Linear Models Applied to Variation in Numbers of Cereal Rust Urediospores

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ABSTRACT

We developed three models to account for the variation in the cumulative numbers of *Puccinia graminis* and *P. recondita* urediospores trapped/cm^2 on microscope slides in the Mississippi River Basin during 1953, 1962, 1963, 1964, and 1965. These were linear multiple regression models derived from (i) a combination of five biological and six climatological variables; (ii) the biological variables alone; or (iii) the climatological variables alone. The biological variables were developed from regression components associated with the numbers of urediospores trapped. The climatological variables were derived from temperature and precipitation records.

The best model for *P. graminis* was one combining both biological and climatological variables. In the spring wheat area, a significant portion of the variation in final cumulative number of urediospores could be accounted for as early as 2 weeks before heading. However, in the winter wheat area, estimates made 2 weeks before heading were significant only for the 7- and 14-day predictions. For *P. recondita*, the model with only bi logical variables accounted for a highly significant portion of the variation in the final cumulative number of urediospores 2 weeks before heading. The model based on the six climatological variables was unsatisfactory for both *P. graminis* and *P. recondita*. Phytopathology 60:246-251.

Cereal rust epidemics in North America have from the turn of the century been studied for their patterns of development and for clues concerning components of predictive value. Except for leaf rust on winter wheat in Oklahoma and Illinois (2), however, no workable forecast scheme has been devised. In Oklahoma, the forecast is based on the number of infections on 1 April, and on the assumption that weather deviations after this date usually have little effect on the rate of increase (2, 3). This forecast has been remarkably successful, but occasionally has led to an overestimate of final severities. Thus, weather deviations after this date can influence rates of increase.

A tendency toward epidemic development of stem rust in the Western Mississippi Basin was noted when disease was observed early in the season. However, epidemics did not develop in all "early rust years" in the period 1921-1962 (5). Lambert (7) observed a correlation between warm growing seasons and destructive epidemics of stem rust in the spring wheat area for the period 1904-1925, but found no correlation with either total precipitation or number of rainy days. Wallin (17), on the other hand, noted that for the period 1904-1960, severe stem rust development in Nebraska, the Dakotas, and Minnesota, was associated with June and July temperature means lower than the 57-year average and with June and July rainfall means higher than the 57-year average. For the same period, there also seemed to be a causal relationship between March precipitation in Texas and Oklahoma and subsequent outbreaks of wheat stem rust in June and July in the upper midwest (16). Craigie (4) also observed that years of medium to heavy rust infection in Canada tended to be years of above-average rainfall or years with a greater frequency of days of rain. No rules for the prediction of stem rust, however, were formulated in these studies.

The usual northern limit of overwintering on the grass hosts for stem rust is north central Texas (15), and for leaf rust, central Kansas (6). The subsequent development of disease in the overwintering areas is a function of both the number of infections that survive and the interaction with environment during the growing season. Development of disease north of the overwintering sites obviously depends upon inoculum produced to the south. Thus, rust development in both areas is dependent upon the amount of initial inoculum. This could explain why, in contrast with some other diseases where abundant primary inoculum is always present, the analyses of climatological relationships alone have not led to satisfactory forecasting systems for rust development.

Generalized curves for numbers of urediospores of cereal rust fungi trapped on slides follow a pattern associated with local production of spores (10), and epidemic development of stem rust has been associated with early infection (5). Furthermore, work with rain samples has shown that early infection of spring wheat was associated with urediospores washed out of the air by rain, and that urediospores were trapped on slides only after rust had been observed locally (12). Thus, even though disease in the upper midwest is dependent upon primary inoculum from the south,

small inputs of urediospores early in the season are all that are required for epidemic development.

With these considerations in mind, we developed linear multiple regression models from biological data in the form of numbers of urediospores trapped on slides and climatological data of temperature and precipitation, to see if acceptable prediction is possible and, if so, to select the most appropriate variables for the development of working models.

MATERIALS AND METHODS.—Greased microscope slides have been exposed daily during a portion of the growing season for more than 40 years at a number of locations in the United States to trap urediospores of cereal rusts. The traps and methodology have been described (10, 15).

