Predicting Stripe Rust Severity on Winter Wheat Using an Improved Method for Analyzing Meteorological and Rust Data

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This research was supported in part by the Climate Dynamics Program, Division of Atmospheric Sciences, National Science Foundation Grants 82-11253 and 85-03115.

Acknowledgement is made to the National Center for Atmospheric Research, Boulder, CO, which is supported by the National Science Foundation, for supplying computer time and research space.

Accepted for publication 28 October 1987 (submitted for electronic processing).

ABSTRACT

Coakley, S. M., Line, R. F., and McDaniel, L. R. 1988. Predicting stripe rust severity on winter wheat using an improved method for analyzing meteorological and rust data. Phytopathology 78:543-550.

An improved method was used to determine more precisely than previous methods the relationship of meteorological factors and stripe rust (caused by *Puccinia striiformis*) on winter wheat cultivars Gaines, Nugaines, and Omar at Pullman, WA. A computer program WINDOW was written and used to analyze meteorological data for 1967–1984 in segments of 21–65 days beginning on 29 July of each year and ending on 24 July of the following year. Meteorological factors were used as the independent x-variables in multiple regression with disease index (DI) used as the dependent y-variable. For each cultivar, four statistical models (two two-variable and two three-variable) provided more accurate predictions than either the local or regional models previously used in the Pacific Northwest. The three-variable models had adjusted $R^2 = 0.73–0.88$, and were 89–100% accurate for predicting rust severity. Contingency quadrants were used to evaluate accuracy of predicted $\widehat{DI}$ versus actual DI. Winter temperature and spring precipitation factors were included in the proposed three-variable models and were positively correlated with DI. Two models for each cultivar were "predictive" in that they could have been used early enough in the season to allow application of fungicides if severe disease had been predicted. The number of days with maximum temperature greater than 25 C was important in each full-season model. For Gaines and Nugaines (cultivars with high-temperature, adult-plant resistance), high temperatures were necessary for their resistance. The frequency of this factor from 21 April to 26 June was highly correlated ($r = -0.88$ and -0.90) with DI. However, for Omar, a cultivar without resistance, that factor was not important until June. Model validation included making DI predictions for 1985 and 1986, years not used in model development. The models should be used with caution whenever input data exceeds the range of the modeled data.

Additional keywords: empirical models, linear regression, quantitative epidemiology

A method for quantifying the relationship between climatic factors and stripe rust of wheat (*Triticum aestivum* L. em Thell), caused by *Puccinia striiformis* West., resulted in the development of statistical models to predict stripe rust severity on winter wheat in the Pacific Northwest (3,4,7). Those models were used in combination with other information on disease occurrence to predict rust severity early in the growing season so that fungicides could be applied in a timely way if necessary (6,12). However, the methods were not applicable to analyzing how climatic factors affect Septoria tritici blotch on wheat, caused by *Mycosphaerella graminicola* Fuckel (Schroeter). Therefore, a general method of analyzing relationships between disease severity and meteorological conditions was sought that could be applied to many different diseases on a wide variety of hosts. The method required that analysis of meteorological data could begin and end on any selected date; that all types of meteorological parameters could be examined; and that nonmeteorological variables could be included in model development. Ideally, the methodology would allow the development of statistical models that could be used to predict disease in time to decide on the use of control measures.

With these goals in mind, a statistical model was developed to predict Septoria tritici blotch in Indiana on day of year (DY) 170 (17 June, 26 days after the average heading date of 22 May). The two meteorological variables in the model were total consecutive days without precipitation between 26 March and 4 May and total consecutive days when the minimum temperature was equal to or less than 7 C between 4 April and 3 May. These variables explained 86% of the variation in disease severity among years. This model predicted disease severity approximately 18 days before heading, which allowed time for application of a fungicide when severe Septoria tritici blotch was predicted (9).

Because the method used to develop the Septoria tritici blotch model was intended to be useful in analyzing other disease data, it was then tested on stripe rust data. This paper describes the use of an improved method to analyze for interactions between meteorological factors and stripe rust severity and to develop statistical models to quantify the relationship between climate and disease. The statistical models developed were evaluated and compared with the previously published models (3,5–7) used to predict stripe rust in the Pacific Northwest.

MATERIALS AND METHODS

Disease data base. Stripe rust severity (percentage of the total leaf and glume surface covered by rust) was recorded for several hundred cultivars and breeding lines of wheat planted in single rows 1.5–3.0 m long at multiple sites in the Pacific Northwest. Each row had more than 100 plants and some sites had multiple rows of a single cultivar. An average value for disease severity along with infection type was recorded for each row at various stages of plant growth. Three winter wheat cultivars were selected from the data base for Pullman, WA: the susceptible cultivar Omar, and the high-temperature, adult-plant resistant cultivars Gaines and Nugaines. Data recorded at growth stages 7 (milk) or 8 (dough) (22) were selected, and disease severity was converted to a 0–9 disease index (DI) (footnote a, Table 1). Disease data were available for 1968 to 1986 for one to four geographically distinct areas around Pullman, and the DI used (Table 1) was an average of available data for each year.

Meteorological data base. Daily maximum and minimum temperature and precipitation data for July 1967 through July 1986 were obtained from the National Climatic Data Center, Asheville, NC; the Pullman meteorological station is located at lat. 117° 12′ W, long. 46° 46′ N at an elevation of 775 m. Negative degree days (NDD) and positive degree days (PDD) were calculated from the daily average Celsius temperature using a base of 7 C (7).

