

## A Model to Estimate Disease on Cereal Leaves at Different Positions from Whole Plant Severity Data

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### ABSTRACT

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A model to estimate wheat leaf rust severity at different positions from the tiller/whole plant rust severity values and disease progress curves was developed. Development of leaf rust on the  $i$ th leaf was expressed as  $dx_{it}/dt = rX_t(1 - x_{it})$  or, in an integrated form,  $x_{it} = 1 - \exp[-rX_t(t - t_i)]$ , where  $x_{it}$  is the rust severity on the  $i$ th leaf at time  $t$ ,  $r$  is the tiller/plant apparent infection rate,  $X_t$  is the tiller/plant rust severity observed at time  $t$ , and  $t_i$  is the time of the  $i$ th leaf emergence. Leaf rust severity data were collected on individual leaves on 10 randomly selected tillers in sequentially inoculated plots and in plots of naturally occurring epidemics of wheat cultivar McNair 1003 during the 1986-87 and 1987-88 wheat-growing seasons. These data were used to study the

relationship between rust on leaves at different positions and mean rust severity per tiller/plant, as well as to evaluate the performance of the above model. The equation predicted leaf rust severity on individual leaves from the whole plant rust severity, and the predicted severities correlated very well with the observed severity ( $r = 0.85-0.99$ ). The severity of leaf rust on flag (F) and F-1 leaves was lower than on F-2 and F-3 leaves. The slopes between any two successive points on the disease progress curves for individual leaves were significantly different from each other, indicating the influence of the amount of inoculum available for different leaf layers and the time of leaf emergence.

*Additional keywords:* Crop model, model coupling, *Puccinia recondita* f. sp. *tritici*, quantitative epidemiology, simulation.

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Recent interest in simulation modeling has resulted in many models to simulate host growth and disease development for different crops (8,17) and diseases (2). Some cereal crop models simulate plant growth by leaf development at different positions on plants (8). Many disease models simulate the overall growth of the pathogen population on a crop, and a few models operate at the level of individual colonies. Thus, the crop growth models and the epidemiological models operate at different levels of the crop system hierarchy.

To study the effects of foliar pathogens on the crop in a simulation model, specific disease information on different leaf layers, with their position along the stem, size, and time of emergence, is needed when combining the crop model with the epidemic model. Such coupling and the application of a crop-disease model is restricted by the unavailability of such specific data. The data are not readily available because, in conventional

crop disease surveys, overall disease on a crop is recorded (7). If a method were developed to estimate foliar diseases on individual leaves from the whole plant disease data, the present deficiency in the application of crop-pest interaction models could be overcome. Such a method would serve as an interface between crop growth simulators and disease simulators and could provide a basis for using the available disease databases in crop-disease modeling. A need for this methodology also was expressed at a recent workshop on modeling crop-pest interactions (7).

The first objective of our study was to develop a theoretical model that could be used to estimate the severity of the leaf rust on individual leaves from the whole plant disease severity or from the whole plant disease progress curve. The second objective of our research was to evaluate model performance by applying the model to 10 sets of data obtained from sequential inoculations of *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* (Eriks. & E. Henn.) D. M. Henderson on the wheat cultivar McNair 1003, which indirectly evaluates the model applicability to the available disease data bases for use in crop-pest interaction models.

## MATERIALS AND METHODS

**Model development.** We first outline the logic of the model and deduce it for a single tiller of a cereal plant. The same logic can be applied to a cereal crop as a whole.

Considering that there are 1, 2, . . . ,  $n$  leaves on a cereal tiller, the time of emergence for each leaf is  $t_1, t_2, \dots, t_n$ , respectively. The proportions of the foliar disease on the corresponding leaves are  $x_1, x_2, \dots, x_n$ , respectively, and the proportion of disease on the whole tiller is  $X$ .

The model was developed based on the following three fundamental equations:

(a) Development of disease ( $x$ ) is a function of time ( $t$ ), such that  $X_t = f(t)$ ,  $x_{1t} = f(t - t_1)$ ,  $x_{2t} = f(t - t_2)$ , . . . ,  $x_{nt} = f(t - t_n)$ . For the  $i$ th leaf, the disease proportion ( $x$ ) at time  $t$ ,  $x_{it} = 0$  for  $t < t_i$  and  $x_{it} = f(t - t_i)$  for  $t > t_i$ .

(b) Tiller disease is the mean of individual disease proportions of leaves,

$$X_t = [x_{1t} + x_{2t} + \dots + x_{nt}] / n. \quad (1)$$

(c) The logistic equation introduced into plant disease epidemiology by Vanderplank (15) can be modified to achieve our objectives,

$$dx/dt = rx(1 - x), \quad (2)$$

where  $(1 - x)$  is the proportion of leaf per tiller that is healthy, and  $r$  is the proportionality constant commonly referred to as the apparent infection rate (15).

