Characterization of Wheat Leaf Rust Epidemics in Louisiana

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ABSTRACT

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Two experiments were conducted to study the effect of time of inoculation on leaf rust progress and to study the spatiotemporal spread of leaf rust in Baton Rouge, LA, during the 1986–1987 and 1987–1988 wheat-growing seasons. Epidemics were generated by sequential inoculation of different plots of a leaf rust-susceptible cultivar, McNair 1003, at 15-day intervals from 1 February to 15 March 1987, and from 1 December 1987 to 1 March 1988. Depending on the time of inoculation, the incubation period after inoculation varied from 8 to 18 days and appeared to be a function of the prevalent temperature. Early inoculations resulted in long, apparently stationary periods of development and greater areas under the disease progress curve (AUDPC). Leaf rust increase in all the plots occurred at the same time in March. The average apparent infection rates (r) of the epidemics were significantly different for different dates of inoculation. The r-values varied from 0.076 to 0.153/day during 1986–1987 and from 0.047 to 0.157/day during 1987–1988. Leaf rust severity was highly correlated with cumulative degree days (>20 C) following inoculation. The spatial and temporal spread of leaf rust was studied on the cultivars Rosen, McNair 1003, and Terral 812, which varied in degree of leaf rust resistance. An inoculum point source was established by transferring two uniformly rusted McNair 1003 seedlings to the center of each plot. Leaf rust spread in time and space was measured by estimating severity on five tillers at 2, 4, and 6 m from the inoculum source. Spatial gradients (g), r, and a velocity parameter (v) were calculated for each cultivar. The logistic model adequately explained the development of leaf rust in time and space. Cultivar resistance affected leaf rust severity and extent of spread. The r- and v-values for Rosen were significantly higher than for Terral 812, whereas g was significantly higher in Terral 812, indicating that Terral 812 was the most resistant cultivar. Yield reductions in all the cultivars were significantly related to AUDPC and distance from focus. The significance of distance of spread in estimating yield reduction is discussed.

Additional keywords: *Puccinia recondita*, quantitative epidemiology, *Triticum aestivum*.

Leaf rust caused by *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* is an important disease of wheat (*Triticum aestivum* L.) in many areas of wheat cultivation (33). In the United States, leaf rust is more severe in certain areas (31) and poses a greater threat to wheat production where virulence to current leaf rust resistance genes has been detected in the pathogen populations (34). In Louisiana, the area under soft red winter wheat cultivation is expanding as a result of the popularity of wheat-soybean rotation (1), and leaf rust has been observed more frequently than any other wheat disease (2).

The association of specific weather conditions with leaf rust development has been studied extensively (5,6,8,12,14,15,19, 40,41). Although temperature affects every stage of the disease cycle (5,12,15,37,38,40,41), viable inoculum, susceptible host, and hours of free moisture are all factors influencing leaf rust development.

Based on the severity of leaf rust on 1 April, Chester (8) developed a forecasting system for Oklahoma. Burleigh et al (7) showed that leaf rust epidemics can be quantified using the numbers of uredinia and urediniospores. Further analysis of these biological variables, along with the meteorological variables, such as minimum temperature and hours of free moisture or number of days of precipitation (13), resulted in the development of regression equations to predict leaf rust severities 14, 21, and 30 days after the date of prediction (6).

Forecasting systems based entirely on weather have also been developed. Coakley and Line (9) reported the influence of climatic variation on the frequency and severity of stripe rust epidemics in the Pacific Northwest of the United States. Higher winter temperatures and lower spring temperatures contributed to an increasing number of epidemics (10). A model for predicting stripe rust on certain cultivars was proposed and refined based on the accumulated winter or spring temperatures (11).

MacKenzie (23) suggested the use of both the apparent infection rate (42) and gradient steepness (18) to characterize slow-rusting components. However, with stem rust of wheat, MacKenzie (23) found no significant differences among gradients for susceptible and slow-rusting wheat cultivars, even though significant differences in the apparent infection rates existed. Attempts to identify a variable that encompasses both the rate and gradient parameters have been successful. More recently, other models to study the spatial dynamics of plant pathogens have been suggested, and the wave theory has been postulated to explain the spread of the disease (26). The gradient steepness (g), the apparent infection rate (r), and the velocity of spread (v) have been related by the formula $g = r/v$. This model was experimentally proven to explain the spread of late blight of potato (27). With oat crown rust (4), isopathic movement of the disease was used to explain spread and to rank horizontal resistance. Inoculum gradients for *P. recondita* have been quantified in terms of the number of urediniospores trapped (3,30) or the number of pustules on plants (28) at various distances around the point source. Gradients measured by disease severity have not been determined.

Winter wheat in Louisiana is normally planted in late October through late November and is harvested by mid-May. In most years, leaf rust appears during the early part of December, although delayed appearance of leaf rust has been noticed in some years. Variation in the time of appearance of leaf rust in Louisiana may be attributable to the source of the primary inoculum (37). Irrespective of the time of disease onset, leaf rust development is generally believed to slow down because of low winter temperatures and to progress faster with the onset of higher temperatures in March. However, experimental evidence to support this speculation is lacking.

In this article, we describe the effects of time of inoculation on disease development, environmental variables that explain the variation in leaf rust development, and the spatiotemporal spread of leaf rust in Louisiana. Preliminary results have been reported (38).

MATERIALS AND METHODS

The data reported in this article are derived from two experiments conducted during both the 1986–1987 and 1987–1988 wheat growing seasons at the Louisiana Agricultural Experiment Station Ben Hur Research Farm located in Baton Rouge, LA.

Experiment I. To study the effects of time of inoculation on disease development and identify environmental variables that explain the variation in leaf rust development, 24 3- × 3-m plots of McNair 1003, a soft red winter wheat cultivar susceptible to the prevalent pathogen populations, were planted in rows 25 cm apart on 5 December 1986 and 20 October 1987. Inclement weather delayed planting in 1986. The plots were separated by a 2.5-m strip of a leaf rust-resistant cultivar, Florida 302, to reduce plot interactions. At planting, the plots were fertilized with 68 kg/ha of N (ammonium nitrate). Two days after planting, the plots were sprayed for weed control with chlorosulfuron at a rate of 0.05 kg/ha. The treatment design consisted of a randomized complete block with three replications.