The following meteorological variables were considered: NDD, PDD, mean maximum temperature (MMAX)(C), mean minimum temperature (MMIN), mean average temperature (MAVE), total precipitation (TPREC) (mm), precipitation frequency (PFREQ), total consecutive days that the minimum temperature was less than 7 C (DL7C), total days that the average temperature was less than 0 C (DL0C), total days that the maximum temperature was greater than 25 C (DG25C), total consecutive days with precipitation (CDWP), and total consecutive days without precipitation (CDWOP).

Consecutive days were counted as described by Shaner and Finney (17); only sequences of two or more days that meet a specified criterion (e.g., CDWP) were counted and summed for a window subset. For example, if there were 5-, 4-, and 2-day periods with precipitation, these would be counted as 4, 3, and 1 CDWP and would be summed to give 8 CDWP.

Data analysis. The WINDOW program for the analysis of the Septoria data (9) was modified to improve its efficiency and flexibility in identifying the climatic variables that were most highly correlated with disease data (8). All calendar dates were converted to DY, in which 1 January = DY 1 and 31 December = DY 365 or 366 in leap years (16,20). For this analysis the starting date was 29 July (DY 210) of one year and the ending date was 24 July (DY 205) of the next year, which was before harvest of the plots in August. The plots were planted each year in the first two weeks of October.

Meteorological data were averaged or summed in variable-length time periods (windows) that were sequentially examined. Each set of windows consisted of nine subsets, the first being the full-length window and the other eight being progressively smaller subsets (Fig. 1). The nine subsets used initially were 65, 60, 55, 50, 45, 40, 35, 30, and 25 days in length (Fig. 1, window set P). To examine specific time periods in more detail, selected window subsets were set only one day shorter than the previous one, e.g., 65, 64, 63,...57 days in length.

TABLE 1. Disease indices for severity of stripe rust on three cultivars of winter wheat at Pullman, WA, from 1968 to 1986

	Disease Index at growth stage 8 (dough state)[a]		
Year	Nugaines	Gaines	Omar
1968	5.00E	6.50E	...
1969	2.00	2.00	3.50
1970	2.00	3.00	7.00
1971	5.00	5.75	8.25
1972	2.50E	4.00E	6.00E
1973	3.00	3.50	7.50
1974	1.00	3.00	5.00
1975	5.75	6.25	7.50
1976	7.00	6.50	7.00
1977	0.00	0.00	3.00
1978	3.50E	6.25E	7.50
1979	3.00	3.00	7.00
1980	4.00	5.50	8.50
1981	7.20	7.50E	9.00E
1982	3.25	2.00	3.50
1983	4.00	5.67	7.83
1984	6.00	6.38	8.38
1985	2.00	2.00	2.00
1986	2.50	2.50	2.50
Mean	3.78	4.52	6.65

[a] The 0–9 scale disease index (DI) is based on converting percent disease intensity to DI where 0 = 0% disease, 1 ≤ 1%, 2 = 1–5%, 3 = 6–20%, 4 = 21–40%, 5 = 41–60%, 6 = 61–80%, 7 = 81–95%, 8 = 96–99%, and 9 ≥ 99%. When disease data were available for growth stage 7 but not stage 8 (those indicated by "E"), the DI for stage 8 was extrapolated based on DI and infection type at stage 7 as described in Coakley et al (7).

Figure 1 gives an example of how the data were sequentially analyzed. The first nine subsets (window A) began on DY 5 and ended 65 days later on DY 69; data for each of the 12 selected climatic variables were assembled for each of the nine subsets of this window. The window was advanced 5 days, and data were assembled for the nine subsets in windows B, C, etc. To examine the data in more detail, windows were then advanced by only 1-day increments. The meteorological data were examined for a year in two segments; in segment I, the first window set began on DY 210 and the last began on DY 365. In segment II (part of which is shown in Fig. 1), the first set began on DY 5 and the last set began on DY 140 and ended on DY 204.

For each meteorological variable, the WINDOW program either calculates a mean (e.g., mean average temperature), counts (e.g., total days with maximum temperature greater than 25 C), or sums a cumulative total (e.g., negative degree days) for the subset.

WINDOW analyzed correlation to determine if any relationship existed between the meteorological factors and disease severity. Data were printed out for windows when the correlation coefficient for at least one variable was significant at $P \leq 0.05$. Windows with the highest correlation coefficients were further analyzed to identify the most precise time period for a variable that would give the highest correlation with disease severity. The window sets were advanced only one day at a time, and each window subset was only one day shorter than the previous subset (8).

Development and evaluation of models. Meteorological factors that were highly correlated with disease severity were selected for multiple regression analysis to determine the mathematical form of the relationship. The Statistical Analysis System (SAS) programs used for regression analysis were REG, RSQUARE, and STEPWISE (15). The independent variables were meteorological factors and the dependent variable was the DI for each year.

