A METHOD OF PREDICTING EPIDEMIC DEVELOPMENT OF *Puccinia Recondita f. sp. tritici*

by 45

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INTRODUCTION

Wheat leaf rust, incited by *Puccinia recondita* Rob. ex. Desm. f. sp. *tritici*, is one of the major barriers to the realization of potential wheat yields in the Great Plains. Sporadic leaf rust epidemics have reduced wheat yields by 30 per cent in some years. Resistant varieties provide the primary means of control, however, changes in the virulence of the parasite population reduce the long term effectiveness of specific resistance.

Chemical control of leaf rust has not been effective or economical because the complex interrelationship between weather, inoculum, rate of disease development, and reduction in yield is not clearly defined. A reliable leaf rust forecast is essential for proper timing of fungicide application to reduce losses in wheat yields.

Extensive work has been done on the epidemiology of leaf rust but few researchers have attempted to forecast the rate of development or the resulting loss in yield. Instead, emphasis has been placed on following the seasonal development of leaf rust by the date of the first appearance of urediospores on spore traps and of uredia in the field, the number and intensity of spore showers, and by climatological records (1,2,12,13,14,15,16,20,24,27).

Leaf rust development has been studied under controlled environmental conditions (4) but development in the field is subjected to environments which fluctuate according to diurnal and seasonal patterns. In addition, short irregular changes in these patterns have an effect on subsequent disease development. This thesis examines the environmental factors which need to be included in a leaf rust prediction equation. Several methods of analyzing different variables are tried and prediction equations in the form $Y = b_1x_1 + b_2x_2 + b_3x_3$ are tested.

REVIEW OF LITERATURE

The first forecast of a plant disease in the United States was issued in 1923 by N. E. Stevens on the keeping quality of the Plymouth County, Massachusetts cranberry crop (25). The forecast was based on the May-June temperatures and the July-August rainfall.

Most forecasts of disease loss have been concerned with potato and tomato late blight. Cook (6,7) developed a forecast for potato late blight which used daily temperature and rainfall to determine the critical period for blight development. Hyre (10) modified Cook's forecasting technique by using a seven day moving mean of temperatures. After eight consecutive days favorable for blight a disease warning was issued. Late blight forecasting systems developed by Cook and Hyre are not applicable to the Midwest because blight conditions can occur without measurable rainfall. Wallin (29) and others (11) have found relative humidity measurements, which include moisture associated with dew formation (9), to be more reliable than precipitation measurements in a forecast system.

Wallin and Riley (30) based forecasts of late blight on information from synoptic weather maps. Scarpa and Raviere (22) related development of downy mildew of lima bean to synoptic weather patterns by use of hourly dew points.

Chester (4) developed a leaf rust forecast for Oklahoma based on the severity of rust on April 1. He stated that weather was not the limiting factor after April 1 but that inoculum and generation time limit leaf rust development. Because a logarithmic increase in leaf and stem rust severity can occur in 4-5 days (21) extremely favorable or unfavorable environmental conditions could invalidate Chester's forecasts.

MATERIALS AND METHODS

Replicated plots of four winter wheat varieties (Triumph, Kharkof, Early Blackhull, Comanche) were planted at 24 experiment stations in Texas, Oklahoma, Kansas, and Nebraska. Three spring wheat varieties (Selkirk, Justin, and either Little Club, Marquis, Lee or Ceres) were planted at 16 experiment stations in North Dakota, South Dakota, and Minnesota for the 1966 crop year (Plate I).