Equation 2 can be written for disease development on the  $i$ th leaf layer as (for detailed derivation, see Appendix)

$$dx_{it}/dt = rX_t(1 - x_{it}), \quad (3)$$

where disease  $x_{it}$  on the  $i$ th leaf at time  $t$  is usually but not necessarily measured on a proportion scale, and a disease asymptote of unity is assumed.

By integrating equation 3 when  $X_t$  and  $r$  are known, we get

$$x_{it} = 1 - \exp[-rX_t(t - t_i)], \quad (4)$$

where  $x_{it}$  is the disease on the  $i$ th leaf at time  $t$ ,  $r$  is the apparent infection rate on the tiller,  $X_t$  is the mean disease on the tiller observed at time  $t$ , and  $t_i$  is the time of the  $i$ th leaf emergence. Equation 4 was used to test model performance by applying it to 10 sets of data obtained from sequential inoculations of McNair 1003 with *P. r. tritici* and to two sets of data on the same cultivar derived from naturally occurring epidemics.

**Data collection.** The data used to test the equation were collected from two experiments conducted during the 1986-87 and 1987-88 wheat-growing seasons at the Louisiana Agricultural Experiment Station Ben Hur Research Farm, Baton Rouge, LA. Experimental details have been described previously (11: experiment I) and are summarized below.

Epidemics were generated on McNair 1003, a soft red winter wheat cultivar susceptible to the prevalent leaf rust pathogen (*P. r. tritici*) populations, by sequential inoculation of the plots with a point source of inoculum at 15-day intervals from 1 February to 15 March 1987 and from 1 December 1987 to 1 March 1988.

In both years, one plot was maintained as a control in which the epidemic was initiated with the natural inoculum. All plots were separated by a 2.5-m strip of a leaf rust-resistant cultivar, Florida 302, to reduce plot interactions. The methodology of inoculation has been described previously (11). Leaf rust progress was assessed in each plot at 5- to 7-day intervals on individual leaves of 10 randomly selected tillers per plot using the modified Cobb's scale (6). Rust severities were estimated on each leaf of the tiller from the time the first pustules were noticed, and estimations continued until leaf senescence. The dates of emergence of flag (F), F-1, F-2, and F-3 leaves were recorded for each plot. For the purpose of clarity, only the results from two dates of inoculation are presented.

**Data analysis.** Leaf rust severities on all leaves were transformed to proportions for further analysis. To study the relationship between leaf rust progress on individual leaves and on the tiller, proportions of leaf rust on the tiller, F-3, F-2, F-1, and F were plotted against days after inoculation.

According to equation 4, at any given time the amount of disease on different leaf layers is dependent on the time of emergence of the corresponding leaves and the amount of available inoculum. When this is true, the slope (absolute rate of disease increase) between any two successive points of the disease progress curve for different leaves would be different. To examine this, the slopes ( $\Delta x_i / \Delta t$ ) or change of disease between the different assessment intervals ( $\Delta t$  is 5-7 days) for the  $i$ th leaf were calculated using the equation

$$\Delta x_i / \Delta t = [x_{i(t+1)} - x_{i(t)}], \quad (5)$$

where  $x_{i(t)}$  and  $x_{i(t+1)}$  are the proportions of leaf rust on the  $i$ th leaf at time  $t$  and on the  $i$ th leaf at time  $t + 1$ , respectively. Analysis of variance was conducted on the slopes for different inoculations. The slopes were plotted against time for individual leaves at different positions as well as for the tiller. The point of origin of the curves for individual leaves was equivalent to the time lag between the emergence of corresponding leaves.

In equation 2, we assumed that  $r$  was the same for all leaf layers. To test this assumption on our data, apparent infection rates on all leaves for different periods of disease assessment were calculated by regression analysis of the logit-transformed leaf rust proportions and time after inoculation. Variance analysis was conducted using the apparent infection rates as dependent variables and leaf layers as independent variables. Significance of the models was evaluated using  $F$  tests (10).

Equation 4 was used to determine the predicted leaf rust severities on individual leaves for all inoculation dates in both years. Calculated leaf rust severities were regressed against observed severities on individual leaves to examine the model performance. The performance was evaluated using coefficients of determination. All analyses were performed using SAS (9).