Experiment II. To study the spatiotemporal spread of leaf rust, three wheat cultivars with similar maturity dates but different degrees of resistance to leaf rust were planted in 9- × 9-m plots in a randomized complete block design with three replications on 5 December 1986 and 17 October 1987. Plot preparation and fertilization were similar to the method described in experiment I. The three cultivars were McNair 1003 (from Rohm and Haas Seeds, Inc., with 83% leaf rust severity based on visual estimation for 3 yr at Baton Rouge), Rosen (Arkansas Agricultural Experiment Station, with 40% leaf rust severity), and Terral 812 (Terral-Norris Seed Co., Inc., with 11% leaf rust severity) (1). Rows were spaced 25 cm apart and oriented perpendicular to the prevailing wind. The plots were separated by a 3-m strip of the leaf rust-resistant cultivar Florida 302 to reduce plot interactions. Stakes were placed 2, 4, and 6 m away from the center of the plots in four diagonal directions for data collection. An isolated 3- × 3-m plot of each cultivar was grown approximately 8 km from these experiments to serve as reference plots to assess the interplot interference in the main experiment.

Inoculation. McNair 1003 was planted in pots 10 cm in diameter and maintained in an air-conditioned greenhouse (21 C). Five days after emergence, the pots were thinned to two seedlings per pot. At Feekes growth stage (GS) 4 (22), seedlings were inoculated with a leaf rust urediniospore suspension (~ 10^6 spores/ml) of race UN2 (common to most of the winter wheat-growing areas) prepared by using an atomizer to suspend urediniospores in distilled water containing two drops of Tween 80 (ICN Nutritional Biochemicals, Cleveland, OH). Plants were then incubated in a dew chamber for 16–18 hr at 18 ± 1 C. Subsequently, the pots were transferred to greenhouse benches and incubated at 21 ± 1 C until uredinia became erumpent. Epidemics were initiated in different plots with rusted seedlings of similar age. Uniformly rusted (~ 60%) seedlings in pots were transferred to the center of plots in experiment I at 15-day intervals beginning on 1 February 1987 and 1 December 1987 and continuing until 15 March 1987 and 1 March 1988, respectively.

To initiate epidemics in experiment II, a point source of inoculum was established by transferring two uniformly rusted (~ 60%) seedlings in pots prepared as described in the previous experiment. The pots were placed in the center of the plots on 4 March 1987 and 17 January 1988, for 1986–1987 and 1987–1988 experiments, respectively. The source plants remained in the plots until the end of the season.

The cultivar Florida 302, planted as a buffer, was sprayed with the leaf rust-specific fungicide butrizol at the rate of 0.98 kg/ha with a hand-held sprayer (model 21, R. E. Chapin Manufacturing Works, Inc., Batavia, NY) to reduce possibilities of leaf rust development. The fungicide was sprayed on 5 February 1987 for the 1986–1987 experiments and on 10 December 1987 for the 1987–1988 experiments.

Disease assessment. In experiment I, for each date of inoculation, the number of days between inoculation and appearance of the first pustule was noted. Plots were then monitored at 3- to 4-day intervals for leaf rust appearance.

Disease progress was measured using the modified Cobb's scale (29) at approximately weekly intervals on 10 randomly selected tillers per plot. Severity estimations were begun from the time the first pustules were noticed in each date of inoculation and continued until leaf senescence.

In experiment II, the first disease assessments were delayed until the disease was well established (GS 5–6). Leaf rust severity estimates were made at 7-day intervals as described above on five randomly selected tillers around the point source and at each sampling distance in four directions. Severity estimates were made until the leaves senesced. Care was taken to minimize the effects of physical movement in plots at disease evaluation and thus lessen interplot interference.

Environmental monitoring. Maximum and minimum temperature and leaf wetness were measured using sensors on a CR21 micrologger (Campbell Scientific Inc., Logan, UT) programmed to test leaves each minute and then average and record data at

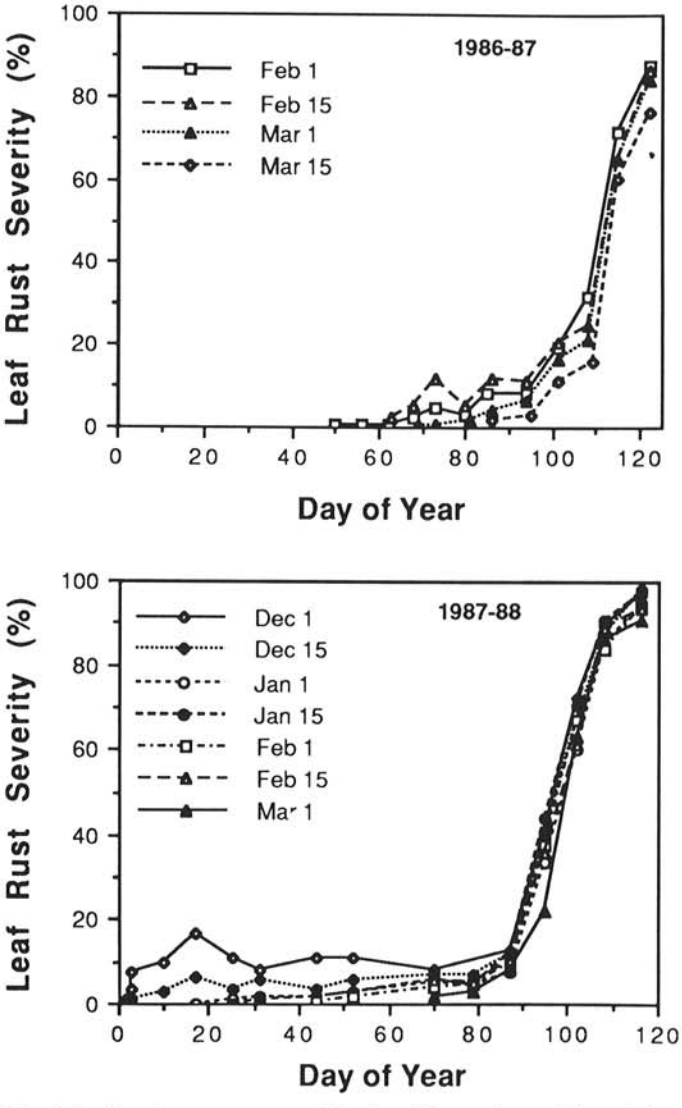

Fig. 1. Leaf rust progress curves following different dates of inoculation on wheat cultivar McNair 1003 during the 1986–1987 and 1987–1988 growing seasons in Baton Rouge, LA.