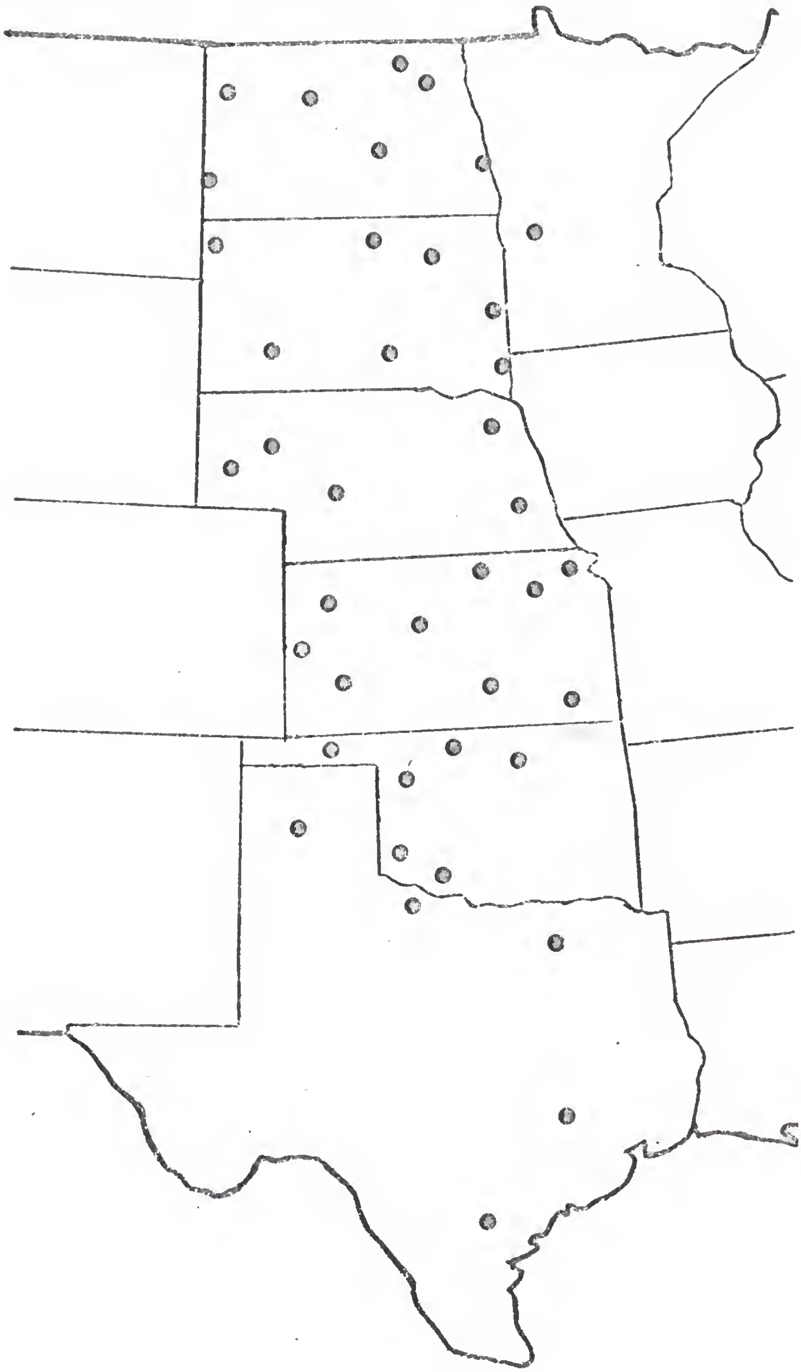
A ten-culm sample was collected weekly from 4 replications of each variety beginning at late tillering and continuing until the crop reached maturity. Samples were placed in padded envelopes or 3-inch mailing tubes and air mailed to the Rust Laboratory in Manhattan, Kansas where leaf rust uredia were counted and recorded as number of uredia per culm. When leaf rust severity reached 1 per cent, (18 uredia per culm) subsequent disease severity estimates were made using the modified Cobb scale (17).

A 40 by 60 ft plot of Bison wheat was planted at 16 locations in August 1966 for a fall epidemiological study. A 40-culm random sample was collected twice weekly beginning when the wheat plants reached the 3 leaf stage and continuing until 31 October.

EXPLANATION OF PLATE I

Location of experiment stations where nurseries were planted in both the winter and spring wheat regions.

PLATE I.



Two wheat varieties were planted in 40 by 60 ft plots at each location in 1967 and 1968. Bison and Baart were used as susceptible varieties at all winter and spring wheat locations, respectively. A second variety, one predominantly grown in the area, was grown at each location. This combination of varieties measured the rate of disease development on a susceptible variety and on a commercial variety which was resistant to portions of the parasite population. Forty culm random samples were collected weekly until boot stage and then twice weekly. Samples were collected daily from the Bison plot at Manhattan in 1968.

Glass rod impaction traps (18), mounted on weather vanes located in or near the nursery, were used to provide a measure of urediospore numbers. Spore numbers were expressed as numbers deposited per cm^2 per day.

Daily maximum-minimum temperature and precipitation records were obtained for the individual locations from the appropriate section of the 1966 Climatological Data (ESSA). Hours of dew were recorded on a Taylor dew meter (26) at Manhattan, Kansas and Langdon, North Dakota in 1966. All 1967-68 weather data were recorded from instruments located on the experiment stations. Hours of dew were recorded at 12 locations in 1967 and 16 locations in 1968.

Methods of Transforming Variables

Analyses of the relationships between uredial numbers and environmental factors were made using simple and multiple regression techniques. Uredial numbers were used as the dependent variable with temperature, moisture, and inoculum used as independent variables. An incubation period of 8–14 days was used in data analysis (4). Therefore, regression programs were structured around temperature, moisture and inoculum (independent variables) recorded 8–14 days before each uredial count (dependent variable).