## RESULTS

**Leaf rust development on individual leaf layers.** Leaves on McNair 1003 emerged at 6- to 9-day intervals under the experimental conditions in Louisiana (Table 1). On the initial dates of leaf rust assessment, leaf rust was present on F-3, F-2, and F-1 leaves in 1986-87, and leaf rust was present on all leaves

TABLE 1. Growth stage at inoculation of wheat cultivar McNair 1003 and dates of leaf emergence for the two representative dates of inoculation

Year	Inoculation		Leaf emergence			
	Date	GS <sup>a</sup>	Flag (F)	F-1	F-2	F-3
1986-87	1 February	3	19 February	11 February	4 February	28 January
	1 March	5	19 February	11 February	4 February	28 January
1987-88	1 February	6	31 January	25 January	18 January	10 January
	1 March	9	31 January	25 January	18 January	10 January

<sup>a</sup>Feekes growth stages (11).

in 1987-88 (Fig. 1). Proportions of leaf rust were highest for the F-3 leaf on all dates of disease assessment (Fig. 1). The proportions of leaf rust decreased with the increase in the position of leaves (Fig. 1). The shapes of the disease progress curves for the individual leaves and for the tiller were very similar except that the point of infection occurred earlier for the F-3 leaf (Fig. 1). During 1986-87 season all leaves senesced at the same time; in 1987-88 the F leaf senesced 1 wk after the other leaves.

**Absolute rate of disease progress on individual leaf layers.** The length of the lag in the curves for absolute rates on individual leaves is equivalent to the time of emergence of individual leaves (Fig. 2). For all leaves in plots inoculated in February of both years, the absolute rate of progress was near 0 for 5 wk. The absolute rate increased earlier for F-3, followed by F-2, F-1, and F (Fig. 2A and B). However, for plots inoculated on 1 March in both years, increases in the absolute rates were noticed from the beginning for all leaves with the exception of F. As the epidemic progressed temporally, the absolute rates increased to a maximum and then declined. The curves for the absolute rates were parabolic for all leaves later in the season. The magnitude of the distance between the arcs decreased with the increase in the height of the leaf layers (Fig. 2). The maximum rates of absolute disease progress for individual leaves occurred at intervals equivalent to the length of the lag.

At any given time, the absolute rate of leaf rust increase for the individual leaves was significantly different among different leaf layers during the epidemic, except for approximately 40% of the time intervals. The *F* tests were significant for most time intervals for the representative dates of inoculation in each of the 2 yr (Table 2).

**Apparent infection rates on individual leaves and the tiller.** Early in the season, the apparent infection rates were low for

all of the leaves and the tiller (Table 3). The rates did not increase linearly with time. They fluctuated with time, reaching a maximum during midseason and declining towards the end of the season. Analysis of variance was conducted to examine if these fluctuations were statistically significant. The apparent infection rates on different leaf layers and the tiller at any given time were not significantly different from each other (Table 4). The *F* tests were not significant for apparent infection rates pooled over individual leaves for all individual dates of inoculations in each of the 2 yr (Table 4). The *F* test for apparent infection rates pooled over all dates of inoculations was significant only for the 1986-87 season (*df* = 179); it was not significant for the 1987-88 season (*df* = 408) (Table 4).

**Results of prediction.** The procedure of estimating leaf rust severities on individual leaves from tiller/plant rust severity is graphically illustrated in Figure 3. Estimated leaf rust severities on individual leaves closely matched with the observed severities. The predictions were highly significant ( $P = 0.0001$ ) for all leaves in plots inoculated on different dates in both years (Table 5). The coefficients of determination for the prediction equations varied between 0.73 and 0.99. In most cases, the equation estimated leaf rust severities on F-3 and F-2 leaves better than on F-1 and F leaves. The intercepts ( $\beta_0$  in Table 5) were close to 0 for the different leaves, and the regression coefficients ( $\beta_1$  in Table 5) were close to 1.

## DISCUSSION

The model described in this paper calculates disease severities on individual leaves from cereal crop whole plant/tiller disease severity data. The model can be used to estimate disease for the whole epidemic period or between any two given intervals. The