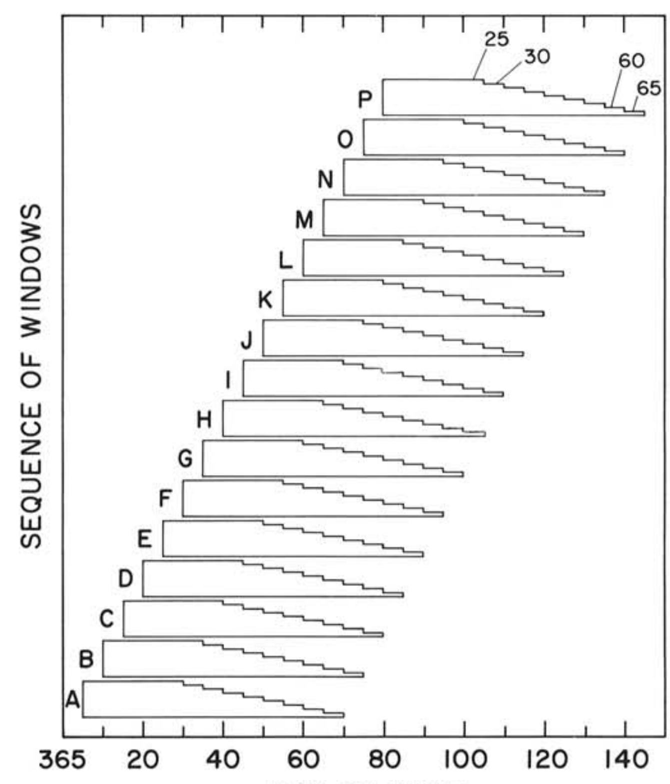

Fig. 1. Diagram of how meteorological data are considered by the WINDOW program. Each set of windows has nine subsets; window set A starts on day of year (DY) 05 and the subsets are 65, 60, 55, 50, 45, 40, 35, 30, and 25 days in length. After the meteorological data are assembled for window set A, the window is advanced 5 days to window set B, where all subsets begin on DY 10. This is repeated for window sets C–P; thus window P begins on DY 80 and ends on DY 144. From Coakley et al (8).

RSQUARE was used to evaluate all possible models up to a maximum of three independent variables. STEPWISE used four regression methods for generating models: forward, backward, stepwise, and maximum R^2 improvement. Two- and three-variable models from STEPWISE and RSQUARE were evaluated to determine whether they appropriately described the relationship between meteorological factors and DI. Each variable was examined as to type of factor. Models that had two overlapping or highly correlated variables were excluded from further evaluation.

The REG procedure of SAS was used to develop the selected models. The models were evaluated for minimization of standard errors of the predictions, stability of the regression coefficient signs, plotting of studentized residuals against predictions and time, variance inflation factors (VIFs) of the coefficients, and the accuracy of the predictions that were made for the years included in development of the model. The best models show stability of regression coefficient signs, random distribution of residuals, and VIFs less than 5. Adjusted R^2 was used to compare the models because it takes into account the number of variables included in the regression and allows comparison of models with different numbers of x-variables.

Model validation determined how the model functioned in its intended use and included analysis of model coefficients and predicted values (21), data splitting using Allen's predicted error sum of squares (PRESS) statistic (9,10,13,19), and collection of new data to check model predictions. Allen's PRESS statistic was calculated using the SAS procedure REG.

The accuracy of the predictions was determined using contingency quadrants (Fig. 2A). When the DI was greater than 5.5 ($\geqslant$ 60% severity), stripe rust was severe without chemical control and yield would be at least 20% lower than if chemical control were used (5). When the DI was 5.5 or less, disease was moderate or light and chemical control would be less beneficial. Figure 2A was used to evaluate how many times the predicted $\hat{DI}$ agreed with the actual DI; in quadrant I, both predicted and actual DI were 5.5 or less, whereas in quadrant IV, both predicted and actual DI were greater than 5.5. If all predictions fell into quadrants I and IV, all predictions of severe disease would be correct. In quadrant II, actual disease was greater than 5.5 but predicted $\hat{DI}$ was 5.5 or less (underprediction). In quadrant III, actual DI was 5.5 or below but the predicted $\hat{DI}$ was greater than 5.5 (overprediction). The percentage accuracy of a model was defined as the total number of years in quadrants I and IV divided by the total number of years for which predictions were made. The percent inaccuracy of the model could also be calculated from the contingency table, either as percent overprediction, underprediction, or total inaccuracy.

RESULTS

Model development. Disease indices for 1968 to 1984 on Nugaines and Gaines and for 1969 to 1984 on Omar wheat (Table 1) were correlated with numerous meteorological factors. The meteorological factors with the highest correlation coefficients (Table 2) were used to develop models to predict disease severity indices.

Regression analysis of the meteorological factors (Table 2) and the disease indices for each cultivar (Table 1) resulted in development of numerous two- and three-variable equations with adjusted R^2 greater than 0.75. Models N-I to N-IV, G-I to G-IV, and O-I to O-IV (Table 3) were selected for Nugaines, Gaines, and Omar, respectively, by the criteria described above. Models I and II for each cultivar and the Pullman NDDZ (PNDDZ) and Regional NDDZ, FDS (RNDDZ) models (footnote a, Table 3; 3,7), are "predictive" because they use factors that occur early enough (4 June or earlier) to decide whether to apply a fungicide when severe stripe rust is predicted ($\hat{DI} > 5.5$). Models III and IV for each cultivar included the meteorological factors with the highest correlation with DI, but they were not considered to be predictive because they could not be used to decide on control practices in a current season. The most important factor, total days with maximum temperature greater than 25 C, ended on DY 177 or 179, which would be too late in the season for application of fungicides.

