Development of Linear Equations for Predicting Wheat Leaf Rust

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ABSTRACT

A stepwise multiple linear regression computer program was used to identify six biological and meteorological variables to predict wheat leaf rust severities 14, 21, and 30 days after the date of prediction (DP). Significant variables were leaf rust severity on DP, growth stage of wheat on the date predicted, average hours of free moisture during 7 days prior to DP, number of days of precipitation ⩾ 0.25 mm during 7 days prior to DP, a fungal growth function, and fungal infection function. Linear equations that combined those variables had R^2 values from 0.722 to 0.527. Equations predicted leaf rust severity within ± 1, 3, and 12%, 14, 21, and 30 days in advance, respectively. Equations with leaf rust severity as an inoculum variable were more accurate than those without an inoculum variable and those with spore numbers as the inoculum variable.

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Resistance offers the most efficient disease control in cereal crops, but producers often must rely on alternative control measures as when known sources of resistance became ineffective. Usually the alternative involves chemical control, but the economics of crop production dictate that the value of chemical control exists principally in the absence of effective resistance.

Efforts to control wheat leaf rust are a prime example of exploiting both resistance and chemicals. Researchers trying to control wheat leaf rust have been unable to relax their efforts because resistance has not remained effective, and chemicals and methods of application have been neither effective nor feasible. Control will be achieved only when both methods are developed to their full potential. The objective of these studies was to develop a method of identifying potential epidemics early enough for fungicides to be applied to reduce epidemic development and, thus, crop loss.

Disease prediction schemes have been developed for downy mildew of lima bean (7), blue mold on tobacco (8), potato late blight (4, 12), and wheat leaf rust (1, 3). Each prediction scheme uses biological-meteorological variables. Downy mildew of lima bean and potato late blight warnings are issued when the number of blight-favorable days reaches a threshold sufficient to initiate epidemics. Epidem (11), a simulator of plant disease epidemics developed for tomato early blight, constructs an epidemic as it occurs and formulates decisions on the progress of disease based on biological inputs. The wheat leaf rust forecasting procedure developed for Oklahoma (3) primarily is qualitative, and differentiates severe from light epidemics. The new procedure for South Dakota (1) has not been widely tested, but should quantitatively differentiate among epidemics. Some measure of success is assured with each system because predictions are based on biological-meteorological parameters.

The science of prediction aims at a mathematical description of relationships among variables in nature. The functional relationships do not always have clearly interpretable biological meaning. Most functional relationships expressed by regression lines are empirically fitted curves, so the functions simply represent the best mathematical fit to an observed set of data. The constants necessary to fit the curves possess no clear inherent meaning. Most plant pathologists look askance at empirically fitted curves, yet when such curves describe the relationship between disease development and biological-meteorological phenomena, the curves have real though temporary value. With sufficient knowledge of phenomena, structural models can be constructed. They are preferred but they may not be better predictors than empirical models. In the studies reported here, we have used linear regression to identify and quantify biological and meteorological variables useful in predicting wheat leaf rust epidemics.

MATERIALS AND METHODS.—Location of wheat nurseries, cultivars, plot size, urediospore-trapping techniques, methods of estimating disease severity, and types of weather measurements taken for 1967 and 1968 were reported previously (6). Investigations in 1970 were confined to Stillwater and Altus, Okla.; Hutchinson, Colby, and Manhattan, Kans.; Alliance, Nebr.; and Rosemount, Minn. In 1969, we also had nurseries at Williston, No. Dak.; and Morris, Crookston, and St. Paul, Minn. Reasoning used in cultivar selection in 1969 and 1970 was similar to that for 1967 and 1968. Combinations of Agent (C.I. 13523), Bison (C.I. 12518), Guide (C.I. 13856), Gage (C.I. 13532), Scout (C.I. 13546), Parker (C.I. 13285), Cheyenne (C.I. 8885), Shawnee (C.I. 14157), Lancer (C.I. 13547), Ottawa (C.I. 12804), and Milam (C.I. 13369) were planted in winter wheat nurseries; and combinations of Baart (C.I. 1697), Mindum (C.I. 5296), Thatcher (C.I. 10003), Chris (C.I. 13751), Crim (C.I. 13465), Manitou (C.I. 13775) and Selkirk (C.I. 13100) were planted in spring wheat nurseries. In 1967 and 1968, we planted two cultivars at each location, but in 1969 and 1970, we planted 3 to 5. All cultivar additions provided disease severity data on commercial cultivars not used previously. The cultivars possessed degrees of specific resistance to *Puccinia recondita* Rob. ex Desm. *tritici* that ranged from 100% effective, as in Agent, to apparently no specific resistance, as in Triumph. Although we did not have a complete range of specificity at each location, we obtained disease severity data on many of the host genotypes extant in winter and spring wheats grown in the Great Plains of the USA.