60-min intervals. The weather data were recorded from the date of first inoculation until final disease assessments were made.

Grain yield. In experiment II, 1-m-row plots of each cultivar were harvested around the point source and at each distance at which disease assessments had been made in four diagonal directions. Each sample was threshed, and final yields were determined at 13% moisture.

Data analysis. Areas under the disease progress curves (AUDPCs) for each date of inoculation in both years from experiment I were calculated according to the procedure described by Shaner and Finney (35). Variance analysis was performed on incubation period and AUDPC data. Mean comparisons were made using Fisher's protected least significant difference test (LSD) (36) at the 5% probability level.

Degree days were used to determine the cumulative effect of temperature on leaf rust development after each date of inoculation during the wheat-growing season. Most studies indicate that the optimum temperature for urediniospore survival (12), growth (31), and sporulation (15,40,41) on susceptible wheat plants is 20 C; one study indicates that it is 16 C (19). Therefore, 20 C was used as a base temperature, from which to calculate degree days. A computer program was written in FORTRAN to compute daily maximum and minimum temperatures and to calculate degree days according to the procedure of Coakley and Line (9). From this data, the cumulative degree days (CDD) from inoculation to final disease assessment were obtained for each date of inoculation. The number of hours of leaf wetness per day from inoculation to final disease assessment was also calculated for each date of inoculation. Mean leaf rust severity per tiller was computed, logit transformations of leaf rust severity were made, and apparent infection rates (42) were calculated by regression analysis of logit disease severity on cumulative degree days for each date of inoculation and days after inoculation as independent variables.

Regression analysis was used to determine the relationships between leaf rust development and biological and environmental variables. Data from different dates of inoculation from both years were combined by dates of disease assessment and analyzed. Logit severity was used as the dependent variable. CDD, hours of leaf wetness, and logit severity 2 wk before the date of prediction were independent variables. Variables that were not statistically significant (*t* tests of partial regression coefficients) were dropped from further analysis.

Leaf rust severity data from experiment II were transformed to logits for further analysis. Severities less than 1% and more than 99% were not used in the analysis. To determine whether there was a directional gradient, data were subjected to analysis of variance by cultivar. In all three cultivars, orientation of the gradient was not a significant source of variation in leaf rust severity. Therefore, data from all four directions were combined for further analysis.

The average apparent infection rates (r) for each cultivar were estimated by regression analysis of logit severity on time. Similarly, gradient parameters (g) were estimated by regression analysis of logit severity on distance (26). The velocity (v) of leaf rust spread on each cultivar was calculated using the method of Minogue and Fry (26). The average rate parameter (r), gradient parameter (g), and velocity parameter (v) were used to compare the three

TABLE 1. Incubation period for leaf rust development, average hours of leaf wetness per day and area under the disease progress curve (AUDPC) for different dates of inoculation of the susceptible wheat cultivar McNair 1003

Year	Dates of inoculation and GS[a] at inoculation		Incubation period (days)[b]	CDD[c]	Hours of leaf wetness/day[d]	AUDPC
1986–1987	1 February	3[a]	18 z	0	11.2	1356 w
	15 February	3	18 z	0	9.0	1397 w
	1 March	5	9 x	2	7.9	1095 x
	15 March	6	9 x	2	6.9	879 y
1987–1988	1 December	3	9 x	2	17.4	2671 w
	15 December	3	10 x	2	17.9	2074 x
	1 January	4	17 z	0	17.4	1898 y
	15 January	5	8 x	1	18.2	1715 z
	1 February	6	9 x	1	17.6	1706 z
	15 February	8	12 y	0	17.4	1694 z
	1 March	9	9 x	2	16.9	1531 z

[a] Feekes growth stage.

[b] Interval between inoculation and first pustule appearance. Figures followed by the same letters are not significantly ($P = 0.05$) different in each year.

[c] Cumulative degree days between inoculation and first pustule appearance.

[d] Average hours of leaf wetness per day during the period from the date of inoculation to the final disease assessment.

TABLE 2. Comparison of regression coefficients and coefficients of determination between logistic models using days after inoculation (Days) and cumulative degree days (CDD) as independent variables for the development of leaf rust as logit-transformed proportion of disease

Year	Date of inoculation	Logit[a]		Slope[b]		R^2[c] (adj.)	
		Minimum	Maximum	Days	CDD	Days	CDD
1986–1987	1 February	−5.36	1.91	0.096	0.171	0.949	0.846
	15 February	−3.85	1.82	0.076	0.149	0.843	0.918
	1 March	−7.13	1.66	0.127	0.197	0.966	0.860
	15 March	−4.41	1.19	0.153	0.156	0.946	0.921
1987–1988	1 December	−9.21	4.59	0.047	0.169	0.633	0.670
	15 December	−6.50	4.59	0.053	0.165	0.737	0.861
	1 January	−5.59	5.29	0.076	0.179	0.775	0.869
	15 January	−7.19	4.82	0.095	0.187	0.829	0.850
	1 February	−4.93	3.32	0.102	0.180	0.902	0.834
	15 February	−3.13	3.44	0.139	0.154	0.907	0.899
	1 March	−4.18	2.94	0.157	0.197	0.955	0.912

[a] Mean of three replications. Logit values calculated as $\ln[x/(1-x)]$, where x is the proportion of the leaf rust severity.