Model evaluation. For models I to IV of each cultivar (Table 3),

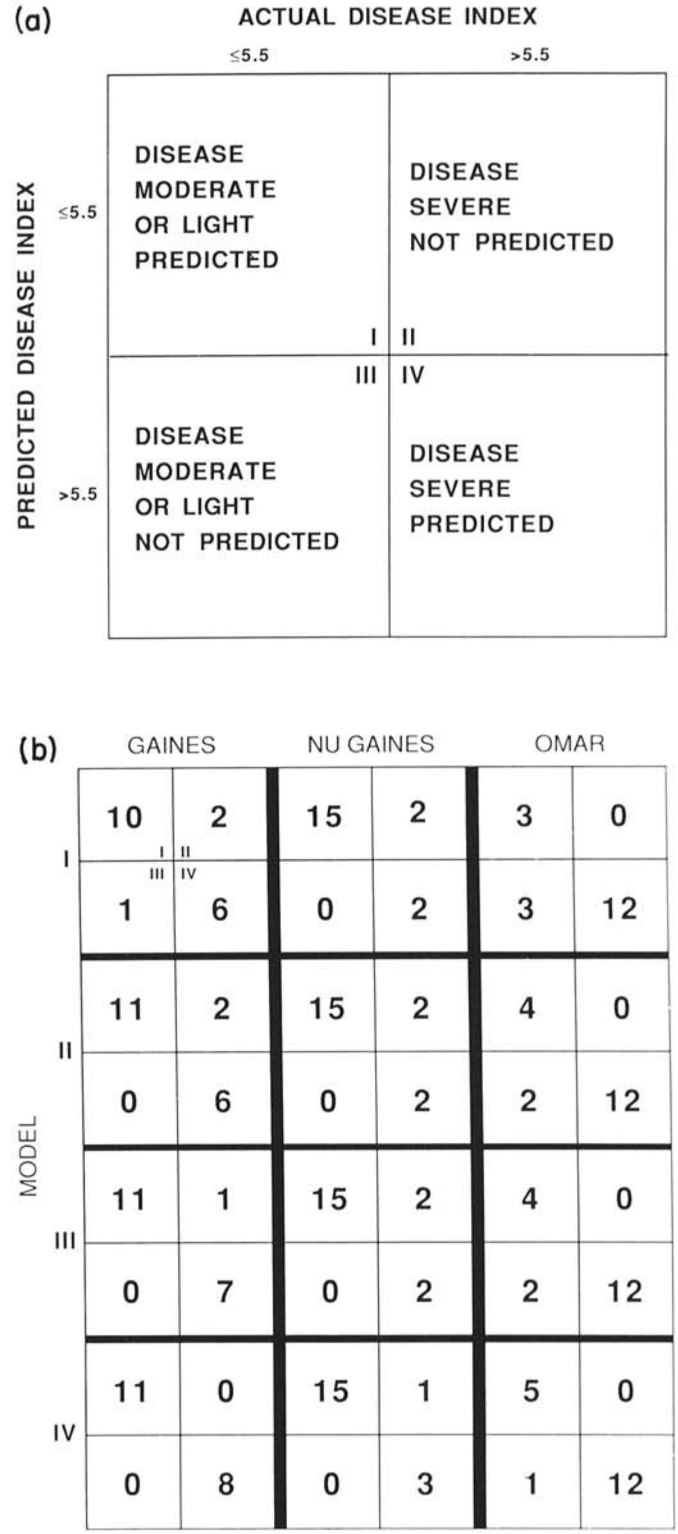

Fig. 2. A, Contingency quadrants used to determine the accuracy of disease predictions relative to actual disease index. In quadrants I and IV, actual disease and predicted disease are in agreement. In quadrant II, disease was severe but an underprediction of disease is made; in quadrant III, disease was moderate or light but an overprediction of disease is made. The accuracy of a model in making correct predictions of severe disease can be calculated as percentage accuracy = quadrant I + quadrant IV/n, where n = total number of predictions. **B,** Actual number of years that fall in each of four quadrants (I, II, III, IV) defined in 2A. Model equations for each cultivar are given in Table 3.

the residuals appeared as random-scatter data points. Had the points shown nonrandom distribution of residuals, they would have been used to diagnose the type of deficiencies in the model.

The VIFs were less than 2.70 for all model coefficients and were frequently close to 1. This indicated that the model coefficients were properly estimated and stable.

A comparison of the two- and three-variable models for the cultivars showed that the addition of the third variable improved the adjusted R^2 from 0 to 6% (Table 3). To evaluate whether this slight increase was important, predicted $\widehat{DI}$ was plotted against actual DI for all models for all cultivars (G-I, G-II, G-III, and G-IV and N-IV and O-IV are given in Fig. 3). The three-variable models (II and IV) for each cultivar were only slightly closer to the slope of 1 than their comparable two-variable models. However, with a two-variable model, there is one less variable to calculate.