Data from Abilene, Denton, and Renner, Texas; Oklahoma City and Stillwater, Oklahoma; Goodland, Manhattan, and Wichita, Kansas; Lincoln and North Platte, Nebraska; Sergeant Bluff, Iowa; Rochester, Minnesota; Cottonwood and Brookings, South Dakota; Bismarck, Fargo, Grand Forks, Minot, and Williston, North Dakota; and Glasgow, Montana, for the years 1953, 1962, 1963, 1964, and 1965 were employed for the development of the model. Not all the stations were represented every year; as a result, data for 72 station-years were usable in this study.

The dependent variables for the linear multiple regression analyses consisted of the log cumulative numbers of urediospores of the appropriate species trapped per cm^2 on microscope slides. The date of prediction (D.P.) was the last date for which data for the independent variables was used in the analyses. The D.P. was related to crop stage at each location, based on estimates of the ripe stage derived from the cooperative regional wheat performance reports.

The biological variables developed from the urediospore data were: X_1 = time in days from the date the first urediospore of the appropriate species was trapped on a microscope slide to the D.P.; X_2 = logarithm of the cumulative number of urediospores of *Puccinia graminis* Pers. trapped per cm^2 on microscope slides up to the D.P.; X_3 = logarithm of the cumulative number of urediospores of *P. recondita* Rob. ex Desm. trapped per cm^2 on microscope slides up to the D.P.; X_4 = slope of the regression of the daily log cumulative numbers of urediospores of the appropriate species trapped per cm^2 on microscope slides on time in days for the 7-day period prior to the D.P.; X_5 = slope of the regression of the daily log cumulative numbers of urediospores of the appropriate species trapped per cm^2 on microscope slides on time in days from the date of first spore trapped to 7 days before the D.P.

The climatological variables derived from meteorological station records of daily maximum and minimum temperatures and precipitation were: X_6 = a rainfall function for the period from 8 to 14 days before the D.P.; X_7 = a rainfall function for the 7-day period prior to the D.P.; X_8 = a spore germination function for the appropriate species for the period from 8 to 14 days before the D.P.; X_9 = a spore germination function for the appropriate species for the 7-day period prior to the D.P.; X_{10} = a fungal growth function for the appropriate species for the period from 8 to 14 days prior to the D.P.; X_{11} = a fungal growth function for the appropriate species for the 7-day period prior to the D.P.

The rainfall function combined a moving average of rainfall and days of rain into one value. It was calculated from the total precipitation in mm in the 7-day period, multiplied by the number of days of precipitation in the period, divided by seven.

The germination and growth functions were both calculated with hourly temperature development equivalents. These equivalents related response of the fungus within its temperature range to that at the optimum temperature. They were derived from a $\sin^2$ function of a third-degree polynomial (13, 14). The equation used to obtain the temperature equivalents was: $Y = \sin^2 (124.72\ x - 64.30\ x^2 + 119.58\ x^3)$ where x equals observed temperature minus minimum temperature for activity)/maximum temperature for activity minus minimum temperature for activity. Thus, the value of Y ranges from 0 at the minimum temperature, to 1 at the optimum, to 0 at the maximum. Temperatures outside the temperature range were assumed to have no negative effect on development. The constants in this equation differ from those given by Schrödter (13).

Values chosen for the cardinal temperatures for germination and for growth of *P. graminis*, derived from the work of Rowell et al. (11) and Lange et al. (8) were: 3, 21, and 30°C; and 10, 30, and 40°C, respectively. For *P. recondita*, the values chosen for the cardinal temperatures for germination and for growth, derived from the review by Chester (3) were: 2, 21, and 30°C; and 5, 25, and 35°C, respectively.

Hourly temperature values were not available for most of the stations. However, at several locations with hourly temperature records, the daily low usually occurred at 6 AM, and the daily high at 4 PM (standard time). The daily low was also usually preceded by a 4-hr period of temperatures close to the low. Hourly temperature estimates, in C, were therefore generated from the daily weather records by assuming a 10-hr linear rise of temperature from the low at 6 AM to the high at 4 PM, followed by a 10-hr linear drop to the next day's low, with a 4-hr constant temperature from 2 to 6 AM. This technique seemed as good as, or better than, the temperature-averaging method proposed by Went (19). It was much simpler than developing equations by means of a Fourier series (18) for the different latitudes and dates represented in the study.