Van der Plank (28) showed that an epidemic can be followed by a logit curve. According to Van der Plank, the logit, ($\log_e \frac{x}{1-x}$), should be used to analyze epidemics caused by pathogens which multiply exponentially such as the rust fungi. Therefore, the logit transformation of uredia and urediospore numbers was used in all regression analysis. Since a maximum value must be assumed to use the logit transformation in any prediction equation, the values 10^6 and 10^7 were selected for weekly spore numbers (WSN) and cumulative spore numbers (CSN), respectively. Because the maximum values selected will not be exceeded in any year, several years' data can be used in the same analysis.

Regression analysis, with uredial numbers (dependent variable) transformed as the logit, was applied to the data using various combinations of the following as independent variables: (1) the logit of the cumulative spore numbers (CSN) 8 days prior to the dependent variable, (2) the logit of the weekly spore numbers (WSN) 8–14 days prior to the dependent variable, (3) the logit of the uredial numbers (UN) observed 8 days prior to the dependent variable, (4) average maximum temperature (MAX) recorded 8–14 days prior to the dependent variable, (5) average minimum temperature (MIN) recorded 8–14 days prior to the dependent variable, (6) average hours of free moisture per day (FM) occuring as dew or rain 8–14 days prior to the dependent variable, and (7) the number of days of measurable precipitation (PREC) recorded 8-14 days prior to the dependent variable.

The transformations were generated by subroutines within simple and multiple regression programs supplied by the Kansas State University Computing Center.

All tests of significance were calculated at the .05 level.

Analysis of Data

A multiple regression program, which also prints out simple correlation coefficients, was used to determine the amount of variation (r^2) in the dependent uredial numbers that was explained by maximum temperature, minimum temperature, and precipitation. In a second analysis of data from Manhattan, Kansas and Langdon, North Dakota, free moisture was expressed as 5 independent variables: (1) average hours of rain per week, (2) average hours of rain per day of occurrence, (3) average hours of dew per week, (4) average hours of dew per day of occurrence, and (5) average hours of free moisture per day.

An attempt was made to express weighted values of temperature and moisture as a degree of favorability for rust development at Manhattan and Langdon in 1966 (Table 1). The weighted values were based on the assumption that the relationship between temperature and disease development follows a normal curve.

Cohen and Yarwood (5) found that the temperature developmental curves of most fungi were asymmetric and skewed to the right with optimum fungal growth at 67 per cent of the temperature range. Schrodter (23) developed an equation to express this skewed curve

Table 1. Temperature and moisture data expressed as degrees of favorability for Leaf Rust development.

Temperature	Degree of Favorability [a]	Temperature (°F)	Hours of Free Moisture	Degree of Favorability [b]
0-32	1	111-115	0	1
33-35	2	106-110	1-3	2
36-40	3	101-105	4-5	3
41-45	4	96-100	6-24	4
46-50	5	91-95		
50-55	6	86-90		
56-50	7	81-85		
60-65	8	76-80		
66-70	9	71-75		

[a] Optimum value is 63 for 8-14 day period

[b] Optimum value is 28 for 8-14 day period

as a $\sin^2$ function of temperature. He simultaneously solved equations for the following properties of Cohen and Yarwood's empirical temperature curves:

1. The optimum temperature for fungal growth occurs at 67 per cent of the temperature range.

2. Fungal growth is 0 at maximum and minimum temperatures.

3. The inflection point of the increasing portion of the temperature curve occurs at 45 per cent of the temperature range.

The resulting equation for the effect of a specific hourly temperature on fungal growth was in the form $Y = \sin^2 (1.28x - 0.00746 x^2 + 0.001266x^3)$ and the temperature equivalent x is given by the equation $x = \frac{t - t_{min}}{t_{max} - t_{min}}$ where t is the observed temperature, t_{min} is the minimum temperature at which fungal growth begins, and t_{max} is the maximum temperature at which fungal growth occurs. R. W. Romig (19) found errors in the calculation of the constants used by Schrodter. He resolved the equations and obtained the following general equation $Y = \sin^2 (124.72x - 64.30x^2 + 119.58x^3)$.

This equation was used to calculate Y values from 1967 hourly temperatures at Manhattan and Stillwater. Hourly Y values were added to give daily Y-sum values which were summed for the 8–14 day period and used as an independent variable instead of average maximum and minimum temperatures.

Two moisture-temperature interactions were used as independent variables: (1) the sum of Y values of hours on which dew was recorded during the 8–14 day period and (2) the daily Y-sum values for days on which at least 4 consecutive hours of dew occurred.

Biologically, three conditions must be met before infection by P. recondita tritici can occur (4).

1. Presence of viable inoculum on susceptible host tissue.

2. Presence of temperatures favorable for urediospore germination and infection of host tissue.

3. Presence of free moisture for spore germination.

Therefore, inoculum was included as an independent variable in the analysis of 1967 data. Epidemic development on each variety was analyzed separately using an IBM 360 stepwise multiple regression program.