The accuracy of each model's predictions was calculated for 1968–1986 for Gaines and Nugaines, and for 1969–1986 for Omar (Fig. 2B). Models III and IV for each cultivar, which were based on

TABLE 2. Meteorological factors most highly correlated with disease index for stripe rust on Nugaines, Gaines, and Omar wheat at Pullman, WA, when using the WINDOW program[a]

	Nugaines			Gaines			Omar		
Meteorological factor[b]	Beginning date (day of year)	Time (days)	Correlation coefficient	Beginning date (day of year)	Time (days)	Correlation coefficient	Beginning date (day of year)	Time (days)	Correlation coefficient
MMIN	276 (10 Oct)	37	0.69a						
	358 (24 Dec)	21	0.71a						
MMAX				004 (4 Jan)	21	0.71a			
PDD							314 (10 Nov)	23	−0.74a
DL0C	360 (26 Dec)	21	−0.74a	363 (29 Dec)	22	−0.81	356 (22 Dec)	49	−0.63b
				001 (1 Jan)	24	−0.74	363 (29 Dec)	24	−0.63b
DG25C	111 (21 Apr)	68	−0.90	113 (23 Apr)	66	−0.88	155 (4 June)	22	−0.86
TPREC	074 (15 Mar)	21	0.80	073 (14 Mar)	23	0.75	072 (13 Mar)	21	0.74a
PFREQ	073 (14 Mar)	43	0.73	069 (10 Mar)	49	0.67a	106 (16 Apr)	48	0.75
	076 (17 Mar)	39	0.72a	073 (14 Mar)	28	0.66a			
	076 (17 Mar)	25	0.69a	079 (20 Mar)	69	0.68a			
	095 (5 Apr)	59	0.74	080 (21 Mar)	38	0.64a			
				095 (5 Apr)	59	0.70a			
				138 (18 Mar)	41	0.76			
CDWP							106 (16 Apr)	49	0.79
							106 (16 Apr)	66	0.82
CDWOP	139 (19 May)	46	−0.78						

[a]The WINDOW subset is designated by the beginning date measured by the calendar day of the year and duration (time) measured by days; e.g., mean maximum temperature with a begining date of 004 and a time of 21 beginning on day 004 (4 Jan) and ending on day 24 (24 Jan). The correlation coefficients (r) are significant at $P \leqslant 0.001$. When an "a" follows the r, $P \leqslant 0.01$; a "b" indicates that $P \leqslant 0.05$.

[b]MMIN = Mean minimum temperature; MMAX = mean maximum temperature; PDD = positive degree days; DL0C = total days average temperature less than 0 C; DG25C = total days maximum temperature greater than 25 C; TPREC = total precipitation; PFREQ = precipitation frequency; CDWP = total consecutive days with precipitation; CDWOP = total consecutive days without precipitation.

TABLE 3. Models[a] for predicting disease index (DI) for severity of stripe rust on Nugaines, Gaines, and Omar winter wheat at Pullman, WA, with the regression coefficients (β), meteorological variables (x), adjusted-R^2 (adj-R^2), and Allen's predicted error sum of squares (PRESS) statistic and percentage (%) accuracy[b]

	Statistic		
Model $\widehat{DI} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3$	Adj-R^2	PRESS	Accuracy (%)
Nugaines model			
PNDDZ = 3.917 − 1.339 NDDZ 335	0.52		79
RNDDZ = 1.997 − 1.150 NDDZ 335 + 0.016 FDS	0.41		82
N-I = 2.932 + 0.220 MMIN 358 + 0.678 TPREC 074	0.76	22.9	89
N-II = 1.660 + 0.429 MMIN 276 + 0.153 MMIN 358 + 0.648 TPREC 074	0.76	26.3	89
N-III = 7.548 + 0.148 MMIN 358 − 0.277 DG25C 111	0.85	12.6	89
N-IV = 5.741 + 0.140 MMIN 358 + 0.301 TPREC 074 − 0.206 DG25C 111	0.88	11.7	95
Gaines model			
PNDDZ = 4.500 − 1.547 NDDZ 335	0.74		79
RNDDZ = 1.575 − 1.417 NDDZ 335 + 0.025 FDS	0.60		76
G-I = −2.187 + 0.454 MMAX 004 + 0.271 PFREQ 095	0.75	23.4	84
G-II = −1.344 + 0.406 MMAX 004 + 0.315 TPREC 073 + 0.182 PFREQ 095	0.76	24.2	89
G-III = 6.752 + 0.322 MMAX 004 − 0.276 DG25C 113	0.88	10.9	95
G-IV = 5.940 + 0.309 MMAX 004 + 0.039 PFREQ 080 − 0.256 DG25C 113	0.88	11.2	100
Omar model			
PNDDZ = 5.909 − 1.832 NDDZ 335	0.60		67
RNDDZ = 2.340 − 1.897 NDDZ 335 + 0.038 FDS	0.71		81
O-I = 10.402 − 0.414 PDD 314 − 0.101 DL0C 356	0.71	27.5	83
O-II = 6.539 − 0.289 PDD 314 − 0.087 DL0C 356 + 0.187 PFREQ 106	0.73	27.9	89
O-III = 8.770 − 0.256 PDD 314 − 0.253 DG25C 155	0.81	23.9	89
O-IV = 10.132 − 0.256 PDD 314 − 0.061 DL0C 356 − 0.199 DG25C 155	0.87	17.3	94

[a]PNDDZ = Pullman NDDZ model (3); RNDDZ = Regional NDDZ, FDS model (7); Models I-IV were developed for each cultivar using the methods described in this paper. NDDZ = standardized NDD accumulated from 1 December to 31 January (3); FDS = first day of spring (previously called JDS) for each location and is defined by the accumulation of ≥40 positive degree days over the next 14 days. For Pullman, FDS = 111 (7). MMIN = mean minimum temperature; MMAX = mean maximum temperature; TPREC = total precipitation; PFREQ = precipitation frequency; DG25C = total days maximum temperature greater than 25 C; DL0C = total days average temperature less than 0 C; PDD = positive degree days.

[b]Based on Figure 2, percentage accuracy = quadrant I + quadrant IV/n, where n = total number of years predictions were made for 1968 to 1986 (1969 to 1986 for Omar) with each model.