The spore-germination function consisted of the daily mean of the sum of the 56 hourly temperature-development equivalents calculated for the hr from 12 midnight to 8 AM for each day in the 7-day period. If less than 4 hr in a given 8-hr period fell within the cardinal temperature range for germination, the development equivalent for germination for that day was set to zero. The fungal growth function consisted of the daily mean of the sum of the 168 hourly temperature-development equivalents for the 7-day period.

Data processing for the development of the predic-

tion model was done in two stages. First, the daily urediospore and weather data for each set of the 72 station-year records were transferred from punch cards to tape to eliminate problems associated with card sorting and to speed subsequent computations. At this time, cumulative spore counts, the hourly temperature estimates, and the rainfall moving averages were computed and stored.

The second step was to generate a single row vector for each station record in a data matrix. This procedure was a useful device for grouping stations for multiple regression calculations. From this point, conventional linear multiple regression methods were employed to calculate the total variance of the dependent variable attributable to regression, the individual partial regression coefficients, and the appropriate tests of significance. This was done for each of three regression models (i) derived from both biological and climatological variables; (ii) derived from biological variables only; and (iii) derived from climatological variables only.

RESULTS.—A wide range of disease development for both species was sampled and included in this study. This is reflected in the totals of the numbers of urediospores trapped at each location (Table 1). The numbers of urediospores trapped at each location, although related to disease development (10), cannot be directly correlated with disease, since the trap-sites were not standardized with respect to the spore sources. Hence, the models presented here are primarily useful in showing the kinds of predictions and the effects of the variables which might be expected, rather than in providing working prediction equations.

There are two other qualifications to the urediospore data. One is that a few stations, notably Brookings, South Dakota, had a bi-modal distribution of urediospores; this suggests more than one major source of inoculum. The second is that urediospore sampling at some of the spring wheat locations, especially in 1953, was discontinued prior to harvest. This means that some urediospore records were incomplete.

Results associated with the regression solutions developed for 2 weeks before heading are presented to illustrate the models. The number of locations with urediospore data this early in the season were: 21 for *P. graminis* in winter wheat; 32 for *P. graminis* in spring wheat; 30 for *P. recondita* in winter wheat; and 32 for *P. recondita* in spring wheat.

Table 2 gives the coefficients of determination for the dependent variable in the regression models, with predictions made 42 days before the ripe stage for successive 14-day periods and the corresponding levels of significance. The change in R^2 values, for each successive 7-day increment in the prediction period, are presented in Figure 1.

With the exception of *P. graminis* in the winter wheat area, R^2 values were significant for both species and for all periods of prediction when all 11 independent variables were used. In the winter wheat area, only the 14-day prediction for *P. graminis* gave a significant R^2 value. The lack of significance of the 28-day and 42-day predictions is probably due to insufficient 42-day *P. graminis* records, rather than to excessive variability associated specifically with the region and the fungus.

The five biological independent variables together gave significant R^2 values for *P. graminis* only with the 14-day predictions. The additional input of the climatological variables helped prediction for longer periods. With *P. recondita*, however, use of the five biological variables gave highly significant R^2 values at all dates of prediction. Thus, even earlier predictions with significance could have been made for *P. recondita*.

TABLE 1. Cumulative number of urediospores of *Puccinia graminis* and *P. recondita* trapped per cm^2 on microscope slides for locations and years included in predictions made 42 days before estimated time of ripe stage