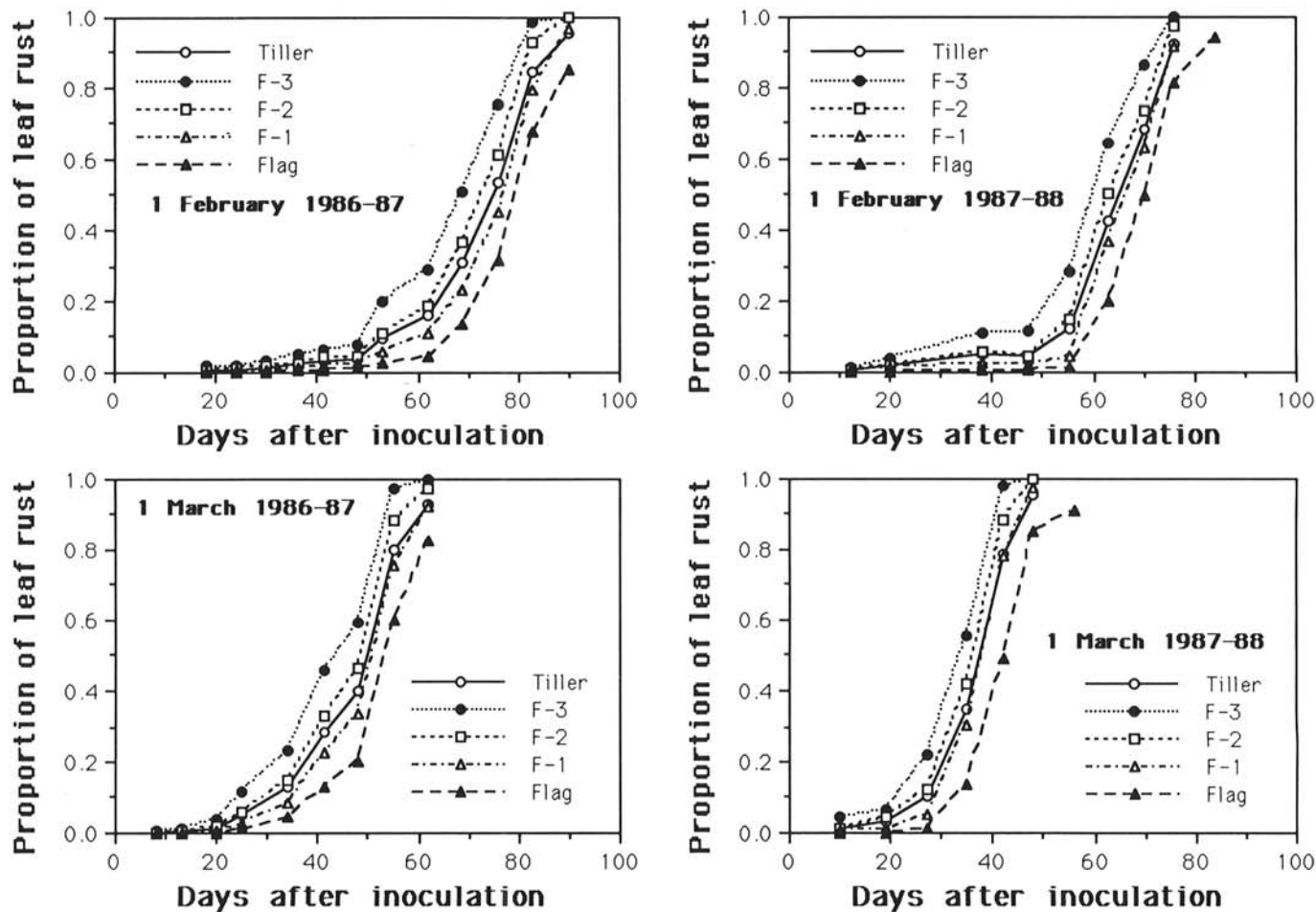


Fig. 1. Progress of leaf rust on individual leaves and the tiller following different dates of inoculation during the 1986-87 and 1987-88 wheat-growing seasons.



model is significant in that it provides a method to fill an important gap in coupling cereal crop growth models with epidemiological models that do not simulate disease development on individual leaf layers. It also serves as a tool to use the disease data collected by conventional disease surveys or whole plant disease data in a crop-disease simulation model.

In wheat, the amount of disease on the top three leaves determines the magnitude of yield (13). Therefore, to study the effects of foliar pathogens on crop yield, disease data on different leaves are necessary. These detailed data are not readily available because conventional disease surveys record overall crop disease (7) and their data is of limited use in a simulation model. The model presented here has the potential to overcome this deficiency by serving as an interface between the data collected in disease surveys and the requirements of a comprehensive simulation model aimed at studying crop-pest interactions.

The logistic equation assumes a constant  $r$  (15). Vanderplank (15) also introduced a biologically realistic rate parameter ( $R$ ) that accounts for the diseased plant tissue actually contributing to the progression of the epidemic. However, Vanderplank (16) disassociated himself from the logistic equation because of the implications of a presumed constant  $r$ . The  $r$  values for leaf rust progress on different leaf layers and the tiller were constant at most disease assessment intervals in plots inoculated at various times during the 2 yr of experimentation (Table 4). Most differences in  $r$  among leaf layers occurred early in the epidemics. This may be attributable to the greater observational error when severities are low. Therefore, it is mathematically reasonable to use  $r$  from the disease progress on the plant/tiller to estimate disease severities on individual leaves as demonstrated in our study. In our model, the amount of inoculum was the same for

each leaf layer as demonstrated by  $rX(1 - x_i)$ , where  $X$  is the proportion of disease on the tiller and the infectious part of which produces the inoculum. The model simulates the commonly asserted fact that inoculum exchange occurs among different leaf layers. In the component  $rX(1 - x_i)$ ,  $X < x_i$  for layers initiated earlier and  $X > x_i$  for layers initiated later in the season. When  $X < x_i$ , some inoculum from lower leaf layers (or leaf layers initiated earlier) will move to the leaf layers initiated subsequently for infection.