We used a stepwise multiple regression computer program to formulate equations to predict leaf rust severities 14, 21, and 30 days after the date of prediction (DP). Stepwise multiple regression analysis regresses exploratorily a variable Y on variables X_1, X_2, X_3, . . . , taking various combinations to obtain a minimum of unexplained residual variance with the fewest independent variables. Any independent variable that does not remove a significant portion of the variation in Y is dropped from the analysis. Therefore, the independent variable that explains the greatest amount of variation (highest coefficient of determination or R^2 value) in the dependent variable enters the program first. Remaining variables are regressed again, and the one with the highest R^2 enters second. That process is repeated until all independent variables are entered. That way, variables are selected that explain most of the variation in disease development.

In our program, the dependent variable (Y) is the $\log_{10}$ per cent leaf rust severity recorded 14, 21, and 30 days after DP. Independent variables are $\log_{10}$ per cent leaf rust severity (disease severity = DS) on DP; $\log_{10}$ cumulative number of urediospores/cm^2 trapped from date the first spore is trapped to DP (cumulative spore numbers = CSN); $\log_{10}$ total number of urediospores/cm^2 trapped during the 7 days immediately before DP (weekly spore numbers = WSN); average minimum temperature (minimum temperature = MIN) during 7 days prior to DP; average maximum temperature (maximum temperature = MAX) during 7 days before DP; a fungal growth function ($\sin^2$ transformation of fungal growth rate = SIN^2) as developed by Schrödter (9) and modified by Dirks & Romig (5); growth stage of wheat (growth stage = GS) on the predicted date where growth stages are expressed as integers on a scale of 1 to 9 (1 = tiller, 2 = joint, 3 = late joint, 4 = boot, 5 = heading, 6 = anthesis, 7 = berry, 8 = dough, and 9 = ripe); average hours of free moisture (free moisture = FM) as dew or rain per day during the 7 days before DP; number of days of rainfall $\geqslant$ 0.25 mm (precipitation = PREC) during the 7 days before DP; logistic rate of rust increase (10) from the date rust was first observed to DP (logistic rate of increase in disease severity = R-DS); logistic increase of daily log cumulative number of urediospores/cm^2 from date first spore trapped to DP (logistic rate of increase of cumulative spore numbers = R-CSN); and an infection function (infection function = IF) where each day is evaluated on the basis of its meteorological and biological favorability for infection and assigned a value of 0 or 1. A day is considered favorable and given a value of 1 when the minimum temperature is $\geqslant$ 4.4 C, with 4 hr of free moisture, and at least one urediospore/cm^2 is trapped. When one of those three measurements is below the minimum, the day is considered unfavorable and given a value of zero. The sum of the daily evaluations from the date rust is first observed to DP is the value of the infection function.

Hourly temperatures used in the fungal growth function (SIN^2) were calculated on the basis of a 10-hr linear rise from a low at 6 AM to a high at 4 PM and a linear drop to the next day's low. We found the highest correlation between temperature equivalents calculated from actual hourly temperatures and those calculated from estimated hourly temperatures when hourly temperatures were estimated on the basis of a 10-hr rise and a 14-hr decline rather than a 10-hr rise, 10-hr decline, and 4-hr constant (5).

Stepwise regression identified combinations of variables that explained a significant amount of variation in disease development. Constant values and partial regression coefficients for those variable combinations with highest R^2 values were used to predict disease severity on cultivars not used in the generation of equations. We tested the precision of the equations by calculating average variation between observed and predicted severities (6). Equations with the highest R^2 and the lowest average variation were selected as working equations.