Crop and location	*P. graminis*					*P. recondita*				
	1953	1962	1963	1964	1965	1953	1962	1963	1964	1965
Winter Wheat										
Abilene, Texas				627					1,645	
Denton, Texas					9					620
Goodland, Kans.			153	4,776	24,640			409	7,597	6,107
Lincoln, Nebr.	406	18,199	255	7,894	4,304	87	4,316	3,043	5,894	6,419
Manhattan, Kans.					1,416					2,910
North Platte, Nebr.	3,251	32,890	2,890	4,731	13,995	136	6,035	3,398	11,266	23,682
Oklahoma City, Okla.	77	182	267	2,041	460	18	19,162	2,499	6,184	4,284
Renner, Texas	748	51	39	1,341	132	361	27,931	888	6,334	15,349
Sergeant Bluff, Iowa	678	2,143	618	1,042	1,523	153	694	559	692	1,583
Stillwater, Okla.					181					1,146
Wichita, Kans.	511	193	337	4,128	1,483	103	4,667	1,614	5,499	4,926
Spring Wheat										
Bismarck, N. Dak.	9,339	1,395	663	1,447	1,176	1,824	2,964	1,357	2,655	4,528
Brookings, S. Dak.	1,472	1,179	262	415	18,359	332	16,364	18,421	612	26,951
Cottonwood, S. Dak.	2,942		319	1,909	3,210	405		330	788	1,970
Fargo, N. Dak.	63	40			296	21	950			2,157
Glasgow, Mont.	136	1,063	2,790	417	7,483	70	1,379	1,292	740	8,538
Grand Forks, N. Dak.	365					189				
Minot, N. Dak.	955	707	1,845	1,187	4,538	1,624	319	764	1,806	996
Rochester, Minn.		2,082	818				201	200		
Williston, N. Dak.	234	2,724	14,531	1,810	15,949	298	1,649	2,060	1,742	5,956

TABLE 2. Coefficients of determination (R^2) of log cumulative spore numbers associated with predictions made 2 weeks before heading

Species and variable class	Winter wheat with prediction of			Spring wheat with prediction of		
	14 Days[a]	28 Days	42 Days[b]	14 Days[a]	28 Days	42 Days[b]
Puccinia graminis						
All	.728**[c]	.676	.674	.777**	.772**	.758*[c]
Biological	.618**	.128	.108	.674**	.276	.362
Climatological	.358	.268	.246	.198	.350	.252
Puccinia recondita						
All	.856**	.717**	.643*	.631*	.517*	.614*
Biological	.817**	.673**	.602**	.549**	.376**	.465**
Climatological	.149	.177	.146	.225	.170	.166

[a] Estimated time of heading.
[b] Estimated ripe stage.
[c] *Significant at the .05 level; **Significant at the .01 level.

The six climatological variables as a group did not give any significant R^2 values at 42 days prior to the ripe stage. With *P. recondita,* the climatological variables used here appear to have little effect. However, with *P. graminis,* the use of climatological variables for prediction for periods longer than 14 days appears useful.

The sums of the R^2 values for the climatological set and the biological set of variables do not exactly equal the R^2 values obtained with all 11 variables, as would be the case if both sets were completely independent. The R^2 values for the biological and climatological variables for *P. graminis* with a prediction interval of 28 and 42 days are less than the values for those R^2 values with all variables. This can result where both positive and negative intercorrelations exist within the variable matrix.

The partial multiple regression coefficients obtained from the model, with all 11 independent variables for *P. graminis* and *P. recondita,* are presented in Table 3. One or more of the coefficients is significant in each individual case. This suggests that if the prediction problem were framed with that variable alone, with all other independent variables of the equation held constant, a significant R^2 value would be obtained for each prediction interval with each rust species in each region. The partial regression coefficients in Table 3 vary with area and rust species as well as prediction period.

The standard error of estimate was calculated for each equation used at 2 weeks before heading. Considering only the equations with significant R^2 values, the standard error of estimate was lowest for the *P. recondita* equations in the winter wheat area. These fell between 15 and 11%. In contrast, the 14-day prediction for *P. graminis* in the spring wheat region had a standard error of estimate of 28%.

