# Calculation of Apparent Infection Rate in Plant Diseases: Development of a Method to Correct for Host Growth

Ajjamada C. Kushalappa and Artémio Ludwig

Visiting professor (titular), Departamento de Fitopatologia, and systems analyst, Centro de Processamentos de Dados, respectively, Universidade Federal de Viçosa, Viçosa, MG, 36 570, Brazil.

Appreciation is expressed to J. C. Zadoks and K. Leonard for suggestions during the preparation of the manuscript. Accepted for publication 12 November 1981.

#### ABSTRACT

Kushalappa, A. C., and Ludwig, A. 1982. Calculation of apparent infection rate in plant diseases: Development of a method to correct for host growth. Phytopathology 72:1373-1377.

The use of the logistic growth model to calculate the apparent infection rate (r) and to characterize plant disease progress was developed by Vanderplank; however, its use resulted in empirical problems. In various coffee rust epidemics, the estimation of Vanderplank's r as well as his  $\rho$  (infection rate corrected for host growth) for intervals within a disease progress curve often gave negative values. These values resulted from rapid host growth, which reduced the cumulative proportion of disease (x). We developed a new method to adequately correct for host growth in calculating a corrected infection rate  $(\rho')$ . Similar correction for the

exponential, monomolecular, and Gompertz growth models also are described. All of these growth models have a basic requirement that the asymptote is constant over the course of the epidemic  $(A/Y_{max} = 1, \text{in which } A$  is the maximum diseased area and  $Y_{max}$  is the maximum host area, and it is assumed that all host area can become diseased by the end of the epidemic). In our method of calculating the intrinsic growth rate of X, the diseased area as a proportion of variable host mass is corrected by a factor  $(Y_1/Y_{max})$ , thus representing X as proportion of the asymptote  $(A \text{ or } Y_{max})$ .

Additional key words: Coffea arabica, epidemiology, Hemileia vastatrix.

Vanderplank (14) suggested the calculation of apparent (logistic) infection rate, r, to quantify the rate of disease development. The r value has been used by plant pathologists to evaluate data on effectiveness of sanitation, fungicide application, and cultivar resistance (2,12,14,15).

Vanderplank proposed two methods to calculate r: one is based on the slope of the regression line obtained by regressing logit x or  $\log_{c}(x/(1-x))$  over time; in the second method the x is estimated at two times during the epidemic and r is the difference in logit x divided by time interval, that is  $r = (\log it x_2 - \log it x_1)/(t_2 - t_1)$ .

Vanderplank suggested quantification of disease as the proportion of host tissue that is diseased at a given time, t,  $(x_t)$ , with  $0 \le x_t \le 1$ . Here the maximum proportion of diseased tissue is 1;  $A/Y_{\text{max}} = 1$ , in which  $Y_{\text{max}}$  is the maximum amount of host tissue and A is the maximum amount of diseased tissue, assuming that at the end of the epidemic all the host is diseased ( $Y_{\text{max}} = A$ ). With the above assumptions,  $Y_{\text{max}}$  may be regarded as constant during the course of an epidemic. However, during the course of an epidemic, not only disease but also the amount of host tissue usually increases. Vanderplank (14, p. 94) stated that it is possible for x to decrease or to be "diluted" by host growth while the disease is actually increasing. Consequently, he suggested a formula to calculate infection rate corrected for host growth ( $\rho$ ):

$$\rho = \frac{1}{t_2 - t_1} \ln \left[ \frac{mx_2 (1 - x_1)}{x_1 (1 - x_2)} \right]$$
 (1)

in which  $m = y_2/y_1$ , y being the host mass. When his formulae were used to estimate r and  $\rho$  at various intervals within a disease progress curve, however, not only r but also  $\rho$  frequently gave negative values. Consequently Kushalappa (7) suggested a new equation to calculate the rate of disease  $(\rho'')$  more adequately corrected for host growth or leaf formation:

$$\rho'' = \frac{1}{t_2 - t_1} \ln \left[ \frac{x_2 (1 - x_1 m')}{x_1 m' (1 - x_2)} \right]$$
 (2)

in which,  $m' = Y_1/Y_2$ , Y being cumulative number of leaves (or host area).

Vanderplank suggested the logistic transformation for compound interest diseases and monomolecular transformation for simple interest diseases. Several authors, however, have cautioned against adopting any transformation until the disease progress curves have been evaluated for their suitability to various transformations (1,5,12).

In this study we report a method for monitoring accurately the growth of a host, and the progress of disease, evidence of a decrease in x with an increase in host tissue, and a procedure to calculate the rate of disease increase corrected for host growth for interval  $(\rho'')$  as well as for the entire disease progress curve  $(\rho')$ .

#### THE MODEL

Collecting data for evaluation of the model. Monitoring disease progress. The data used were obtained from a study designed to elaborate a prediction model for coffee rust development. The progress of rust (Hemileia vastatrix Berk & Br.) on one hectare of Coffea arabica L. 'Mundo Novo' in Viçosa, in Minas Gerais was quantified by marking four branches in each of 15 trees selected at random. Data for individually mapped leaves on each branch were noted at 14-day intervals from September 1978 to August 1980. Notation included presence or fall of a leaf on a given node, and presence and absence of rust. The leaf area was estimated using a diagrammatic scale representing 10, 30, 50, 70, and 90 cm<sup>2</sup> surface area (A. C. Kushalappa, unpublished). The rust severity was scored as proportion of leaf area rusted using a diagrammatic scale (9). The data were analyzed using a computer program LEAFAL (10) to obtain the number of current and fallen leaves with and without rust, and leaf area rusted at each date of reading (these parameters could also have been calculated manually). The disease progress was monitored as the cumulative proportion of leaves or leaf area rusted  $(x_t)$ . At each time, t,  $x_t$  was calculated from (11):

$$x_t = \frac{X_{ct}}{Y_{ct}} = \frac{X_{\text{cut}} + X_{\text{fct}}}{Y_{\text{cut}} + Y_{\text{fct}}}$$
(3)

in which,  $X_t$  is the number of leaves or total proportion of leaf area rusted;  $Y_t$  is the number of leaves; the subscripts: c is the

cumulative, cu is the current or present on a given day, and fc is the cumulative total removed by leaf fall (present on  $t_1$  fallen by  $t_2$ ).