RESULTS.—Table 1 gives coefficients of determination (r^2) for each variable that entered the stepwise program for winter and spring wheats, respectively. With one exception, DS had the highest r^2 of any variable, indicating that leaf rust severity 14, 21, and 30 days after DP is primarily a function of the amount of leaf rust present on DP. WSN and CSN had higher r^2 values than other variables, except DS, for the 14-day prediction; however, as the predictive period lengthened, GS, IF, SIN^2, and MIN increased their ranking relative to CSN and WSN.

Individual r^2 values can be misleading in stepwise regression. DS has the highest r^2 and is the first variable to enter the program for both winter and spring wheats; but GS, which usually does not have the second highest r^2, enters next as the second most useful variable in prediction. Of all remaining variables, combinations of PREC, FM, SIN^2, and IF, along with DS and GS, offered the best predictions on winter wheats, whereas combinations of DS, GS, MIN, PREC, SIN^2, and IF were best on spring wheats. Generally, MAX, R-DS, and R-CSN were not significant variables. By omitting DS as an independent variable, we permitted CSN or WSN to enter as the primary biological variable; however, all variable combinations that included CSN or WSN had lower R^2 values than those with DS.

Partial regression coefficients for variables in our

TABLE 1. Simple coefficients of determination (r^2) for independent variables used in stepwise regression of *Puccinia recondita tritici*

Predictive period (days)	Independent variables												
	DS[a]	CSN	WSN	MIN	MAX	SIN²	GS	IF	FM	PREC	R-DS	R-CSN	N
						Winter wheat							
14	0.570	0.423	0.430	0.209	0.059	0.196	0.144	0.328	0.024	0.011	0.043	0.077	321
21	0.459	0.261	0.265	0.273	0.113	0.245	0.148	0.261	0.009	0.008	0.067	0.058	296
30	0.337	0.082	0.122	0.249	0.113	0.177	0.215	0.187	0.020	0.006	0.097	0.008	229
						Spring wheat							
14	0.524	0.338	0.384	0.004	0.002	0.016	0.258			0.004	0.030	0.001	277
21	0.509	0.235	0.284	0.017	0.002	0.043	0.278			0.022	0.163	0.004	221
30	0.296	0.229	0.211	0.158	0.067	0.216	0.283			0.035	0.095	0.011	140
30	0.302	0.373	0.345	0.171	0.066	0.161	0.033	0.394	0.051	0.189	0.043	0.032	46

[a] DS = $\log_{10}$ per cent disease severity; CSN = $\log_{10}$ cumulative spore numbers; WSN = $\log_{10}$ total number of spores trapped during 7 days prior to date of prediction; MIN = minimum temperature; MAX = maximum temperature; SIN² = sin² fungal growth function; GS = wheat growth stage; IF = infection function; FM = hours of free moisture; PREC = precipitation; R-DS = infection rate; R-CSN = logistic increase of cumulative spore numbers; N = number of observations.

TABLE 2. Constant value, variables, and their partial regression coefficients for predicting *Puccinia recondita tritici* on winter wheat

Equation	Variables									Predictive period (days)
	K[a]	FM	PREC	DS	GS	IF	SIN²	N	R^2	
1[b]	-3.3998	0.0606		0.7675	0.4003		0.0077	321	0.722	14
2	-5.2304				0.4726	0.0826	0.0125	321	0.560	14
3	-3.4663	0.0285	0.0681	0.6243	0.4105		0.0128	296	0.707	21
4	-4.9145				0.4505	0.0763	0.0163	296	0.572	21
5	-3.5420	0.0736	0.0963	0.5409	0.4912		0.0088	229	0.669	30
6	-4.8639	0.0475			0.5107	0.2795	0.0129	229	0.554	30

[a] K = constant term; FM = free moisture; PREC = precipitation; DS = $\log_{10}$ per cent disease severity; GS = wheat growth stage; IF = infection function; SIN²=fungal growth function; N = number of observations that went into generation of equation; MIN = minimum temperature; R^2 = coefficient of determination for equations.

[b] Equations 1, 3, and 5, for 14-, 21-, and 30- day predictions, respectively, with rust present on date of prediction; equations 2, 4, and 6 for 14-, 21-, and 30-day predictions, respectively, with no rust present on date of prediction.

