and leaf wetness duration requirements for development of the gray leaf spot differs from the diseases of field crops, but the functional relationship between temperature and leaf wetness duration in the gray leaf spot pathosystem is consistent with those demonstrated for these diseases.

Development of disease predictive models in the turfgrass pathosystem has been limited to only brown patch and anthracnose (7,10,25). A preliminary report (20) on the influence of temperature and leaf wetness duration on the severity of gray leaf spot of a forage crop (Italian ryegrass) has provided some information. Of the four temperature regimes (5, 15, 25, and 35°C) tested, 25°C was reported to be most favorable to gray leaf spot development. Of the six leaf wetness periods (0 to 72 h at 12-h intervals), number of lesions reportedly increased up to 12 h and remained at a similar level at longer leaf wetness periods; however, the interactions between the temperature and leaf wetness duration were unclear. Of the two temperature regimes (22 and 29°C) tested on gray leaf spot of perennial ryegrass turf, 29°C was reportedly more favorable to disease development (15); however, the leaf wetness duration effect was not tested in that study. In our study, the highest disease incidence and severity were observed at 28°C. The results of temperature effects on gray leaf spot development were similar to that reported in annual forage ryegrass and perennial ryegrass turf.

Gray leaf spot did not develop in plants that were air dried immediately after spraying the leaves with conidial suspension,

which indicates that free moisture is required for gray leaf spot development on the ryegrass leaves. Although 20°C was least favorable for gray leaf spot development, symptoms developed on plants that were exposed to the shortest leaf wetness duration (3 h) under such conditions. Gray leaf spot incidence increased with an increase in leaf wetness duration at 20°C; however, it remained relatively low until after 12 to 15 h of continuous leaf wetness, when a dramatic increase was observed. Only 50 to 60% leaf blades developed symptoms when exposed to 36 h of leaf wetness at 20°C. The relationship between disease incidence and leaf wetness duration at 20°C was quadratic. The effect of temperature on severity of gray leaf spot also showed a similar pattern. The disease severity was extremely low (0.1 index) at 3 h leaf wetness duration at 20°C, and remained virtually unchanged by extending leaf wetness period to 9 h.

In this study, regression analysis showed that gray leaf spot severity can be estimated by disease incidence (Fig. 3). In turfgrass disease management, information on disease incidence

TABLE 3. Estimated parameters for equation 2 for effects of temperature and leaf wetness duration on incidence of gray leaf spot of perennial ryegrass

Parameter	Parameter estimate	P value
b_0	2,685.71	<0.0001
b_1	-338.13	<0.0001
b_2	13.73	<0.0001
b_3	-0.18	<0.0001
b_4	6.21	<0.0001
b_5	-0.07	<0.0001
b_6	-0.08	<0.0001

TABLE 4. Estimated parameters for equation 2 for the effects of temperature and leaf wetness duration on severity of gray leaf spot of perennial ryegrass

Parameter	Parameter estimate	P value
b_0	350.09	<0.0001
b_1	-43.33	<0.0001
b_2	1.74	<0.0001
b_3	-0.02	<0.0001
b_4	0.28	<0.0001
b_5	-0.006	<0.0001
b_6	-0.002	0.0027

Fig. 2. A surface response for disease incidence and severity based on polynomial model (equation 2).

serves as an indicator for assessing the distribution of the disease, but not necessarily the extent of damage to turf in a given area. For example, an extremely high disease incidence (percent blades symptomatic) may include only specks or necrotic spots that will likely depict an off-color turf or diffuse-blighted area without causing significant damage to turf. On the other hand, disease severity serves as an indicator for assessing the extent of damage or death of turf. The information on disease severity will be highly desirable in order to determine whether the leaf blades are completely blighted, partially blighted, or have only necrotic spots or specks (off-color turf). Incidence data are easier to collect from the plant population in roughs and fairways than the severity data (percent leaf area necrotic) by sampling the plants in cup-cutter samples or the clippings already collected by mowers. Because gray leaf spot initially develops as specks that enlarge to necrotic spots during the early stage of epidemics, estimation of disease severity by incidence data at this stage of disease development will serve as a valuable tool for management of gray leaf spot, particularly during the periods of warm temperature and extended period of free moisture in the turf canopy.