Statistical analysis of 1967 data was hindered by lack of degrees of freedom for individual locations. Therefore data from winter wheat locations where dew records were available were pooled according to variety (Bison or second variety) and analyzed. Then data from all 1967 winter wheat varieties were pooled and analyzed as one variety. The same procedure was followed for data from 1967 spring wheat and 1968 winter and spring wheats. Finally, data from 1967 and 1968 were pooled and analyzed by variety.

Beta values obtained in the analysis of pooled data were used to predict leaf rust severity on nurseries not included in the regression analysis.

EXPERIMENTAL RESULTS

Data presented in Table 2 are representative of the analyses of all 1966 weather variables. Maximum or minimum temperature explained the most variation in uredial numbers but a Fishers Z test (8) showed no significant difference between coefficients of determination (r^2). Addition of a second independent weather variable in a multiple regression model was significant in reducing the amount of unexplained variation at two locations (Table 2).

Partitioning free moisture as 5 independent variables did not significantly increase r^2 values over those obtained in a simple linear regression model. The method used to determine the degree of favorability of weather data for rust development did not account for more variation than was previously explained by minimum temperature.

Disease development was negatively correlated with maximum and minimum temperatures at all 1966 fall locations. Minimum temperature explained a significant amount of the variation in uredial numbers at 15 of 16 locations. However, additional variables needed to be included in the regression model since 60 to 90 per cent of the variation in uredial numbers was unexplained by regression analysis of 1966 weather data.

Minimum temperature was significantly correlated with leaf rust development at all 1967 winter wheat locations and at 3 of 4 spring wheat locations. Hours of dew were significant at 3 winter wheat and 2 spring wheat locations.

Analysis of 1967 data showed that minimum temperature was effective in reducing variation in uredial numbers in both 1966 and 1967. However, 50 to 90 per cent of the variation in a simple regression model remained unexplained when average weekly weather variables were used. Because average weather variables mask the wide ranges and amplitudes observed in weather patterns, they have limited use in a simple regression model.

Table 2. Coefficient of determination (r^2) values for regression analysis of 1966 weather data.

Simple Regression (r^2)

Location	Variety	Max Temp	Min Temp	Precipitation
Denton, Texas	Triumph	.695*	.539*	.419
Cherokee, Okla.	Triumph	.676*	.689*	.130
Manhattan, Kans.	Triumph	.479*	.588*	.259
Langdon, N.D.	Ceres	.529*	.768*	.042

Multiple Regression (R^2)

Location	Max Min Temp	Max Temp Prec	Min Temp Prec	Max Min Prec	% Leaf Rust Severity
Denton, Texas	.703	.823	.902*a	.908*a	3
Cherokee, Okla.	.773	.739	.709	.774	5
Manhattan, Kans.	.710*	.502	.598	.725	30
Langdon, N.D.	.774	.875*a	.822	.875	50

* Indicates significance at .05 level.

a Indicates significant increase in amount of variation explained by addition of variable in a multiple regression model.

An inoculum variable was entered into the stepwise multiple regression equation first at most locations. A weather variable entered the stepwise equation next and significantly reduced the unexplained variation at 50 per cent of the locations (Table 3). Inoculum coefficients of determination (r^2) were not significantly greater than those for minimum temperature at most locations (Table 4). Also coefficients of determination for UN, WSN, and CSN were not significantly different indicating that any of the inoculum variables could be substituted in the regression equation (Table 4). A larger number of observations may have shown that significant differences exist between the inoculum variables and between inoculum and minimum temperature.

Substitution of Y-sum values for average maximum and minimum temperatures and creation of moisture-temperature interactions did not significantly increase the amount of variation explained (R^2) at either Manhattan or Stillwater (Table 5).

Whether a $\sin^2$ transformation of hourly temperatures will be of value in a prediction equation cannot be ascertained from the analysis of two locations using 1967 data.

Analysis of 1967, 1968, and 1967-68 pooled data indicate that a difference does exist in the amount of variation (R^2) explained by the different inoculum variables (Table 6). The R^2 for UN was always higher than the R^2 for either WSN or CSN in the winter wheat region. R^2 values for WSN and CSN were higher than the R^2 for UN in the spring wheat region in 1968 and 1967-68 but not in 1967 (Table 6).

Minimum temperature was always equal to or better than maximum

Table 3. Coefficients of determination (R^2) obtained in analysis of 1967 data and the order the variables entered the stepwise multiple regression program.