[b] Slopes from regression of logit x = days after inoculation and logit x = cumulative degree days (>20 C) accumulated from the date of inoculation.

[c] All regressions significant at $P = 0.0001$.

cultivars using the LSD test at $P = 0.05$. Comparisons of r, g, and v between years were also made using the LSD test at $P = 0.05$.

The AUDPCs at each distance from the focus in experiment II were calculated for each cultivar. The yield at different distances was used as the dependent variable, and distances and the AUDPCs at each distance were used as independent variables to predict yield. Coefficients of determination were used to evaluate the models.

TABLE 3. Intercept and partial regression coefficients for cumulative degree days (CDD), average hours of leaf wetness per day (HLWT), and observed leaf rust severity 2 wk before prediction (PD) used to predict leaf rust development in Baton Rouge, LA

Variable	Partial regression coefficient	$P > t$	R^2[a](adj.)
—[b]	−1.574 ± 0.274[c]	0.0001	0.905
PD	0.264 ± 0.028	0.0001	. . .
CDD	0.116 ± 0.007	0.0001	. . .
HLWT	−0.023 ± 0.014	0.1047	. . .

[a] Significant at $P = 0.0001$.

[b] Intercept.

[c] Standard error of parameter.

RESULTS

Experiment I: Leaf rust development. The disease present at the first observation was considered for analytical purposes to be the amount of initial disease. Inoculations on 1 and 15 February 1987, 1 and 15 December 1988, and 1 and 15 January 1988 resulted in long, apparently stationary periods of development (lag period). Leaf rust inoculations after this period resulted in progressive reduction in the lag period (Fig. 1). During this apparently stationary period of leaf rust development, there was little degree day accumulation. Leaf rust increase in plots inoculated at different times occurred at the same time in March (day of year = 80–85) and subsequently progressed in a similar manner in both seasons (Fig. 1).

Incubation period varied from 9 to 18 days in 1986–1987 and from 8 to 17 days in 1987–1988 (Table 1). Significant differences were found in the incubation periods following different dates of inoculation that appeared to be a function of the temperature following inoculation (Table 1). Significant differences were also noticed in AUDPCs resulting from the different dates of inoculation each year (Table 1). Early inoculations resulted in significantly higher AUDPCs. The AUDPCs varied from 879 to 1,356 during 1986–1987 and from 1,530 to 2,671 during 1987–1988.

Apparent infection rates. The logistic model fitted the data using either days after inoculation or CDD as the time variable.