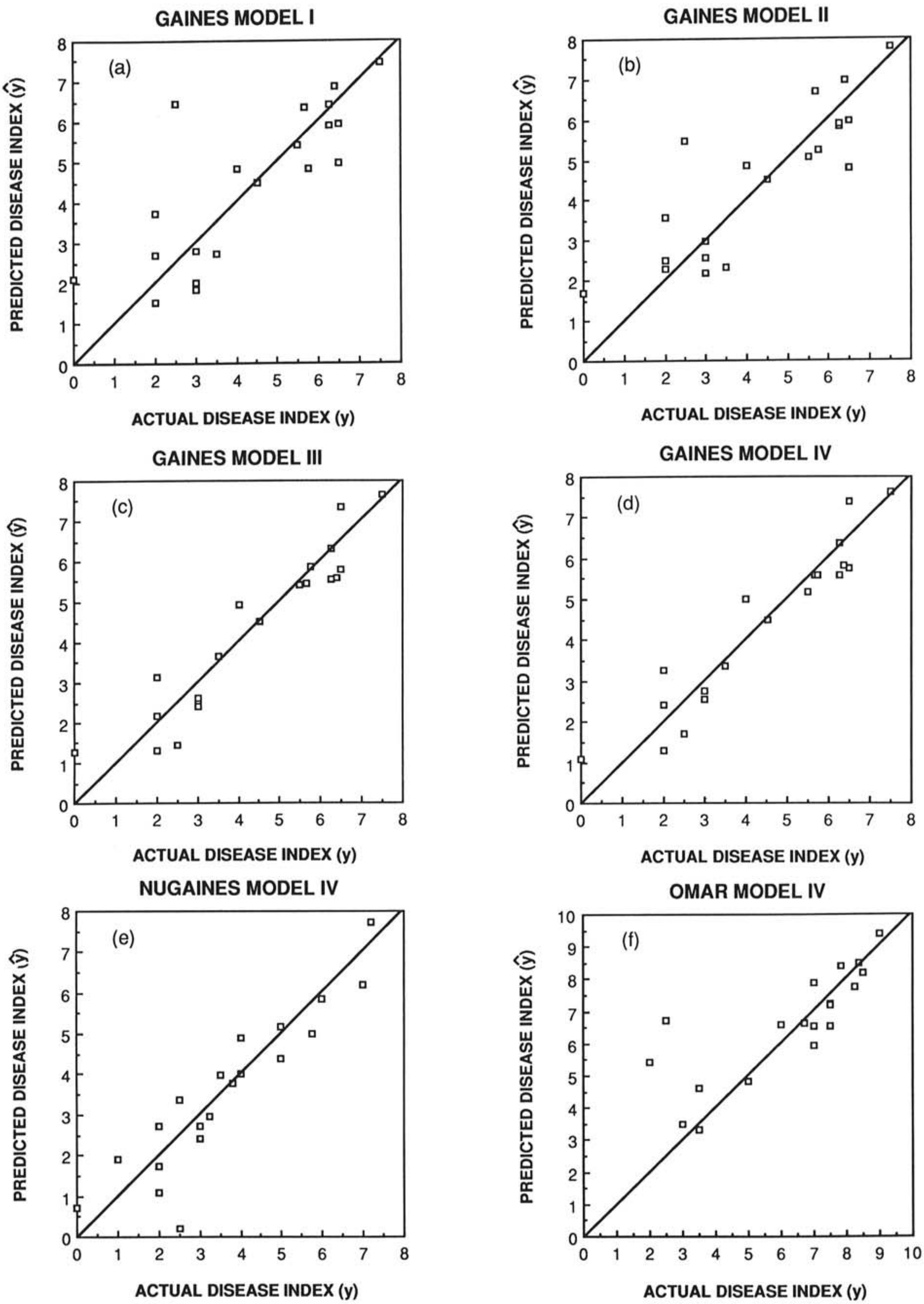

Fig. 3. Relationship between actual disease index (DI) and predicted $\hat{DI}$ on winter wheat for 1968–1986 at Pullman, WA. Predictions in (a) to (d) are for Gaines models G-I to G-IV; (e) is for Nugaines N-IV; and (f) is for Omar O-IV described in Table 3. The slope of the line = 1 and would occur if DI = $\hat{DI}$ in all cases.

the meteorological factors for the full season, improved the accuracy of the predictions the most for Gaines and the least for Nugaines (Table 3) when compared with models I and II for each cultivar. A comparison of actual DI versus predicted D$\hat{I}$ for all models showed that predictions were consistently closer to actual DI for models III and IV than for the other models (for Gaines, see Fig. 3A–D).

Model validation. Models N-III and N-IV and G-III and G-IV had PRESS statistics that were about one-half the size of those for models N-I, N-II, G-I, and G-II (Table 3).