In most situations, the inoculum arrives before leaf emergence, and the infections remain latent on the emerged leaves. In Louisiana, the epidemic onset time varies from early December to February, depending on the source of primary inoculum (12). The leaf rust epidemics in our study (11) were generated to cover this range by inoculating the plots at different times. Each year, epidemics in one plot developed from the natural inoculum. The model using the tiller disease severities from different inoculations predicted the leaf rust severities on individual leaves well. We have outlined an approach to predict disease severities on individual leaves from the plant/tiller disease data and have demonstrated its applicability by using it on the leaf rust data. The applicability of the model to the available data bases depends on knowledge of time of leaf emergence as well as uniform susceptibilities of different leaves, which is a cultivar-specific characteristic. The disease on the tiller is usually calculated as an unweighted mean of disease on individual leaves. However, using the mean weighted for different leaf sizes may improve the prediction on individual leaves.

While the  $r$  values were constant, the slopes (instantaneous disease growth rate) calculated using equation 5 (the absolute rates) were variable for different leaves (Table 2). The absolute

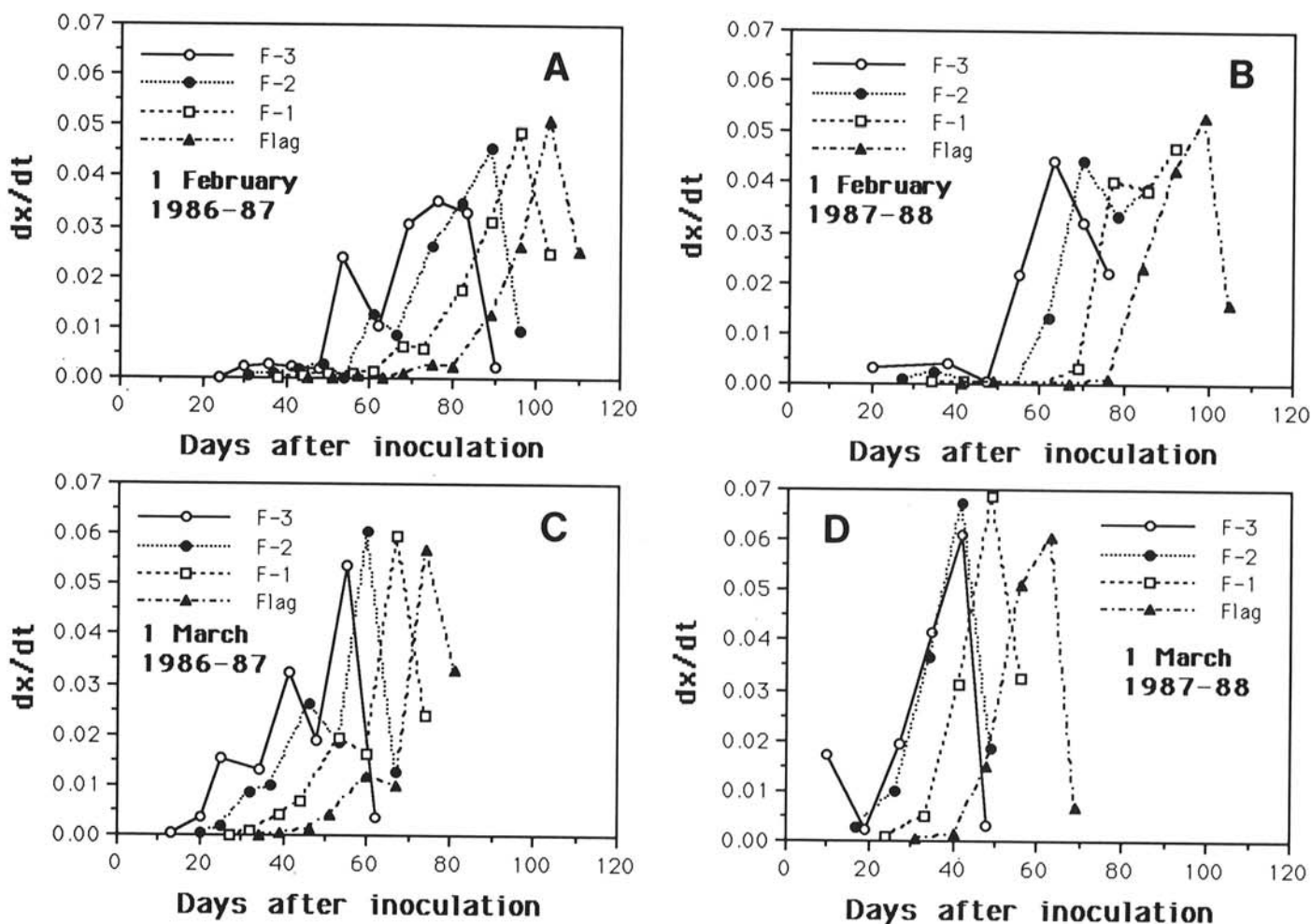


Fig. 2. Relationship between time and absolute rate of wheat leaf rust progress on individual leaves in four plots inoculated on 1 February or 1 March of 1987 or 1988.