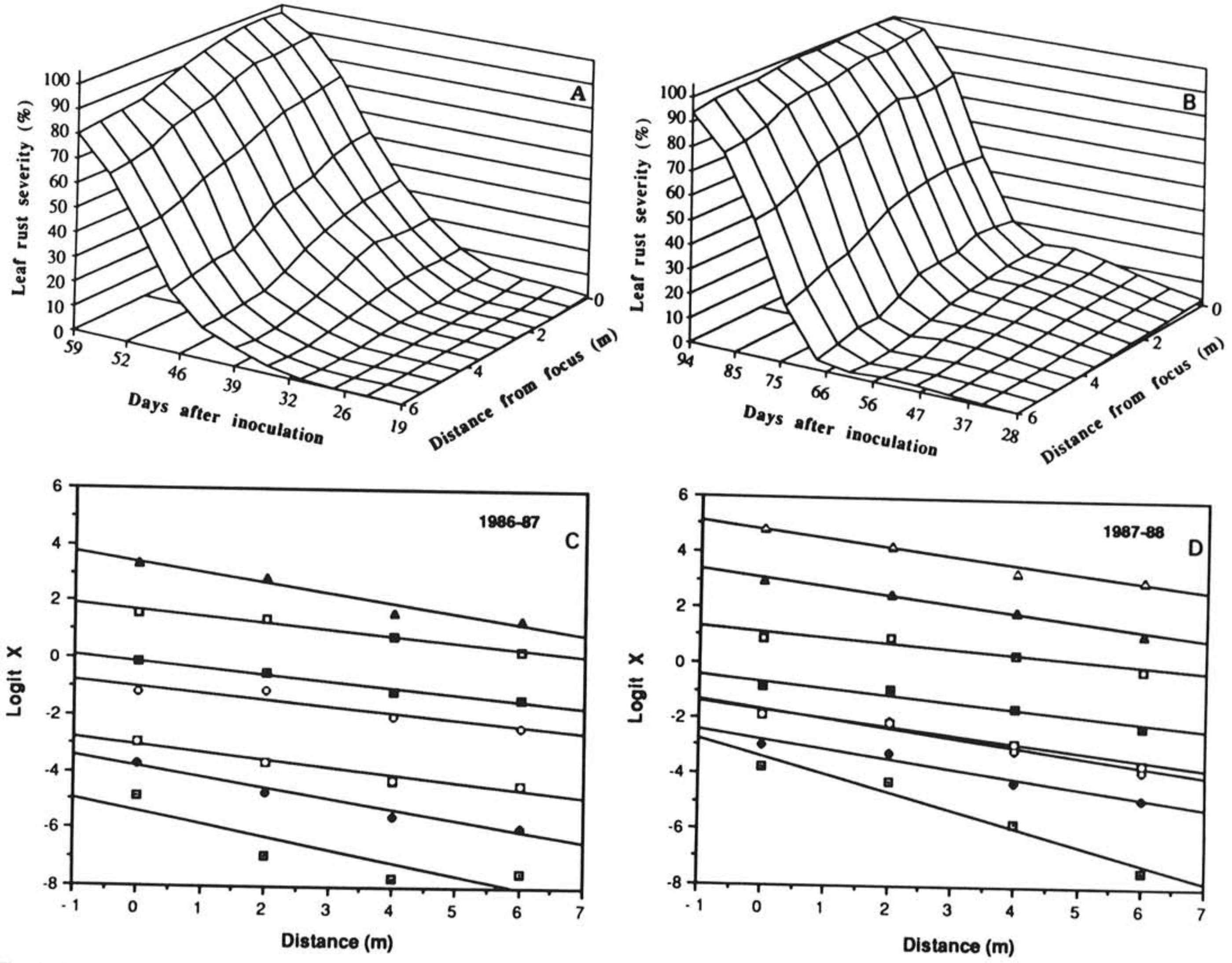

Fig. 2. Development and spread of leaf rust on wheat cultivar Rosen during 1986–1987 and 1987–1988. Leaf rust severity by time and distance during 1986–1987 (**A**) and 1987–1988 (**B**). Leaf rust severity as a function of distance from the point of inoculation at 19 and 28 (dotted squares), 25 and 36 (solid diamonds), 32 and 55 (closed dotted squares), 40 and 63 (dotted diamonds), 46 and 71 (solid squares), 53 and 79 (open squares), 59 and 86 (solid triangles), and 94 (dotted triangles) days after inoculation during 1986–1987 (**C**) and 1987–1988 (**D**).

In both years, apparent infection rates calculated using days after inoculation as the independent variable were significantly different for different dates of inoculation (Table 2). The apparent infection rates ranged from 0.096 to 0.153/day during 1986–1987 and from 0.047 to 0.157/day during 1987–1988. Calculated apparent infection rates between successive dates of disease assessment were similar from 12 April to 2 May 1987 and from 28 March to 26 April 1988. When CDD was used as the independent variable, the apparent infection rates standardized. The apparent infection rates calculated from regression analysis using CDD as the independent variable were 0.149–0.197/DD during 1986–1987 and 0.154–0.197/DD during 1987–1988. When time (days) was used as the independent variable, the coefficients of determination for epidemics initiated on different dates of inoculation ranged from 0.843 to 0.966 during 1986–1987 and from 0.633 to 0.955 during 1987–1988. When CDD was used as the independent variable, the coefficients of determination improved for early dates of inoculation during 1987–1988 and remained comparable for other dates of inoculation (Table 2).

Factors affecting leaf rust development. Regression analysis using biological and environmental variables to predict leaf rust severity indicated that the disease present 14 days before prediction and CDD would explain most of the variability in leaf rust development in Louisiana (R^2 = 0.905, Table 3). The partial regression coefficients associated with these two variables were highly significant. The coefficient for hours of leaf wetness per day was not significant (Table 3). The regression model after dropping hours of leaf wetness per day was also highly significant ($P = 0.0001$). The regression equation based on the disease present on the date of prediction and CDD predicted leaf rust development accurately for different dates of inoculation for most of the season. The plots of residuals showed normal distribution. The average number of hours of leaf wetness per day varied from 6.9 to 11.2 during 1986–1987 and from 16.9 to 18.2 during 1987–1988 (Table 1).

Experiment II: Cultivars and leaf rust development. Response surfaces of leaf rust severity from initial disease assessment to final disease assessment are presented in Figures 2–4 for each cultivar at various distances from the point source of inoculum. For Rosen, the final leaf rust severity observations on plants around the point source of inoculum showed leaf rust severity to be more than 95% in both years and to be lower at the farthest sampled distance from the source in both years (Fig. 2A and B). A similar trend was noticed in the other two cultivars each year (Fig. 3A and B; 4A and B).

Differences in degree of cultivar resistance were also noticeable in the average apparent infection rates. The apparent infection rates for Rosen were significantly higher than those for McNair 1003 and Terral 812 during 1986–1987. However, during 1987–1988, the apparent infection rate for Terral 812 alone was