The interactive effects between temperature and leaf wetness duration on gray leaf spot development in perennial ryegrass was consistent with the findings of a previous study on gray leaf spot of tall fescue (31), where a minimum of 4 h leaf wetness duration was sufficient to cause infection at 26 and 28°C but not at 24°C. In tall fescue, 28°C was the most favorable temperature for the development of gray leaf spot among the three temperatures tested (24, 26, and 28°C). Disease incidence increased in tall fescue with an increase in temperature and leaf wetness durations, and there were significant interactions between temperature and leaf wetness duration. In tall fescue, the relationship between disease incidence and leaf wetness duration was best described by a linear model at 20°C and a quadratic model at 28°C. Our study also showed a similar relationship described by a linear model at 20°C for both disease incidence and severity; however, it was described by a cubic model at the temperatures of 24 to 32°C.

Our model predicts the development of gray leaf spot when temperature is in the range of 28 to 31°C during the summer and when free moisture is present in the turf canopy. The effects of temperature and moisture are highly interdependent. Gray leaf spot is a late summer disease that is often misdiagnosed by turf managers as a drought stress problem, and the disease is greatly favored when irrigated in order to alleviate the problem. Prudent irrigation practices during the warm periods of summer are critical in order to reduce the leaf wetness duration in the turf canopy. The temperature and leaf wetness duration-based model may be used

as a tool in devising a spray schedule that accurately indicates the timing of fungicide application. This model could serve as an important component of a gray leaf spot forecasting system. Information on the effects of various additional cultural and meteorological factors may be useful in order to develop a comprehensive gray leaf spot forecasting system.

ACKNOWLEDGMENTS

This research was funded by the Golf Course Superintendents Association of America and the Pennsylvania Turfgrass Council. We thank F. Moorman and N. Kabir for technical assistance.

LITERATURE CITED

1. Bain, D. C., Patel, B. M., and Patel, M. V. 1972. Blast of ryegrass in Mississippi. Plant Dis. Rep. 56:210.
2. Campbell, C. L., and Madden, L. V. 1990. Introduction to Plant Disease Epidemiology. John Wiley & Sons, New York.
3. Carisse, O., Kushalappa, A. C., and Cloutier, D. C. 1992. Influence of temperature, leaf wetness, and high relative humidity on sporulation of *Cercospora carotae* on carrot leaves. Phytopathology 82:602-606.
4. Carver, R. B., Rush, M., and Lindberg, G. D. 1972. An epiphytic of ryegrass blast in Louisiana. Plant Dis. Rep. 56:157-159.
5. Chungu, C., Gilbert, J., and Townley-Smith, F. 2001. *Septoria tritici* blotch development as affected by temperature, duration of leaf wetness, inoculum concentration, and host. Plant Dis. 85:430-435.
6. Cochran, W. G., and Cox, G. M. 1992. Experimental Design. 2nd ed. John Wiley & Sons, New York.
7. Danneberger, T. K., Vargas, J. M., and Jines, A. L. 1984. A model for weather-based forecasting of anthracnose on annual bluegrass. Phytopathology 74:448-451.
8. Dernoeden, P. H. 1996. Perennial ryegrass and gray leaf spot. Golf Course Manag. 64:49-52.
9. Evans, K. J., Nyquist, W. E., and Latin, R. X. 1992. A model based on temperature and leaf wetness duration for establishment of *Alternaria* leaf blight of musk melon. Phytopathology 82:890-895.
10. Fidanza, M. A., Dernoeden, P. H., and Grybauskas, A. P. 1996. Development and field validation of a brown patch warning model for perennial ryegrass turf. Phytopathology 86:385-390.
11. Gross, M. K., Santini, J. B., Tikhonova, I., and Latin, R. 1997. The influence of temperature and leaf wetness duration on and infection of perennial ryegrass by *Rhizoctonia solani*. Plant Dis. 82:1012-1016.
12. Harmon, P., Rane, K., Ruhl, G., and Latin, R. 1999. First report of gray leaf spot on perennial ryegrass in Indiana. Plant Dis. 84:492.
13. Kato, H., and Kozaka, T. 1974. Effect of temperature on lesion enlargement and sporulation of *Pyricularia oryzae* in rice leaves. Phytopathology 64:828-830.
14. Kaur, S., Kaur, P., and Padmanabhan, S. Y. 1977. Influence of temperature on the development of blast in rice. Indian Phytopathol. 30:544-546.
15. Landschoot, P. J., and Hoyland, B. F. 1992. Gray leaf spot of perennial ryegrass turf in Pennsylvania. Plant Dis. 76:1280-1282.
16. Magboul, A. M., Geng, S., Gilchrist, D. G., and Jackson, L. F. 1992. Environmental influence on infection of wheat by *Mycosphaerella graminicola*. Phytopathology 82:1407-1413.
17. Malca, I., and Owen, J. H. 1957. The gray leaf spot disease of St. Augustinegrass. Plant Dis. Rep. 41:871-875.
18. McCarty, B. 2000. Perennial ryegrass on golf courses: Friend or foe? Grounds Maint. Jan. 67-74.
19. Monroe, J. S., Santini, J. B., and Latin, R. 1997. A model defining relationship between temperature and leaf wetness duration, and infection of watermelon by *Colletotrichum orbiculare*. Plant Dis. 81:739-742.
20. Moss, M. A., and Trevathan, L. E. 1987. Environmental conditions conducive to infection of ryegrass by *Pyricularia grisea*. Phytopathology 77:863-866.
21. Nutter, F. W., and Cole, H. 1983. Disease forecasting system for warm weather Pythium blight of turfgrass. Plant Dis. 67:1126-1128.
22. Rotem, J. 1978. Climatic and weather influences on epidemics. Pages 317-337 in: Plant Disease: An Advanced Treatise. Vol. 2. H. G. Horsfall and E. B. Cowling, eds. Academic Press, New York.
23. Schuh, W., and Adamowicz, A. 1993. Influence of assessment time and modeling approach on the relationship between temperature-leaf wetness periods and disease parameters of *Septoria glycines* on soybeans. Phytopathology 83:941-948.
24. Schumann, G. L. 1999. First report of gray leaf spot (*Pyricularia grisea*) on perennial ryegrass (*Lolium perenne*) in New England. Plant Dis. 83:1073.