Location	Variety	R^2 value and order						
Manhattan, Kans.	Bison	CSN	FM	PREC	WSN	UN	MAX	MIN
		.769	.835	.850	.882	.893	.893	.895
Goodwell, Okla.	Bison	UN	PREC*	MIN	MAX	WSN	PREC	CSN
		.814	.906	.922	.933	.935	.935	.937
Stillwater, Okla.	Bison	WSN	MAX*	FM	PREC	CSN	MIN	UN
		.872	.912	.922	.949	.955	.956	.956
Denton, Texas	Bison	UN	MIN	PREC	CSN	FM	WSN	MAX
		.745	.819	.897	.912	.931	.939	.941
Colby, Kans.	Bison	CSN	MAX	WSN	UN	PREC	MIN	FM
		.702	.821	.880	.891	.901	.933	.937
Eureka, S. Dak.	Baart	UN	PREC	MIN	CSN	MAX	FM	WSN
		.867	.956	.958	.960	.964	.966	.966
Langdon, N. Dak.	Baart	CSN	PREC*	WSN	UN	MIN	MAX	FM
		.863	.935	.962	.972	.972	.972	.972
Beresford, S. Dak.	Selkirk	PREC	UN	WSN	FM	CSN	MAX	MIN
		.766	.874	.937	.955	.994	.994	.994

* Addition of the independent variable significantly reduces the unexplained variation.

Table 4. Coefficients of determination (r^2) for analysis of 1967 weather and inoculum data.

		Inoculum			Temperature		Moisture		N
Location	Variety	UN	WSN	CSN	MAX	MIN	FM	PREC	
Manhattan, Kans.	Bison	.758	.691	.769	.067	.500	.005	.006	18
Goodwell, Okla.	Bison	.813	.759	.780	.476	.602	.401	.486	12
Stillwater, Okla.	Bison	.731	.872	.840[a]	.104	.376	.010	.001	17
Denton, Texas	Bison	.745	.666	.698	.073	.624	.733	.160	11
Colby, Kans.	Bison	.594	.544	.702	.202	.504	.098	.050	11
Eureka, S. Dak.	Baart	.867	.465	.408	.415	.298	.678	.750	12
Langdon, N. Dak.	Baart	.667	.663	.863	.625	.501	.028	.085	11

a r^2 for CSN at Stillwater, Okla. was significantly greater than r^2 for minimum temperature.

Table 5. Comparison of Multiple Regression Coefficients using $\sin^2$ transformation of hourly temperatures vs. average maximum and minimum temperatures at Manhattan and Stillwater.

Location	Variety	Independent Variables	R^2 value	N
Manhattan, Kans.	Bison	UN - Y sum - FM	.864	18
		UN - Y sum - Y sum hour - FM	.874	18
		UN - Y sum - Y sum day - FM	.868	18
Stillwater, Okla.	Bison	UN - Y sum - FM	.870	17
		UN - Y sum - Y sum hour - FM	.885	17
		UN - Y sum - Y sum day - FM	.872	17
Pooled data	Bison	UN - Y sum - FM	.819	35
Pooled data	Bison	UN - Min - FM	.824	35
Pooled data	Bison	UN - Max - FM	.781	35

Table 6. Coefficients of determination (R^2) obtained from pooled data using various combinations of independent variables.

Year	Variety	Independent variables in equation	R^2	N
Winter wheat				
1967	Bison	UN, MIN, PREC	.802	165
	Bison	WSN, MIN, PREC	.669	165
	Bison	CSN, MIN, PREC	.685	165
1968	Bison	UN, MIN, PREC	.820	220
	Bison	WSN, MIN, PREC	.714	220
	Bison	CSN, MIN, PREC	.719	220
1967-68	Bison	UN, MIN, PREC	.811	385
	Bison	WSN, MIN, PREC	.677	385
	Bison	CSN, MIN, PREC	.675	385
Spring Wheat				
1967	Baart	UN, MIN, PREC	.678	36
	Baart	WSN, MIN, PREC	.508	41
	Baart	CSN, MIN, PREC	.556	77
1968	Baart	UN, MIN, PREC	.599	36
	Baart	WSN, MIN, PREC	.811	41
	Baart	CSN, MIN, PREC	.795	77
1967-68	Baart	UN, MIN, PREC	.633	36
	Baart	WSN, MIN, PREC	.707	41
	Baart	CSN, MIN, PREC	.715	77

temperature in explaining variation. No difference could be detected between the R^2 of precipitation and hours of dew. Small differences in the R^2 values were noted between years and between varieties within years but no definite pattern could be detected.

Statistical tools to evaluate the difference between equations are not available. Therefore the beta coefficients (b) obtained in the regression equations for all combinations of inoculum, moisture, and temperature were used to predict leaf rust at several locations during 1968. Data used were not from the varieties involved in the formulation of the prediction equations. Beta coefficients used in the prediction equation $Y = b_1x_1 + b_2x_2 + b_3x_3$ are shown in Table 7.