rates are controlled by amount of inoculum and time (2). In our model, both of these factors were accounted for by the developmental times of different leaves.

Simulation of disease focus expansion is extremely complex (14) and, therefore, most simulation models do not include this component. Our model assumes homogeneous distribution of the disease in the crop and calculates the severity of the disease based on the time of emergence of individual leaves. Jeger (3) deduced relationships between Vanderplank's (15) apparent infection rate ( $r$ ) and the infection rate ( $R$ ), accounting for the time lag attributable to the latent period. For simulation models using  $R$ , our model can be modified to calculate  $R$  using the available techniques (3).

An idealized prediction equation would have an intercept of 0 and a slope of unity (5). In the prediction equations for individual leaves from our model, the intercepts varied from -0.047 to 0.189, and the slopes varied from 1.06 to 1.25 (Table 5). Even though the model predictions were almost always better for F-3 and F-2 leaves, the model does provide satisfactory results on all leaves. This could be due to the fluctuations in  $r$  during the season. Therefore, when applying the model,  $r$  values may be calculated for each interval of the disease progress curve to estimate the severity of each layer more precisely. Johnson and Teng (4) also emphasized using infection rate parameter ( $r$ ) as a variable in modeling early blight of potato to describe more realistically the crop and disease interaction. Similarly, to reflect the true infection rates on the late-appearing host tissue, Berger's (1) daily cohort model considers the daily increase in host tissue in calculating infection rates.

TABLE 2. Analysis of variance<sup>a</sup> for the absolute rate ( $\Delta x_i/\Delta t$ ) of leaf rust increase on leaves at different positions at given time intervals in two inoculation dates during 1986-87 and 1987-88 wheat-growing seasons

Year	Inoculation date	Time interval (days)	$P > F$	Significance <sup>b</sup>
1986-87	1 February	18	0.445	NS
		24	0.954	NS
		30	0.039	*
		36	0.016	**
		41	0.091	NS
		48	0.716	NS
		53	0.029	*
		62	0.009	**
		69	0.007	**
		76	0.051	*
1986-87	1 March	8	0.364	NS
		13	0.078	NS
		20	0.033	*
		25	0.024	*
		34	0.002	**
		41	0.001	**
		48	0.091	NS
		55	0.663	NS
		62	0.009	**
		76	0.089	NS
1987-88	1 February	38	0.026	*
		47	0.954	NS
		55	0.026	*
		63	0.127	NS
		70	0.023	*
		76	0.031	*
		90	0.015	*
1987-88	1 March	19	0.118	NS
		27	0.025	*
		35	0.049	*
		42	0.545	NS
		48	0.015	*

<sup>a</sup>Rate was the dependent variable and position number was the independent variable.

<sup>b</sup>Significance of  $F$  test at probabilities of 0.05 and 0.01 for \* and \*\*, respectively. NS indicates not significant.

TABLE 3. Apparent infection rates of leaf rust progress on the tiller and individual leaves at different time intervals after inoculation for two representative dates of inoculation during 1986-87 and 1987-88 wheat-growing seasons