Fig. 3. Relationship between gray leaf spot incidence and severity across four temperatures and 12 leaf wetness durations.

25. Schumann, G. L., Clarke, B. B., Rowley, L. V., and Burpee, L. L. 1994. Use of environmental parameters and immunoassays to predict Rhizoctonia blight and schedule fungicide applications on creeping bentgrass. *Crop Prot.* 13:211-218.
26. Shaner, G. 1981. Effects of environment on fungal leaf blight of small grains. *Annu. Rev. Phytopathol.* 19:273-296.
27. Smiley, R. W., Dernoeden, P. H., and Clarke, B. B. 1996. *Compendium of Turfgrass Diseases*. The American Phytopathological Society, St. Paul, MN.
28. Sullivan, M. J., Damicone, J. P., and Payton, M. E. 2002. The effects of temperature and leaf wetness period on the development of spinach white rust. *Plant Dis.* 86:753-758.
29. Suzuki, H. 1975. Meteorological factors in the epidemiology of rice blast. *Annu. Rev. Phytopathol.* 13:239-256.
30. Uddin, W. 1999. Gray leaf spot 'blasts' U.S. golf course turf. *Golf Course Manag.* 67:52-56.
31. Uddin, W., Burpee, L. L., and Stevenson, K. L. 1998. Influence of temperature and leaf wetness duration on development of gray leaf spot (blast) of tall fescue. (Abstr.) *Phytopathology* 88:S90.
32. Uddin, W., and Viji, G. 2002. First report of gray leaf spot of perennial ryegrass in sports field in California. *Plant Dis.* 86:75.
33. Valent, B., Crawford, M. S., Weaver, C. G., and Chumley, F. G. 1986. Genetic studies of fertility and pathogenicity in *Magnaporthe grisea* (*Pyricularia grisea*). *Iowa State J. Res.* 60:569-594.
34. Vargas, J. M., Jr. 1994. *Management of Turfgrass Diseases*. Lewis Publishers, Ann Arbor, MI.
35. Vincelli, P., and Dixon, E. 2002. Resistance to Q₀I (Strobilurin-like) fungicide in isolates of *Pyricularia grisea* from perennial ryegrass. *Plant Dis.* 86:235-240.
36. Wu, L., Damicone, J. P., Duthie, J. A., and Melouk, H. A. 1999. Effects of temperature and leaf wetness duration on infection of peanut cultivars by *Cercospora arachidicola*. *Phytopathology* 89:653-659.

Erratum

A correction was made to this article on October 10, 2005.
The parameter estimates in Tables 3 and 4 were incorrect.