Logits of observed and predicted uredial numbers are illustrated in Table 8. Variances ($\Sigma y - \hat{y}/n - 1$) between observed and predicted leaf rust severities were calculated and used to determine which prediction equation was most precise. Variances were always smaller using prediction equations formulated from pooled data of all 1967-68 varieties. Prediction equations using uredial numbers as the inoculum variable were more precise than either weekly spore numbers or cumulative spore numbers. WSN and CSN equations always under-predicted the leaf rust severities in both winter and spring wheat equations.

Precipitation used with UN and MIN over-predicted leaf rust severity on spring wheat varieties. Hours of free moisture were not available at locations used to test the spring wheat equations. Hours of free moisture used with UN and MIN would slightly under-predict while use of precipitation with UN and MIN would over-predict leaf rust severity on winter wheat

Table 7. Beta Coefficients (b) used in testing prediction equations obtained from analysis of 1967-68 pooled data.

	UN	WSN	CSN	MIN	FM	PREC
Winter wheats						
Equation 1	0.8345			-0.0020	0.0746	
Equation 2	.8528			.0055		0.3288
Equation 3		0.8057		- .0041	.1084	
Equation 4		.8189		.0071		.3134
Equation 5			0.8107	- .0003	.0763	
Equation 6			.8198	.0076		.2386
Spring wheats						
Equation 2	.8312			.0453		-.2076
Equation 4		.9067		- .0573		-.1591
Equation 6		.9621		- .0710		-.1719

Table 8. Cologarithum of logits of observed and predicted leaf rust severity on Bison during 1968 at Manhattan. Prediction equations formulated from 1967-68 pooled data of all winter wheat varieties.

Date	Observed Severity	Predicted Severities using					
		UN MIN FM	UN MIN PREC	WSN MIN FM	WSN MIN PREC	CSN MIN FM	CSN MIN PREC
29 April	-6.34	-9.91	-8.01	-5.57	-4.67	-5.24	-4.50
30	-5.19	-8.94	-8.03	-5.50	-4.85	-5.07	-4.50
1 May	-5.22	-9.01	-8.37	-6.00	-5.59	-5.14	-4.76
2	-4.93	-8.94	-8.71	-5.43	-5.45	-5.00	-4.94
3	-5.31	-8.93	-8.71	-5.43	-5.46	-5.00	-4.95
6	-5.17	-4.61	-4.98	-5.72	-6.43	-4.99	-5.46
8	-5.06	-3.68	-4.34	-5.47	-6.47	-4.94	-5.62
9	-5.09	-3.37	-4.09	-4.69	-5.76	-4.69	-5.43
10	-5.05	-3.94	-4.73	-4.26	-5.38	-4.61	-5.41
13	-4.55	-4.10	-4.93	-4.53	-5.41	-4.86	-5.51
14	-5.27	-3.91	-4.54	-4.19	-4.90	-4.63	-5.17
15	-4.53	-4.01	-4.17	-4.19	-4.41	-4.63	-4.79
16	-4.29	-4.14	-4.21	-4.39	-4.53	-4.69	-4.80
17	-3.15	-4.00	-4.48	-4.25	-4.19	-4.49	-4.42
20	-3.74	-3.43	-2.76	-3.68	-3.21	-4.09	-3.70
21	-3.64	-4.18	-3.37	-3.16	-2.45	-3.74	-3.19
23	-1.90	-3.30	-2.84	-2.39	-2.05	-3.10	-2.82
24	-2.73	-2.35	-2.20	-2.10	-2.06	-2.83	-2.80
27	-1.94	-3.07	-3.36	-2.35	-2.62	-2.97	-3.17

Table 8. (cont.)

Date	Observed Severity	Predicted Severities using					
		UN MIN FM	UN MIN PREC	WSN MIN FM	WSN MIN PREC	CSN MIN FM	CSN MIN PREC
28 May	-1.49	-2.90	-3.62	-2.29	-3.01	-2.82	-3.36
29	-2.01	-1.52	-1.82	-2.64	-2.97	-2.84	-3.09
31	-2.09	-2.14	-2.21	-2.88	-3.01	-2.70	-2.79
3 June	-1.73	-1.26	-0.85	-2.58	-2.37	-2.41	-2.21
4	-1.40	-0.82	-1.09	-2.12	-1.99	-2.18	-2.04
5	-1.78	-1.17	-1.22	-1.94	-2.23	-2.04	-2.22
6	-1.79	-1.17	-1.55	-1.86	-2.47	-2.01	-2.43
7	-1.16	-1.16	-0.80	-2.06	-1.92	-2.08	-1.93
10	-0.87	-1.02	-1.30	-0.98	-1.42	-1.52	-1.83
11	-0.80	-0.75	-1.01	-0.83	-1.25	-1.37	-1.66
12	0.22	-1.07	-1.32	-0.33	-0.72	-1.01	-1.28
13	0.06	-1.08	-1.32	-0.28	-0.65	-0.96	-1.21

varieties.