Year	Date inoculated	Time (days)	Apparent infection rates <sup>a</sup>						
			Flag	F-1	F-2	F-3	Tiller		
1986-87	1 February	24	0.000	0.047	0.051	-0.009	0.020		
		30	0.133	0.110	0.070	0.091	0.089		
		36	0.295	0.095	0.080	0.073	0.102		
		41	0.018	0.054	0.081	0.053	0.071		
		48	0.139	0.062	0.003	0.040	0.043		
		53	0.149	0.167	0.192	0.229	0.199		
		62	0.072	0.078	0.071	0.072	0.084		
		69	0.165	0.127	0.134	0.131	0.138		
		76	0.157	0.142	0.142	0.159	0.277		
		83	0.215	0.221	0.439	0.434	0.351		
1986-87	1 March	90	0.147	0.282	...	...	0.196		
		13	0.000	0.000	0.139	0.162	0.140		
		20	0.021	0.062	0.114	0.236	0.163		
		25	0.028	0.076	0.169	0.332	0.246		
		34	0.034	0.057	0.089	0.133	0.108		
		41	0.047	0.088	0.137	0.209	0.142		
		48	0.032	0.062	0.087	0.118	0.072		
		55	0.177	0.303	...	...	0.260		
		62	0.205	0.333	...	...	0.269		
		1987-88	1 February	20	0.051	0.055	0.075	0.120	0.098
38	0.069			0.043	0.068	0.058	0.059		
47	-0.013			-0.018	-0.033	0.004	-0.009		
55	0.115			0.108	0.152	0.115	0.124		
63	0.335			0.262	0.150	0.101	0.155		
70	0.132			0.079	0.054	0.043	0.067		
76	0.083			0.061	0.046	0.024	0.050		
84	0.018			...	...	...	0.018		
1987-88	1 March			19	0.218	0.102	0.108	0.046	0.071
				27	0.181	0.173	0.133	0.151	0.149
		35	0.291	0.222	0.153	0.114	0.154		
		42	0.186	0.137	0.108	0.082	0.115		
		48	0.092	0.037	0.020	0.003	0.033		
		56	0.008	...	...	...	0.008		

<sup>a</sup>Mean of three replicates.

<sup>b</sup>Leaves senesced.

TABLE 4. Analysis of variance for the apparent infection rates of wheat leaf rust progress (dependent variable) on different leaves (independent variable) pooled over all dates of inoculations and for all individual dates of inoculations in 1987 and 1988

Source of variation	Year	df	Mean square	$P > F$
Pooled	1986-87	4	0.0193	0.0229
Error	1986-87	175	0.0066	
1 February	1986-87	4	0.0038	0.2817
Error	1986-87	50	0.0029	
15 February	1986-87	4	0.0074	0.3840
Error	1986-87	45	0.0069	
1 March	1986-87	4	0.0097	0.5704
Error	1986-87	22	0.0132	
15 March	1986-87	4	0.0015	0.7582
Error	1986-87	25	0.0033	
Pooled	1987-88	4	0.0098	0.5169
Error	1987-88	404	0.0120	
1 December	1987-88	4	0.0016	0.9937
Error	1987-88	71	0.0021	
15 December	1987-88	4	0.0015	0.8803
Error	1987-88	63	0.0050	
1 January	1987-88	4	0.0012	0.9847
Error	1987-88	47	0.0128	
15 January	1987-88	4	0.0009	0.9882
Error	1987-88	42	0.0114	
1 February	1987-88	4	0.0059	0.5237
Error	1987-88	32	0.0073	
15 February	1987-88	4	0.0052	0.5143
Error	1987-88	22	0.0062	
1 March	1987-88	4	0.0057	0.3396
Error	1987-88	22	0.0047	

All of the models developed so far estimate population level(s) from elements in the lower levels of hierarchy. Our work is unique because it uses the population level to estimate elements in the lower levels of hierarchy. Our model provides a shortcut to estimate disease severities on individual leaves in cereals from the whole plant/tiller disease severity data. However, a limitation of the model is that it is not applicable to splash-dispersed diseases because the spread of such diseases depends on rain events. Applying the model to these diseases would violate one of the assumptions (the environment, with respect to all properties that perceptively affect the organisms, is uniformly constant in time) of the logistic equation (15).

## APPENDIX

The proof for the equation  $dx_i/dt = rX(1 - x_i)$  (eq 3 in the text) is provided below.

The equation can be proved by both partition and synthesis approaches or by the relative value of disease  $x$  and absolute value of diseased leaf.  $N$  and  $X$  used below represent the population number of diseased leaves or incidence/severity per leaf.

Let there be  $n_i$  diseased leaves at layer  $i$  and let  $x_i$  be the proportion of disease at layer  $i$ , where  $i = 1, 2, \dots, m$  and  $n_{\max}$  is the maximum number of leaves at a layer. Here  $m$  represents maximum layers of leaves and is not to be confused with  $n$ , which is the number of diseased leaves.

We have known conditions:

$$dX/dt = (dx_1/dt + dx_2/dt + \dots + dx_m/dt)/m \quad (1a)$$

$$X = (x_1 + x_2 + \dots + x_m)/m \quad (1b)$$

$$dN/dt = dn_1/dt + dn_2/dt + \dots + dn_m/dt. \quad (2)$$

**Proof 1.** Synthesis with relative disease value.

$$dx_1/dt + dx_2/dt + \dots + dx_m/dt = rX(1 - x_1) + rX(1 - x_2) + \dots + rX(1 - x_m) = rX(m - (x_1 + x_2 + \dots + x_m))$$

Divide both sides by  $m$ .

$$(dx_1/dt + dx_2/dt + \dots + dx_m/dt)/m = rX(m - (x_1 + x_2 + \dots + x_m))/m$$