TABLE 3. Constant value, variables, and their partial regression coefficients for predicting *Puccinia recondita tritici* on spring wheat

Equation	Variables									Predictive period (days)
	K[a]	MIN	PREC	IF	DS	GS	SIN²	N	R^2	
1[b]	–2.0327				.7482	.3603		277	.636	14
2	–1.7804		.1294		.6978	.3447		221	.621	21
3	–1.9784				.7181	.3487	.0141	140	.569	30
4	–3.0194	.0540		.1970				46	.527	30

[a] K = constant term; MIN = minimum temperature; PREC = precipitation; IF = infection function; DS = $\log_{10}$ per cent disease severity; GS = wheat growth stage; SIN² = sin² fungal growth function; N = number of observations that went into generation of equation; R^2 = coefficient of determination for equations.

[b] Equations 1, 2, and 3 for 14-, 21-, and 30-day predictions, respectively, with rust present on date of prediction; equation 4 for 30-day prediction with no rust on date of prediction.

working equations are shown in Tables 2 and 3. From the stepwise analysis, six equations emerged that would accurately predict leaf rust on winter wheats and four that predict for spring wheats. Equations 1, 3, and 5 (Table 2) and 1, 2, and 3 (Table 3) predict leaf rust severity 14, 21, and 30 days after DP on winter and spring wheats if rust is present on DP. If no leaf rust is present on DP in winter wheats, equa-

TABLE 4. Number of uredia of *Puccinia recondita tritici* per tiller and crop growth stage on date of prediction for wheat cultivars

Location	Cultivar and crop	DP[a]	Uredia/ tiller	Growth stage
Altus, Okla.	Bison wheat	16	6	Late joint
Manhattan, Kans.	Bison wheat	16	4	Early joint
Colby, Kans.	Scout wheat	9	5 of 10	Boot
Hutchinson, Kans.	Parker wheat	16	0	Late joint
Hutchinson, Kans.	Guide wheat	16	0	Late joint
Manhattan, Kans.	Shawnee wheat	16	0	Late joint
Fargo, No. Dak.	Baart wheat	16	8	Late joint
Rosemount, Minn.	Baart wheat	16	1	Late joint
Rosemount, Minn.	Chris wheat	16	1 of 10	Late joint
Rosemount, Minn.	Larker barley	16	0	Late joint
Rosemount, Minn.	Garland oats	9	1 of 10	Late joint

[a] DP = Date of prediction expressed as days before heading.