Use of beta coefficients for UN, MIN, and FM in a winter wheat prediction equation accurately predicted rust severities of 1 to 20 per cent on Bison and Ottawa (Table 9). Use of either FM or PREC would under-predict rust severities above 40 per cent.

Leaf rust severities of 1 to 30 per cent were slightly over-predicted on all spring wheat varieties and final severities were heavily over-predicted.

DISCUSSION

Environment is a complex term that includes many factors which must be above a minimum threshold for disease development to occur. To study the interrelationships of the independent variables (weather and inoculum) with disease development, the independent variables must be limiting or fluctuating between the minimum and optimum conditions necessary for disease development.

A change in one environmental factor may alter the effect of the other factors on disease development. An example of this is precipitation which washes inoculum from the air, reduces light intensity, lowers temperatures, and increases the probability of dew occurrence for several succeeding days. Since dew occurs more frequently than rain, hours of dew were a more accurate measure of the moisture available for leaf rust development as evidenced by the more precise prediction of leaf rust severities (Table 9). However, precipitation measurements could be substituted if dew records were not available. Precipitation measurements caused leaf rust severities to be over-predicted, because in the Great Plains rain

Table 9. Observed and predicted leaf rust severities on Bison and Ottawa in 1968. (Per cent)

Date	Bison			Ottawa		
	Observed Severity	Predicted Severity using UN MIN FM	Predicted Severity using UN MIN PREC	Observed Severity	Predicted Severity using UN MIN FM	Predicted Severity using UN MIN PREC
29 Apr	0.2	0.01	0.03	0.2	0.01	0.03
30	0.5	0.01	0.03	0.5	0.01	0.03
1 May	0.5	0.01	0.02	0.5	0.01	0.02
2	0.7	0.01	0.02	0.4	0.01	0.02
3	0.5	0.01	0.02	0.4	0.01	0.02
6	0.5	1.0	0.6	0.3	0.9	0.6
8	0.6	2.0	1.0	0.4	2.0	1.0
9	0.6	3.0	2.0	0.5	2.0	0.9
10	0.6	2.0	0.8	0.4	2.0	0.7
13	1.0	2.0	0.7	0.3	0.8	0.4
14	0.5	2.0	1.0	0.5	1.0	0.7
15	1.0	2.0	2.0	0.8	1.0	1.0
16	1.0	2.0	1.0	2.0	1.0	1.0
17	4.0	2.0	2.0	4.0	1.0	1.0
20	2.0	3.0	6.0	1.0	1.0	2.0
21	3.0	1.0	3.0	2.0	1.0	3.0
23	13.0	4.0	5.0	5.0	4.0	9.0
24	6.0	9.0	10.0	7.0	9.0	10.0
27	12.0	4.0	3.0	14.0	3.0	2.0
28	18.0	5.0	3.0	15.0	4.0	2.0

Table 9. (cont.)

Date	Bison			Ottawa		
	Observed Severity	Predicted Severity using UN MIN FM	Predicted Severity using UN MIN PREC	Observed Severity	Predicted Severity using UN MIN FM	Predicted Severity using UN MIN PREC
29 May	12.0	18.0	14.0	15.0	6.0	4.0
31	11.0	10.0	10.0	15.0	12.0	11.0
3 June	15.0	22.0	30.0	18.0	24.0	33.0
4	20.0	31.0	38.0	20.0	27.0	34.0
5	14.0	24.0	23.0	21.0	28.0	27.0
6	14.0	24.0	17.0	15.0	28.0	21.0
7	24.0	24.0	30.0	29.0	27.0	34.0
10	30.0	26.0	21.0	37.0	30.0	24.0
11	31.0	32.0	27.0	39.0	32.0	27.0
12	56.0	25.0	21.0	56.0	33.0	28.0
13	52.0	25.0	21.0	58.0	27.0	22.0
Variance		0.76	1.09		0.43	0.63

usually falls on consecutive days and then skips several days or weeks (9).

Since dew usually occurs when daily temperatures are at or near the minimum, minimum temperature is a more accurate measure of the temperature affecting disease development than maximum temperature. In the early part of the growing season, which is the most important for control of leaf rust, the minimum temperature is below or fluctuates across the temperature threshold for leaf rust development, while maximum temperature is at or near the developmental optimum and therefore does not limit disease development.