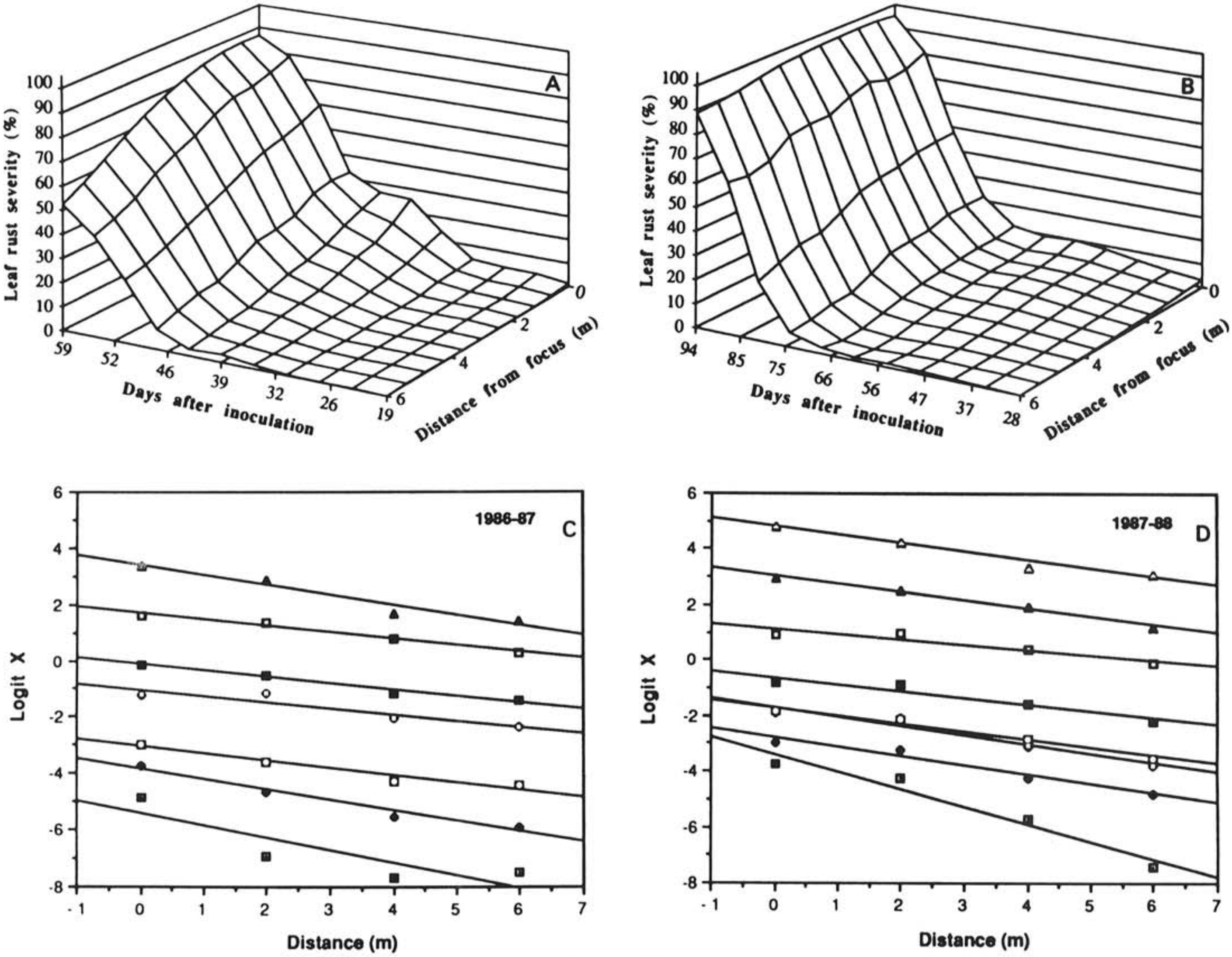

Fig. 3. Development and spread of leaf rust on wheat cultivar McNair 1003 during 1986–1987 and 1987–1988. Leaf rust severity by time and distance during 1986–1987 (**A**) and 1987–1988 (**B**). Leaf rust severity as a function of distance from the point of inoculation 19 and 28 (dotted squares), 25 and 36 (solid diamonds), 32 and 55 (closed dotted squares), 40 and 63 (dotted diamonds), 46 and 71 (solid squares), 53 and 79 (open squares), 59 and 86 (solid triangles), and 94 (dotted triangles) days after inoculation during 1986–1987 (**C**) and 1987–1988 (**D**).

significantly lower than that of Rosen, and the apparent infection rates were intermediate for McNair 1003. The apparent infection rates were 0.171–0.236/day during 1986–1987 and 0.076–0.117/day during 1987–1988 (Table 4).

Gradients. In both years, differences in gradients with direction were not observed in any of the cultivars tested. Leaf rust severities on isolated plots used to assess interplot interference were less than 10% on 15 April in both years. The final disease assessments were made on 26 April 1987 and 16 April 1988. It appears that there was little movement of inoculum between plots. Higher levels of infection in plants along the edges of plots, sometimes associated with the interplot interference, were also not observed in any plots.

A statistically poor fit was consistently observed when Gregory's log-log model (18) was applied to the data (R^2 = 0.07–0.76). The logit-linear model (25) gave the best fit for the data, and the coefficient of determination for all the fitted lines was greater than 0.9. The disease gradient in Terral 812 was initially quite steep and became flatter over time (Fig. 4C and D). In Rosen and McNair 1003, only the primary disease gradients were steep, and, thereafter, any gradient was representative of gradients from any other date of disease assessment (Fig. 2C and D; 3C and D). The apparent infection rates in the three cultivars showed no association with distance (data not shown).

Cultivar resistance was also discernible with both the gradient and the velocity parameters (Table 4). There was little variation in the estimated average gradient parameter between seasons for Rosen and McNair 1003. For Terral 812, the gradient parameter was higher during 1987–1988 than during 1986–1987. The gradient parameter values for Terral 812 were significantly higher when compared with Rosen and McNair 1003 both years (Table 4). The velocity of spread from the focal center was also slow in Terral 812 compared with that in Rosen and McNair 1003 (Table 4). The velocity parameter for McNair 1003 was intermediate between Terral 812 and Rosen. The velocity of leaf rust spread on all the cultivars was higher during 1986–1987 when compared with 1987–1988 (Table 4).

Grain yield. The highest-yielding cultivar was McNair 1003, followed by Terral 812 and Rosen. The predicted grain yield in the absence of leaf rust as indicated by the intercept was 116, 102, and 84 g/m in McNair 1003, Terral 812, and Rosen, respectively (Table 5). As the distance from the focal center increased, AUDPC decreased and yield increased. Yield and AUDPC were significantly inversely correlated ($r = -0.74$; $P = 0.0001$), whereas yield and distance from the focal center were significantly positively correlated ($r = 0.59$; $P = 0.0002$). Correlation between AUDPC and distance was low, albeit significant ($r = -0.33$; $P = 0.0461$). Regression analysis of the yield data pooled from both years showed that the relationship between AUDPC and yield reduction was linear (Table 5). All regression coefficients were significant ($P = 0.026$–0.002), and the models explained 41–64% of yield variance (Table 5). Distance from the focus was also