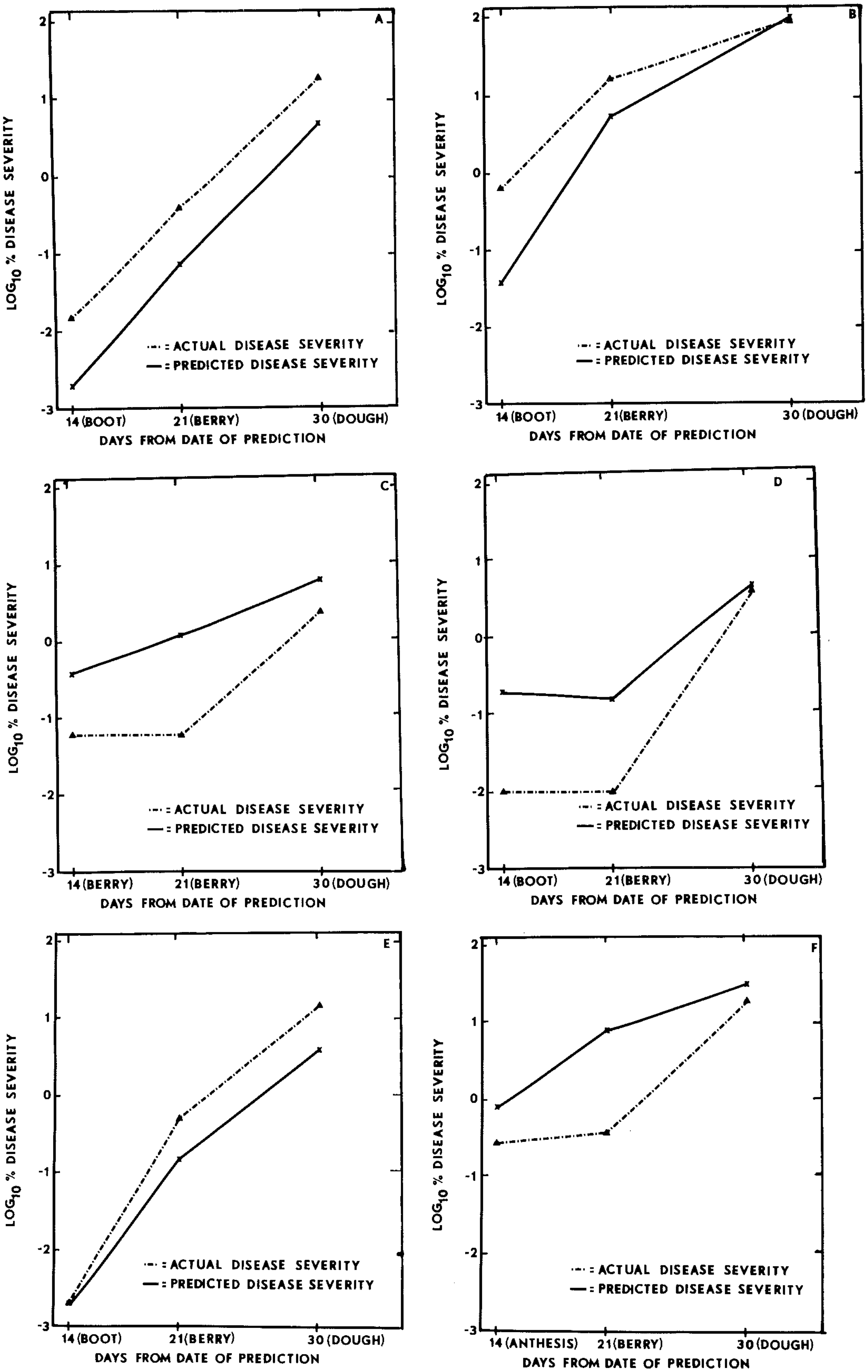
tions 2, 4, and 6 (Table 2) are superior predictors over those with DS. Therefore, equations based on GS, IF, and SIN^2 predicted leaf rust severity 14 and 21 days in advance; and GS, IF, SIN^2, and FM predicted leaf rust 30 days in advance on winter wheats when there was no disease on DP. Usually, we have leaf rust on DP in spring wheats; in the few instances when rust is not present, IF and MIN adequately predict 30 days in advance (equation 4, Table 3).

We tested the accuracy of our equations by predicting leaf rust severity on 34 winter wheat cultivars, 4 spring wheat cultivars, 1 spring oat cultivar, and 1 spring barley cultivar, and calculated the average variation between actual and predicted severities for winter wheats but not for spring wheats, the oat cultivar, and the barley cultivar.

The average variation for leaf rust severities on winter wheats was 1, 3, and 12% for 14, 21, and 30 days, respectively. The accuracy of our predictions is best illustrated in Fig. 1 and 2. Predicted severities for Bison wheat at Altus, Okla. (Fig. 1-A); Bison at Manhattan, Kans. (Fig. 1-B); and Scout at Colby, Kans. (Fig. 1-C) were calculated with equations 1, 3, and 5 (Table 2), as leaf rust was present on DP (Table 4). Predicted severities for Parker at Hutchinson, Kans. (Fig. 1-D); Guide at Hutchinson, Kans. (Fig. 1-E); and Shawnee at Manhattan, Kans. (Fig. 1-F) were calculated with equations 2, 4, and 6 (Table 2), as no leaf rust was present on DP (Table 4). We made all predictions when the wheat was in late joint, except at Colby where it was in boot. Predicted severities on spring cultivars were calculated with equations 1, 2, and 3 (Table 3).