The models also were validated by making predictions for 1985 and 1986 (years that were not included in model development and years when severity of stripe rust was unusually low) and comparing predicted D$\hat{I}$ with observed DI (Table 4). Using the criterion of model accuracy, all models for all cultivars (except O-III) correctly predicted D$\hat{I}$ in 1985. For 1986, models G-III and G-IV and all Nugaines models correctly predicted D$\hat{I}$, whereas the Omar models consistently overpredicted D$\hat{I}$ (Table 4). Accurate predictions can be expected only for the range of meteorological factors included in model development (Table 5). When the models are applied to new meteorological data, their values should be compared with the model's existing range. For Omar in 1985, the DLOC starting on DY 356 was 48 days, whereas the range in O-I, O-II, and O-IV was 11–43 days (Table 5). In this case, the predicted D$\hat{I}$s for these models were closer to actual DI than was the overprediction made by O-III which did not include a winter temperature factor. In 1986, the DG25C factors in the Gaines and Nugaines models II and IV were 24 and 25 days, respectively. Model development included only a range of 2–19 days (Table 5) for this factor. The effect in this case was to reduce predicted D$\hat{I}$ below that which occurred. For Nugaines, N-III predicted a D$\hat{I}$ = −0.3 which is outside the possible disease range. However, the predictions for N-III and N-IV and G-III and G-IV were accurate in that actual DI was very low and did not require any control measures.

Comparison of newly developed models with Pullman and regional NDDZ models. Predictions from the models for each cultivar were compared with the PNDDZ (3) and RNDDZ models (7). The PNDDZ models have been used since 1979 and the RNDDZ models (Table 3) have been used since 1981 to predict D$\hat{I}$ in the Pacific Northwest. Both the PNDDZ and RNDDZ models correctly predicted D$\hat{I}$ for all cultivars in 1985 and 1986, but the RNDDZ model overpredicted D$\hat{I}$ on Omar in 1986.

When the predictive models were compared on the basis of percentage accuracy, models I and II on all cultivars were 83–89% accurate. In contrast, the PNDDZ and RNDDZ models were only 67–81% accurate (Table 3). The values of adjusted R^2 were consistently greater for models I–IV of each cultivar than for models PNDDZ and RNDDZ (Table 3).

TABLE 4. Comparison of actual disease index (DI) and predicted D$\hat{I}$ for 1985 and 1986 using the Pullman NDDZ model (PNDDZ); Regional NDDZ, FDS model (RNDDZ); and models I, II, III, and IV (Table 3) for each cultivar

		Predicted D$\hat{I}$[a] using models:					
Year	Actual DI	PNDDZ	RNDDZ	I	II	III	IV
Nugaines							
1985	2.0	2.2	2.3	3.9	3.4	2.2	2.7
1986	2.5	3.5	3.5	2.7	2.7	−0.3	0.2
Gaines							
1985	2.0	2.5	2.5	1.5	2.3	2.2	2.4
1986	2.5	4.0	4.0	6.4*	5.5	1.5	1.7
Omar							
1985	2.0	3.5	4.0	4.9	4.9	6.6*	5.4
1986	2.5	5.4	6.0*	8.4*	8.7*	6.0*	6.7*

[a] Predicted D$\hat{I}$s followed by an asterisk are when the prediction was for severe disease, but the actual disease was light.

TABLE 5. Unit of measurement, mean value, standard deviation, and range of x for each meteorological factor of models I to IV (Table 3) for Nugaines, Gaines, and Omar winter wheat

Meteorological factor[a]	Unit of measurement	Mean value	Standard deviation	Range of x
Nugaines				
DG25C 111	days	9.94	4.9	2–19
MMIN 276	C	2.14	0.8	0.15–3.53
MMIN 358	C	−6.83	3.6	−15.29–2.00
TPREC 074	cm	3.47	1.6	0.66–7.03
Gaines				
DG25C 113	days	9.94	4.9	2–19
MMAX 004	C	1.59	2.4	−4.23–6.25
TPREC 073	C	3.79	1.6	0.69–7.03
PFREQ 080	days	16.41	4.8	6–25
PFREQ 095	days	22.12	3.9	16–31
Omar				
DG25C 155	days	6.06	4.7	0–15
PDD 314	PDD	2.29	2.6	0–9.2
DL0C 356	days	27.81	8.0	11–43
PFREQ 106	days	17.12	2.7	12–22

[a] MMIN = Mean minimum temperature; MMAX = mean maximum temperature; TPREC = total precipitation; PFREQ = precipitation frequency; DG25C = total days maximum temperature greater than 25 C; DL0C = total days average temperature less than 0 C; PDD = positive degree days.

DISCUSSION

The WINDOW program to identify the meteorological factors that affect disease development was successfully used to identify the meteorological factors that affect stripe rust severity. Meteorological factors that we identified were included in regression analysis, resulted in equations for cultivars Nugaines, Gaines, and Omar (models I–IV, Table 3), and were more accurate for predicting DI than PNDDZ and RNDDZ models (3,7) which we had previously used.

For each cultivar, model II is proposed as a more accurate model for the Pullman location and should replace the PNDDZ and RNDDZ models currently used; these new models predict D$\hat{I}$ early enough for chemical control. The method for analyzing meteorological data will be used to develop new regional models to replace the RNDDZ models now used in the Pacific Northwest.

The three-variable models (II and IV) for each cultivar had a higher percentage accuracy than their comparable two-variable models (I and III), except for model N-I and N-II which were both 89% accurate (Table 3).