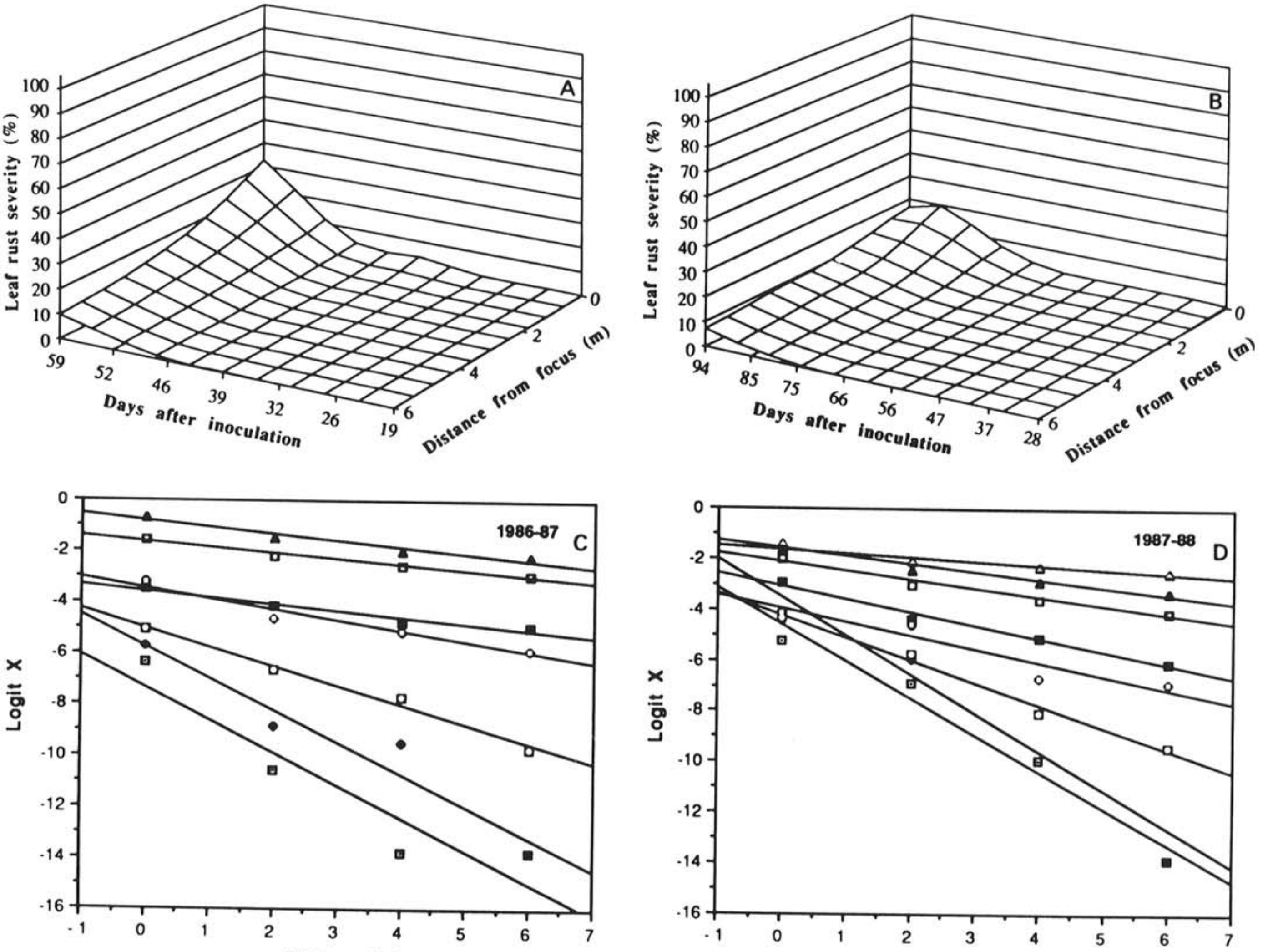

Fig. 4. Development and spread of leaf rust on wheat cultivar Terral 812 during 1986–1987 and 1987–1988. Leaf rust severity by time and distance during 1986–1987 (**A**) and 1987–1988 (**B**). Leaf rust severity as a function of distance from the point of inoculation 19 and 28 (dotted squares), 25 and 36 (solid diamonds), 32 and 55 (closed dotted squares), 40 and 63 (dotted diamonds), 46 and 71 (solid squares), 53 and 79 (open squares), 59 and 86 (solid triangles), and 94 (dotted triangles) days after inoculation during 1986–1987 (**C**) and 1987-1988 (**D**).

a useful predictor of yield and statistically explained the variation in yield as much as or better than AUDPC (Table 5).

DISCUSSION

Temperature affects survival (12,37), latent period (14,15,19,40), growth (31), infectious period (40), and sporulation (15,40,41) of the leaf rust fungus. Analysis of variance of the data on latent period following different dates of inoculation indicated significant differences (Table 1), probably caused by the prevalent temperatures following inoculation. However, leaf rust progress was retarded during early spring irrespective of the time of inoculation. During this period of retardation, there was little degree day accumulation; therefore, temperature during this period was not favorable for leaf rust progress. Departure from optimum temperature during early spring also may have resulted in the lengthening of latent periods between successive infection cycles and a shortening of the infectious period and sporulation. In all the inoculated plots, increases in leaf rust were observed at the same time during March of both years (Fig. 1). Increase in degree day accumulation also began at this time, once again indicating that temperature may be the factor affecting leaf rust development.

Burleigh et al (6) used fungal growth and infection functions as predictors of leaf rust development in their equations to forecast leaf rust. These variables were the SIN^2 transformations of the temperature response curve accounting for periods of favorable temperature for fungal growth and infection. We used degree days, another temperature transformation. Much of leaf rust development in Louisiana appears to be associated with the leaf rust severity on the day of prediction and CDD from the date of inoculum arrival (Table 3). These two variables explained more than 90% of the variation in leaf rust development.

The partial regression coefficient for hours of leaf wetness per day was not significant in the regression analysis. Under optimal temperature conditions, *P. recondita* f. sp. *tritici* requires only 3–4 hr of leaf wetness for spore germination and infection (32). Adequate moisture periods in the form of frequent rain and dew (Table 1) are available during the wheat growing season in Louisiana. Moisture requirements are typically satisfied; therefore, this may not be a limiting factor for leaf rust development. In rainfall-deficient seasons, however, moisture periods may emerge as a factor influencing leaf rust development in Louisiana.

Sequential inoculations of plots of McNair 1003 were essentially inoculations at different growth stages. Although early inoculations resulted in larger AUDPCs, growth stages themselves did not have a direct effect on leaf rust development. The value of growth stages in a predictive equation, therefore, may be limited. However, Burleigh et al (6) indicated that growth stage in the predictive equation may improve predictions. The early infections, however, seem to have a greater deleterious effect on yield, depending on the cultivar used (39).