DISCUSSION.—We compared the predicted values of cumulative numbers of urediospores with the actual

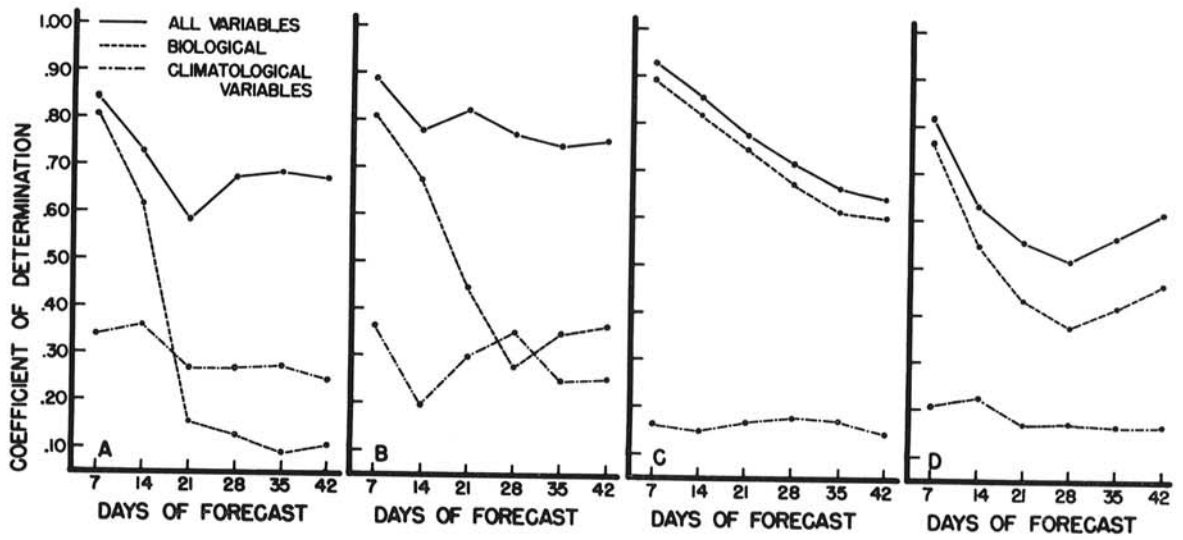

Fig. 1. Variation in the log cumulative numbers of spores attributable to regression on data available 42 days prior to harvest; **A)** *Puccinia graminis* in the winter wheat region; **B)** *P. graminis* in the spring wheat region; **C)** *P. recondita* in the winter wheat region; and **D)** *P. recondita* in the spring wheat region. The biological variables are developed from regression components associated with the numbers of urediospores trapped on microscope slides; the climatological are derived from temperature and precipitation records in the 2-week period prior to the date of prediction.

TABLE 3. Partial regression coefficients for prediction of numbers of spores of *Puccinia graminis* and *P. recondita* made 42 days before ripe stage

Variable	Winter wheat with prediction of			Spring wheat with prediction of		
	14 Days[a]	28 Days	42 Days	14 Days[a]	28 Days	42 Days
			P. graminis			
X_1[b]	.003	.042**[c]	.038**	.040**	.007	.008
X_2	.663**	—.349	—.559*[c]	.817**	.784**	.701**
X_3	—.057	—.247	—.207	.128	.311	.190
X_4	—2.805	—4.543	—4.297	1.019	—2.005	1.407
X_5	—.278	.856	.042	—.326	—5.013**	—5.228**
X_6	.659	2.025**	1.728**	.392	—.093	.375
X_7	1.318	3.128**	2.354**	—.470	1.201	.945
X_8	—.096	—.233	—.097	—.470**	—.374*	.349
X_9	—.477	—.850**	—.855**	.430*	.827**	.544**
X_{10}	.034	.090	.059	.210*	.182	.156
X_{11}	.252	.510**	.558**	—.249**	—.475**	—.357**
			P. recondita			
X_1[b]	—.014	.005	.003	.028*[c]	.020	.027*
X_2	—.160	.235*	—.209	—.102	.150	.190
X_3	1.289**[c]	.731**	.601**	.539**	.247	.189
X_4	—.673	—.157	—.056	1.410	2.794*	3.022**
X_5	.302	1.395	.934	.650	.211	.447
X_6	—.252	.020	.053	.300	.238	.093
X_7	—.256	—.829*	—.579	—.876*	—.224	—.269
X_8	.338	.072	.057	—.331*	—.325*	—.291
X_9	.256	—.025	—.121	.496*	.690**	.660**
X_{10}	—.093	—.002	—.003	.104	.107	.079
X_{11}	—.113	.024	.059	—.216*	—.316**	—.299**

[a] Estimated time of heading.