DISCUSSION.—In developing prediction equations, our primary concern was to see if biological and meteorological variables shown to affect rust development could serve as predictors over a range of environments so we could construct general equations to predict leaf rust severity based on those variables. Major biological and meteorological variables that affect leaf rust development are well documented (3). Amount of inoculum, temperature, and moisture are paramount and are represented in our model by DS, SIN^2, FM, PREC, and IF. The only variables that need explanation are GS and SIN^2. Growth stage of the crop on the date predicted does not seem to have any clear biological meaning. Our rationale for using GS was that the amount of rust usually is related to the crop growth stage. As the crop matures, more rust occurs. Understandably, GS does not cause rust to occur and, in that sense, it is an artifact. We believe the value of GS in predicting is due to the linear scale on which it is constructed. For that reason, it serves as a useful predictor of a disease that also progresses linearly. The SIN^2 transformation of the temperature response curve (5) enables us to predict severe epidemics more accurately than with nontransformed temperature. That is principally because a linear relationship exists between rust development and the frequency of favorable temperatures (not mean temperature) for fungal growth. Undoubtedly, we have not included all possible biological and meteorological variables that affect rust development, as our equations account for only 67 to 71% of the variation in disease progress. Variables that might account for the remaining 29 to 33% of unexplained variation could be interactions and variables not cataloged. We consider the prediction system presented as preliminary. Predictions more than 30 days in advance are needed to allow more lead time to issue forecasts and to apply fungicides. Models designed for longer predictions require identification of additional variables. Acceptable accuracy in prediction would differentiate between epidemics that require control and those that do not. It is evident that both biological and meteorological variables are necessary for acceptable

Fig. 1. Actual and predicted severity of *Puccinia recondita tritici* on **A)** Bison wheat at Altus, Okla. **B)** Bison wheat at Manhattan, Kans. **C)** Scout wheat at Colby, Kans. **D)** Parker wheat at Hutchinson, Kans. **E)** Guide wheat at Hutchinson, Kans. **F)** Shawnee wheat at Manhattan, Kans.


A
LOG10 % DISEASE SEVERITY
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-1
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—·— : ACTUAL DISEASE SEVERITY
— : PREDICTED DISEASE SEVERITY
14 (BOOT) 21 (BERRY) 30 (DOUGH)
DAYS FROM DATE OF PREDICTION
B
LOG10 % DISEASE SEVERITY
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—·— : ACTUAL DISEASE SEVERITY
— : PREDICTED DISEASE SEVERITY
14 (BOOT) 21 (BERRY) 30 (DOUGH)
DAYS FROM DATE OF PREDICTION
C
LOG10 % DISEASE SEVERITY
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—·— : ACTUAL DISEASE SEVERITY
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14 (BERRY) 21 (BERRY) 30 (DOUGH)
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—·— : ACTUAL DISEASE SEVERITY
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14 (BOOT) 21 (BERRY) 30 (DOUGH)
DAYS FROM DATE OF PREDICTION
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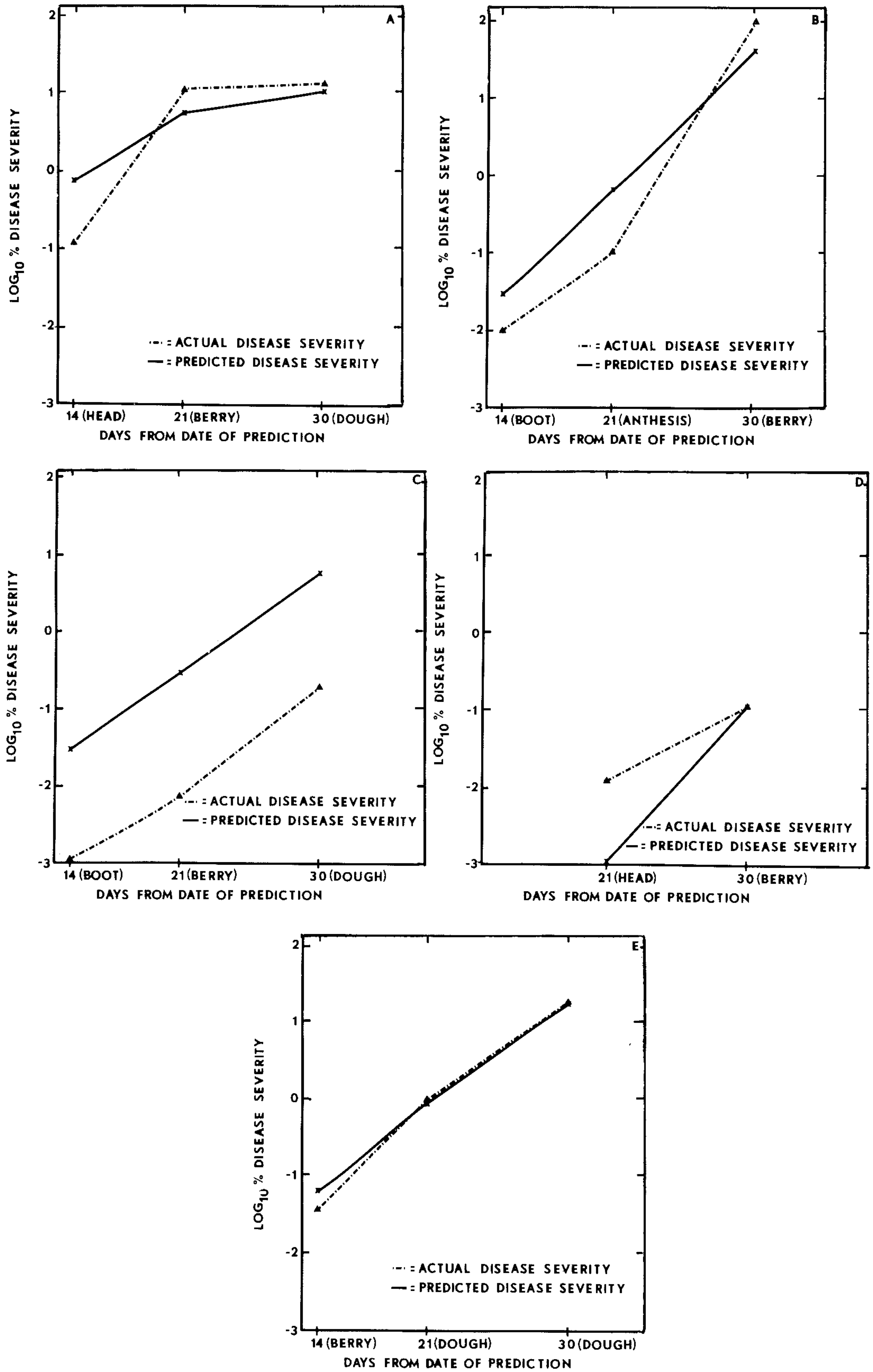
14 (ANTHESIS) 21 (BERRY) 30 (DOUGH)
DAYS FROM DATE OF PREDICTION