Apparent infection rates calculated from the logistic equation (42), using days after inoculation as the independent variable between successive dates of disease assessments for different dates of inoculation, were similar during late season from 12 April to 2 May 1987, and from 28 March to 26 April 1988. However, early inoculations resulted in significantly lower apparent infection rates (Table 2). This apparent difference may have been the artifact of using days as the time variable in the logistic equation, since all days are not equally favorable (24) for leaf rust development. We used CDD as the independent variable, which accounts for favorability of temperature for leaf rust development. Apparent infection rates for the three common dates of inoculation between years in experiment I were significantly different when days were used as the dependent variable. However, calculated apparent infection rates using CDD remained comparable between years and were not significantly different (Table 2). The percentage variation in leaf rust development explained by this variable also improved for early dates of inoculation when CDD was used as the independent variable. Variables like CDD may work to standardize the apparent infection rates so that comparisons can be made among years and cultivars (24).

Cultivar resistance influenced leaf rust severity and the extent of disease spread. Increasing levels of resistance reduced leaf rust severity and spread. Increase in leaf rust severity and spread occurred in March once the temperatures became favorable for disease development. The average apparent infection rates and the average velocity parameter for different cultivars were higher during 1986–1987 than during 1987–1988 (Table 4). This increase in apparent infection rate and velocity may have resulted from the delayed inoculation of plots during 1986–1987, which may have reduced the leaf rust development lag period.

The development of leaf rust in time and space and relative resistance of different cultivars to leaf rust can be depicted by three-dimensional response surface methods. However, for valid statistical comparisons of the cultivars, parameter estimates from empirically fitted models are necessary. Cultivar differences were detected in both three-dimensional response surfaces and the parameter estimates. Terral 812 consistently developed low leaf rust severity, and spread from the point of inoculation was delayed. This cultivar, in contrast to the other two cultivars, also had a steeper gradient, a lower apparent infection rate, and a lower velocity of spread, indicating that it was the most resistant of

TABLE 4. Estimated values of the average gradient parameter (*g*), the apparent infection rate (*r*), and the velocity of spread (*v*) for three cultivars infected with *Puccinia recondita* f. sp. *tritici* during 1986–1987 and 1987–1988 wheat growing seasons

	g (m^{-1})		r (day^{-1})		v (m/day)	
Cultivar	1986–1987	1987–1988	1986–1987	1987–1988	1986–1987	1987–1988
Rosen	0.356 a[a]	0.346 a	0.236 a	0.117 a	0.615 a	0.338 a
McNair 1003	0.358 a	0.311 a	0.171 b	0.098 ab	0.483 ab	0.315 a
Terral 812	0.670 b	0.787 b	0.180 b	0.076 b	0.289 b	0.096 b

[a] Values followed by the same letter within a column are not significantly different ($P = 0.05$) by Fisher's protected least significant difference test.

TABLE 5. Comparison of regression equations used to predict plot yield with distances and areas under the disease progress curve (AUDPC) at different distances from the focus as predictors

Cultivar	Predictor (X)	Regression equation	R^2 (adj.)	$P > F$
Rosen	Distance from focus	38.69 + 3.910 ×	0.54	0.0063
	AUDPC	84.16 − 0.022 ×	0.41	0.0258
McNair 1003	Distance from focus	48.86 + 5.890 ×	0.54	0.0063
	AUDPC	116.45 − 0.047 ×	0.51	0.0096
Terral 812	Distance from focus	63.45 + 5.530 ×	0.64	0.0019
	AUDPC	101.63 − 0.139 ×	0.64	0.0018

the cultivars studied to the leaf rust races employed. In McNair 1003, even though the terminal severities were as high as for Rosen, the apparent infection rates and the velocity parameters during 1986–1987 were between those of Rosen and Terral 812. This suggests that leaf rust develops more slowly on McNair 1003 than on Rosen. Differences in the gradient parameter between McNair 1003 and Rosen were not significant. Several other workers (4,20,23) were also unable to differentiate between cultivars based on the gradient parameter alone. Therefore, apparent infection rate, velocity parameter, and gradient parameter may all need to be compared to detect cultivar differences. All the parameter estimates and the three-dimensional response surfaces indicated that Rosen was the most susceptible cultivar.

Aylor (3) hypothesized that for rust urediniospores, which depend on wind gusts to become airborne, diffusion may dominate dispersal; therefore, the power model may explain a gradient better than the exponential model. Fitt et al (16) fitted 325 sets of data to both power models and exponential models and made similar conclusions. Gradients of *P. recondita* urediniospores described by Roelfs were modeled better by log-log transformation of the power law equation (30) and, similarly, Mundt (28) obtained superior fit using the log-log transformation of the modified power law equation. In our study, logit-linear transformation (25) consistently gave a better fit and the range of estimated gradient parameter values are in agreement with those of Aylor (3), but the magnitude of the gradient estimations may have been influenced by the range of distance chosen for our experiment (3,27). This may also have been the result of our measuring the severity of leaf rust as against the number of spores.

The traveling wave theory that has been advanced to explain the spread of diseases (26) assumes that the gradient steepness and velocity are constant over time and that the rate of increase is constant over distance. Gradients for all the cultivars were constant over time in our experiments (Fig. 2C and D; 3C and D; 4C and D), and the apparent infection rates were uniform over distance. These results support the traveling wave concept. Uniformity of the apparent infection rates also indicates that significant movement of inoculum did not occur as a result of our frequent disease assessments in the plots. Similar observations were made by Fried et al (17) on wheat powdery mildew.

Most studies on disease spread have not included a determination of the relationship between disease spread and yield. In this study, as the distance from the point source increased, the AUDPC decreased and the plot yield increased. The AUDPC explained 41–64% of yield variance (Table 5). Distance can be thought of as related to yield indirectly through AUDPC, and yet, distance explained higher yield variance (54–64%) than did AUDPC. This can possibly be explained by one of the assumptions of regressions that states that the independent variable is measured without error (36). Distance is controlled by the experimenter and is usually measured without error. However, AUDPC is calculated using subjective disease assessments and may not be as accurate. Crop loss models are developed on the assumption that distribution of rusts in plots is homogeneous. These models do not account for spatial heterogeneity (21) resulting in under- or overprediction of losses. Under such circumstances, distance from the primary disease foci identified early in the season may be a useful predictor of yields.

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