Disease development has been followed by use of spore numbers (18) but even though R^2 values for WSN and CSN were slightly higher than R^2 values for UN in the spring wheat region, WSN and CSN prediction equations always substantially under-predicted leaf rust severities. The same trend occurred in the winter wheat region especially with CSN as the inoculum variable. This is not to say that only UN can be used in a prediction equation, but only that the logit transformation of spore numbers cannot be used. The terminal values, 10^6 and 10^7, used in the analysis of spore data mask the smaller increases in spore numbers. When 10^7 is used spore numbers are analyzed as multiples of 100. If 10^6 is used, spore numbers are analyzed as multiples of 10. Use of logit transformations of spore data should therefore be restricted to epidemics where the final spore numbers are known. Terminal values for spore numbers cannot be determined before the epidemic has run its course because environmental factors affect the number of spores produced and deposited at a location. In contrast, the logit can be used for UN since the upper limit of infection is defined as 100 per cent.

Regression analyses of spore numbers with time in days indicate that no significant difference exists between r^2 values obtained using the logit and the $\log_{10}$ transformations (3). A maximum value for spore numbers is not needed with a $\log_{10}$ transformation since there is no upper limit to the population. Therefore, it is suggested that a $\log_{10}$ transformation of spore data be used in future analyses to develop an equation which will accurately predict leaf rust severities.

Prediction equations based on data from geographical areas having similar temperature, moisture and crop maturity patterns should be more effective in a fungicide control program than predictions based on data from the entire winter or spring wheat region.

Subsequent studies to refine leaf rust prediction equations should consider using an incubation period of 10 to 16 or even 14 to 21 days since the critical period for rust control occurs early in the growing season when minimum temperature deviates farthest from the optimum. As minimum temperature deviates from the optimum the incubation period is lengthened. The ability to use 5 or 30 day weather forecasts to predict disease development would greatly enhance the value of any prediction used as the basis for a fungicide control program.

In conclusion, the only true test of a prediction equation is how accurately it will forecast leaf rust development. Prediction equations developed from these studies of environmental factors will accurately predict leaf rust severities below 30 per cent. Equations generated from 1967 or 1968 data would not accurately predict leaf rust severity in either year. However, when data from all varieties in 1967, a year of light leaf rust, and 1968, a year of heavy leaf rust, were pooled, the resulting equation would accurately predict leaf rust severity. This is apparently due to the inclusion of data from a year in which the weather and inoculum variables were marginal for leaf rust development with one in which the environmental conditions were optimal at many locations. The environmental conditions of the locations being predicted were within the extremes of these two years.

Prediction equations have been defined in precise terms, but their actual application must be modified in some situations. For instance a severe freeze, which kills the infected host tissue and reduces the inoculum load, will negate the effect of the inoculum as a variable. A change in the resistance of varieties or in pathogenicity of the parasite population will affect any disease forecast. With increased experience in disease forecasting, it should be possible to overcome these obstacles to accurate forecasts.

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A METHOD OF PREDICTING EPIDEMIC DEVELOPMENT OF *Puccinia recondita* f. sp. *tritici*

by

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A stepwise multiple regression computer program was used to formulate equations to predict the rate of epidemic development of Puccinia recondita f. sp. tritici. Equations were generated for winter and spring wheat areas by analysis of inoculum and weather data from 24 winter wheat and 16 spring wheat locations. Both equations were in the form $Y = b_1X_1 + b_2X_2 + b_3X_3$ where X_1, X_2, and X_3 were a measure of inoculum (uredial numbers, weekly and cumulative urediospore numbers), temperature (average maximum and minimum temperature), and moisture (hours of dew and days of precipitation), respectively. Data for these independent variables were recorded 8–14 days prior to the measurement of the dependent variable (uredial numbers). Uredial and urediospore numbers were transformed as logits, $\log_e \frac{X}{1-X}$ where X = numbers of uredia or urediospores/cm^2 and 1 = 100 per cent for uredial numbers, 10^6 for weekly spore numbers, and 10^7 for cumulative spore numbers.

Analysis of data from individual locations was of little value in determining the independent variables to be used in the prediction equations. However, when data from all winter wheat locations were pooled, coefficients of determination (R^2) indicated that uredial numbers, minimum temperature, and either hours of dew or days of precipitation explained over 70 per cent of the variation in epidemic development. R^2 values indicated that in the spring wheat area weekly or cumulative spore numbers could be substituted for uredial numbers in the prediction equation.

Beta coefficients (b) obtained in the analysis of 1967–68 pooled data were used to predict leaf rust development at several 1968 locations. Data from these locations were not used to generate the prediction equations. Leaf rust development between 1 and 30 per cent severity could be predicted within ± 5 per cent using beta coefficients of uredial numbers, minimum temperature, and hours of dew. Predictions made at severities greater than 30 per cent were 15-20 per cent low.

Logit transformations of spore numbers significantly under predicted leaf rust development at all locations.