[b] X_1 = time in days from the date the first urediospore of the appropriate species was trapped on a microscope slide to the D.P.; X_2 = logarithm of the cumulative number of urediospores of *Puccinia graminis* Pers. trapped per cm^2 on microscope slides up to the D.P.; X_3 = logarithm of the cumulative number of urediospores of *P. recondita* Rob. ex Desm. trapped per cm^2 on microscope slides up to the D.P.; X_4 = slope of the regression of the daily log cumulative numbers of urediospores of the appropriate species trapped per cm^2 on microscope slides on time in days for the 7-day period prior to the D.P.; X_5 = slope of the regression of the daily log cumulative numbers of urediospores of the appropriate species trapped per cm^2 on microscope slides on time in days from the date of first spore trapped to 7 days before the D.P.; X_6 = a rainfall function for the period from 8 to 14 days before the D.P.; X_7 = a rainfall function for the 7-day period prior to the D.P.; X_8 = a spore germination function for the appropriate species for the period from 8 to 14 days before the D.P.; X_9 = a spore germination function for the appropriate species for the 7-day period prior to the D.P.; X_{10} = a fungal growth function for the appropriate species for the period from 8 to 14 days prior to the D.P.; X_{11} = a fungal growth function for the appropriate species for the 7-day period prior to the D.P.

[c] *Significant at the .05 level; **Significant at the .01 level.

values to discover how much of the variation could be accounted for by regression. The models were developed from the entire set of data. The equations were not applied to independent urediospore sequences, primarily because of limitations in the biological inputs.

Analyses with the variables presented here suggest that acceptable predictions, based on statistical significance, of cumulative numbers of urediospores of *P. graminis* and *P. recondita* can be made 2 weeks before the heading stage. Furthermore, numbers of urediospores deposited on impaction traps correlate with disease severity (1); thus, the substitution of disease severity for spore numbers as the dependent variable in these models seems feasible.

The five biological variables measured the age of the epidemic to the D.P., the rate of increase of the epidemic during two periods, the severity of the epidemic on the D.P. (as measured by the cumulative numbers of urediospores), and the severity of the other rust species. These can be reduced to two variables: (i) a severity function; and (ii) either an age function or a rate of increase function. These should be adequate biological variables for satisfactory prediction.

Climatological variables should be retained in a working model, especially in the case of *P. graminis*. However, inspection of the models reported here suggests that the earlier-period temperature variables, i.e., X_8 and X_{10}, did not help very much. This may be because the earlier temperature effects are integrated into the later biological inputs. The same rationale applies to the precipitation function. In effect, only climatological variables derived from data in a short period prior to, or after, the date of the last biological input would provide an independent contribution to the multiple regression.

It seems likely now that the two biological variables mentioned above and the three climatological variables

from the 7-day period prior to the D.P. would have been as effective as the 11 variables used. This would have increased the error degrees of freedom, and possibly would have resulted in improved statistical significance. Models with the reduced number of variables were not constructed, since this paper is concerned primarily with an examination of regression approaches to prediction rather than with the development of a working model.

Other useful functions for the prediction model might be a dew function and a soil moisture function. The former might be a better variable than precipitation with regard to infection. The latter would indicate potential yield (20), and would help relate prediction to yield loss.

The equations generated from these analyses varied with the length of the prediction interval, the area, and the species of rust. Therefore, the development of specific prediction equations seems preferable to the development of a single generalized prediction equation.

The models presented here have dealt with each rust species independently. Clearly, control measures must also take into account the effect of both diseases together, as well as individually. A model combining both stem and leaf rust, in which the joint effect of both diseases on loss are properly apportioned, seems a worthwhile objective. To this end, we need to know whether or not there is interaction or if the effects of both diseases are additive.

Finally, biological variables derived from the numbers of spores trapped on rods or cylinders, rather than on slides, should give added leverage to prediction. The threshold of detection of urediospores with rods is lower, and there is less day-to-day variation (9), a factor that should lead to improved precision. A standardized location of the cylinder traps with respect to spore source would further minimize uncontrolled variation among and within locations, and perhaps might lead to the development of equations for actual prediction.

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