The signs of all β-coefficients and the identity of the meteorological factors (Tables 2 and 3) agree well with what is known about the epidemiology of this disease. Fall temperature was recognized as being important for development of stripe rust the following year, and this knowledge was used along with monitoring data and the PNDDZ and RNDDZ models to predict rust. The effect of fall temperature was not quantifiable in the earlier analysis of meteorological data (4). By using the WINDOW program, mean minimum temperature for 3 October to 8 November was positively correlated with stripe rust development on Nugaines. We speculate that the higher temperatures in the days following planting of the crop in October resulted in earlier emergence and faster growth of seedlings, which provided more time and leaf area for infection and increase of stripe rust in the fall. These results were obtained at Pullman. It is highly probable that both temperature and precipitation may be important at locations in the Pacific Northwest where the crop is planted in late August and early September. Summer temperature in the Pacific Northwest does not limit survival of *Puccinia striiformis*. However, there are other regions of the world where summer maximum temperatures are extremely high and may be important in limiting disease oversummering. Whenever the range of input data exceeds that included in model development, the stripe rust models cannot be expected to make the correct predictions of DI, although the predictions made may be useful to some degree.

Low winter temperatures often limit stripe rust development by eliminating fall-infected foliage as well as healthy foliage and by delaying sporulation (1). Our models show the importance of winter temperatures to disease development in all cultivars. Models I, II, III, and IV for each cultivar are similar to the PNDDZ and RNDDZ models in that, except for O-III, all have a winter temperature factor. The winter factors were different for each cultivar but were for shorter time periods (21–49 days) than for the PNDDZ and RNDDZ models which used a NDDZ factor for the same 62-day period for each cultivar. The winter component of the models usually occurs in late December and January, which is usually the coldest period of the year. However, in the 1985 to 1986 growing season (identified as 1986 in Table 4), the coldest period of the year occurred in November and December. The result was that the predictions of $\hat{DI}$ for Omar were higher than actual DI because the model does not take into account when the coldest period occurs.

The DG25C was important in limiting disease in all cultivars. However, the length of time important for Omar began later in the season (4 June) and was shorter (22 days) than for Gaines and Nugaines. For Gaines and Nugaines, DG25C began on 23 April and 21 April and continued for 66 and 68 days, respectively. Both Gaines and Nugaines have adult-plant resistance that requires high temperatures to induce and maintain (14) and they start to show high-temperature resistance early in the spring. We postulate that from late April until early June, the effect of higher temperatures (as measured by DG25C) was primarily important in triggering the host resistance on Gaines and Nugaines. Omar is considered susceptible with little or no high-temperature resistance. However, Omar shows a very low level of resistance late in the season as indicated by infection type and rust development. This may be one reason for the importance of DG25C in June. Also, the number of days with temperatures greater than 25 C are more frequent in June. Shaner and Powelson (18) reported that constant or mean temperatures above 22 to 25 C inhibited the stripe rust fungus. We think that the higher temperatures from early to late June directly limited the fungus and thereby were unfavorable to infection.

The models that included DG25C have a much higher adjusted R^2 than those without this factor. However, the percentage accuracy of these models (III and IV) was only 0–6% greater than those for the predictive models I and II (Table 3). Model IV for each cultivar is proposed as being the best full-season model. If accurate long-term temperature forecasts for late April to late June were available, models III and IV also might be useful in making predictions of DI early enough to allow application of control when appropriate.

Attempts to include a precipitation factor in the PNDDZ and RNDDZ models were not successful; only precipitation frequency for the month of June was found to be significantly correlated ($r = 0.59$, $P = 0.05$). Using WINDOW, we found numerous spring precipitation factors highly correlated with DI (Table 2). Models I, II, and IV for Gaines and Nugaines and model II for Omar all included a precipitation factor. These results support the report that frequent precipitation in the spring was important to the development of stripe rust epidemics in the Pacific Northwest (11), but are in contrast to our earlier models which indicated that the effect of precipitation on DI could not be quantified except under drought conditions (5).

Our earlier results suggested that the degree of resistance of a cultivar affects the percentage response that can be explained by meteorological factors. In the present study, the application of WINDOW shows that 87–89% of the variation in DI on these three cultivars from year to year can be explained by three factors (Table 3). This is probably because the new analysis technique allows examination of variable-length segments of meteorological data. In the earlier work, the meteorological data were analyzed mainly in blocks of months, cumulative months, or seasons. Because there is no biological reason why either the pathogen or the host should respond on a calendar basis, it is not surprising that the cultivars appeared to have different degrees of response to climatic conditions. The cultivars responded to different kinds of factors but the total extent of response was approximately the same. Ideally, models should be keyed to phenological time scales, such as heading date, which was used for Septoria (9); however, such data were not available for this study.

The program WINDOW has been successfully applied to identifying meteorological factors important to the development of two foliar diseases of wheat. This suggests a wide variety of possibilities for its application. The technique should be applicable to identifying the meteorological factors that are important to development of other diseases on other hosts. Unfortunately, the results of our studies (Coakley and McDaniel, *unpublished*) suggest that the best predictive models are obtained with a minimum of 10 years of data, because this number gives a reasonable range of values for the meteorological factors to be used in model development.

The methods we described for analyzing meteorological data and quantifying the relationship between climatic factors and disease severity may have general application to studies of other organisms and their interaction with their environment. For example, WINDOW might be used to examine long-term climatic records and to help explain why a specific disease changes over time (2). Models developed could be used to evaluate other regions for the probability of disease under current or changing climatic conditions. WINDOW and associated methodology also can be used to quantify populations or productivity of other types of organisms in terms of climatic conditions. With minimal modification, this technique could be used to analyze the effect of meteorological conditions on specific aspects of disease development over a growing season. In that case, hourly meteorological data could be used in place of daily data, and much more information on disease development could be included.

The program WINDOW is written in FORTRAN and runs on a Cray computer. At present, WINDOW is not available for distribution due to constraints of time and money.

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