From equations 1a and b, we have

$$dX/dt = rX(1 - X).$$

**Proof 2.** Partition with absolute value of diseased leaves.

$$\begin{aligned} dN/dt &= rN((N_{\max} - N)/N_{\max}) \\ &= rN(mn_{\max} - (n_1 + n_2 + \dots + n_m))/mn_{\max} \\ &= rN((n_{\max} - n_1)/n_{\max} + (n_{\max} - n_2)/n_{\max} + \dots + (n_{\max} - n_m)/n_{\max})/m \\ &= rN((n_{\max} - n_1)/mn_{\max} + (n_{\max} - n_2)/mn_{\max} + \dots + (n_{\max} - n_m)/mn_{\max}) \end{aligned}$$

From equation 2,

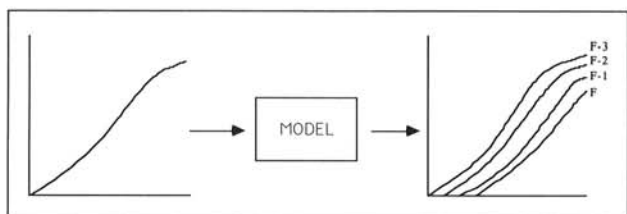
$$\begin{aligned} dn_1/dt + dn_2/dt + \dots + dn_m/dt \\ = rN((n_{\max} - n_1)/mn_{\max} + (n_{\max} - n_2)/mn_{\max} + \dots + (n_{\max} - n_m)/mn_{\max}) \end{aligned}$$

So,  $dn_i/dt = rN((n_{\max} - n_i)/mn_{\max})$ .

Dividing both sides by  $n_{\max}$ , we have  $dx_i/dt = rX(1 - x_i)$ .

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**Fig. 3.** Disease progress curves for individual leaves derived from the disease progress curve obtained from the whole plant severity data, using  $x_{it} = 1 - \exp[-rX_t(t - t_i)]$ , where  $x_{it}$  is the disease on the  $i$ th leaf at time  $t$ ,  $r$  is the apparent infection rate on the tiller,  $X_t$  is the mean disease on the tiller observed at time  $t$ , and  $t_i$  is the time of leaf emergence.

**TABLE 5.** Summary regression analysis results of predicting proportions of leaf rust severities on different wheat leaves using the model  $x_{it} = 1 - \exp[-rX_t(t - t_i)]^a$

Year	Date inoculated	Leaf	Mean square	$P > F$	$R^2$ (adjusted)	$\beta_0 \pm SE$	$\beta_1 \pm SE$
1986-87	1 February	F-3	57.43	0.0001	0.97	$-0.047 \pm 0.005$	$1.11 \pm 0.031$
		F-2	50.39	0.0001	0.97	$-0.010 \pm 0.005$	$1.08 \pm 0.038$
		F-1	44.14	0.0001	0.93	$0.027 \pm 0.007$	$1.09 \pm 0.047$
		Flag	38.30	0.0001	0.88	$0.063 \pm 0.008$	$1.15 \pm 0.057$
1986-87	1 March	F-3	49.07	0.0001	0.91	$-0.063 \pm 0.008$	$1.06 \pm 0.019$
		F-2	43.79	0.0001	0.93	$-0.040 \pm 0.009$	$1.11 \pm 0.019$
		F-1	39.84	0.0001	0.92	$-0.011 \pm 0.009$	$1.16 \pm 0.044$
		Flag	35.33	0.0001	0.88	$0.027 \pm 0.011$	$1.25 \pm 0.056$
1987-88	1 February	F-3	34.84	0.0001	0.93	$0.021 \pm 0.036$	$1.16 \pm 0.068$
		F-2	31.58	0.0001	0.86	$0.089 \pm 0.045$	$1.16 \pm 0.096$
		F-1	28.14	0.0001	0.79	$0.139 \pm 0.051$	$1.16 \pm 0.124$
		Flag	29.88	0.0001	0.73	$0.189 \pm 0.057$	$1.06 \pm 0.127$
1987-88	1 March	F-3	28.83	0.0001	0.98	$-0.103 \pm 0.024$	$1.09 \pm 0.040$
		F-2	27.77	0.0001	0.99	$-0.051 \pm 0.015$	$1.08 \pm 0.027$
		F-1	27.11	0.0001	0.99	$-0.014 \pm 0.013$	$1.07 \pm 0.026$
		Flag	27.14	0.0001	0.96	$0.032 \pm 0.025$	$1.13 \pm 0.050$

<sup>a</sup> $x_{it}$  is the disease on the  $i$ th leaf at time  $t$ ,  $r$  is the apparent infection rate on the tiller,  $X_t$  is the mean disease on the tiller observed at time  $t$ , and  $t_i$  is the time of leaf emergence.

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