A
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LOG10 % DISEASE SEVERITY
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: ACTUAL DISEASE SEVERITY
: PREDICTED DISEASE SEVERITY
14 (HEAD)
21 (BERRY)
30 (DOUGH)
14 (BOOT)
21 (ANTHESIS)
30 (BERRY)
21 (HEAD)
14 (BERRY)
21 (DOUGH)
DAYS FROM DATE OF PREDICTION

Fig. 2. Actual and predicted severity of *Puccinia recondita tritici* on **A)** Baart wheat at Fargo, No. Dak. **B)** Baart wheat at Rosemount, Minn. **C)** Chris wheat at Rosemount, Minn. **D)** Larker barley at Rosemount, Minn. **E)** Crown rust on Garland Oats at Rosemount, Minn.

accuracy of predictions. Even when DS was purposely omitted from our model, the presence of IF was required for acceptable accuracy. Buchenau (1) also used biological and meteorological variables to predict leaf rust in South Dakota. Although Dirks & Romig (5) predicted number of *P. recondita* urediospores rather than disease severity, models based on biological or biological-meteorological variables predicted with equal accuracy. Our experience with spore numbers (2) lead us to hypothesize that we might predict amount of disease with numbers of spores as well as with disease severity estimates because numbers of urediospores deposited on impaction traps correlated with disease severity. Nevertheless, when spore numbers rather than disease severities were used in our model, R^2 values were 0.10 lower.

The principal difficulty with spore numbers is that impaction traps are exposed to spores from endogenous and exogenous sources, and the vicissitudes of weather might cause deposition of more or fewer spores than expected from a given level of infection proximal to the trap. The remedy may involve standardizing trap locations, isolating plots, and including both spore numbers and disease severity estimates as inoculum variables.

The equations we present here are general and designed to predict over a range of environments in the Great Plains of the USA. Although improved accuracy of prediction might be achieved by generating equations for areas with similar precipitation and temperature patterns, a certain danger exists in that approach. Equations based only on meteorological data marginal for disease development would not accurately predict severe epidemics in an abnormally favorable season. To ensure acceptable accuracy in predicting severe and light epidemics in areas of infrequent occurrence, we sacrificed maximum obtainable accuracy for all monitoring sites by pooling climatic and disease data from all recording locations. That enabled us to predict degrees of development at any site.

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