Monitoring host growth. The host growth was monitored as the cumulative proportion of the maximum leaf area or the leaves formed  $(y_t)$ . The  $y_t$  was calculated (11):

$$y_t = Y_{ct}/Y_{\text{max}}$$
 in which  $Y_{ct} = Y_{cut} + Y_{fct}$  (4)

in which,  $Y_{\text{max}}$  is cumulative total number of leaves or leaf area formed by the end of the study. The  $Y_{ct}$  was determined as described above. Throughout this study, capital letters are used in equations to indicate number and small letters to indicate proportion, except the K, r, and  $\rho$  which are units per time.

Calculation of  $\rho'$ , the corrected rate of disease increase. Mathematics of the model. The logistic growth model is obtained from the differential equation

$$dX/dt = rX(A-X)$$

which yields the logistic growth model:

$$X_i = A/(1 + be^{-kt})$$

in which  $X_i$  is the diseased area, A is asymptote or the maximum diseased area to which X can attain in the disease progress curve sought, k is a constant equal to rA where r is apparent infection rate (14), t is time, and b is the initiating position parameter equal to  $(A/X_0) - 1$  in which  $X_0$  is diseased area at  $t_0$ . This equation can be applied to host growth by replacing the diseased area by host area. After further derivation:

$$k = rA = \frac{1}{t_2 - t_1} \left[ \ln \frac{X_2}{A - X_2} - \ln \frac{X_1}{A - X_1} \right]$$
 (5)

Here, X increases asymptotically to A. When X is divided by A, the asymptote or the maximum to which the X can increase in the disease progress curve sought, then

$$k = r \frac{A}{A} = \frac{1}{t_1 - t_2} \left[ \ln \frac{\frac{X_2}{A}}{\frac{A}{A} - \frac{X_2}{A}} - \ln \frac{\frac{X_1}{A}}{\frac{A}{A} - \frac{X_1}{A}} \right]$$
 (6)

For  $x_i = X_i/A$ ,

$$k = r$$
 (1) =  $\frac{1}{t_2 - t_1} \left[ \ln \frac{x_2}{1 - x_2} - \ln \frac{x_1}{1 - x_1} \right]$  (7)

In equations 6 and 7 it is assumed that the amount of host tissue, Y, did not increase during the epidemic so that  $A = Y_{\text{max}}$  and X increases asymptotically to  $Y_{\text{max}}$ . Under these conditions in which host area is constant throughout the epidemic, the diseased area may be estimated as the proportion of host area, and equation 7 is similar to that of Vanderplank's apparent infection rate (14).

When the host area itself  $(Y_t)$  increases with time, then the host area available for disease development during the course of an epidemic is less than  $Y_{\text{max}}$ .

In equation 5, when the amount of disease is divided by the amount of host tissue  $(X_t/Y_t)$ , and when  $Y_{\text{max}} > Y_2 > Y_1$  and  $A = Y_{\text{max}}$ , then

$$k' = r \quad \frac{A}{Y_{\text{max}}} = \frac{1}{t_2 - t_1} \left[ \ln \frac{\frac{X_2}{Y_2}}{\frac{A}{Y_2} - \frac{X_2}{Y_2}} - \ln \frac{\frac{X_1}{Y_1}}{\frac{A}{Y_1} - \frac{X_1}{Y_1}} \right]$$
(8)

Here,  $k' \neq k = r(A/A)$ .

When  $x_t$ , the proportion of host area diseased, is represented as  $X_t/Y_t$  the derivatives become very complex and no simple solution

as in equation 7 is possible because  $(A/Y_2)/(A/Y_{\text{max}}) \ge 1$ . However, if X is expected to increase asymptotically to  $Y_{\text{max}}$  independent of host growth, then  $A = Y_{\text{max}} = Y_f$ , and equation 8 = equation 7. Here r is an intrinsic growth rate of X and not of the diseased proportion of the variable host tissue. However, this would call for the estimation of diseased area  $(X_f)$ .

Equation 8 allows estimation of the diseased area as proportion of variable host area  $(X_t/Y_t)$ . The value  $X_t/Y_t$  can be corrected for variable host area by multiplying it with a factor  $(Y_t/Y_{max})$ . When this is done and the corrected disease proportion is represented as a proportion of the asymptote as in equations 6 and 7, equation 8 yields:

$$k' = r'(1) = \rho' = \frac{1}{t_2 - t_1} \left[ \ln \frac{x_2 y_2}{1 - x_2 y_2} - \ln \frac{x_1 y_1}{1 - x_1 y_1} \right]$$
 (9)

in which  $x_t = X_t/Y_t$ ; and  $y_t = Y_t/Y_{max}$ . Note: in equation 9, r'(1) = r  $(A/Y_{max}) = \rho'$ , whereas in equation 7 the r(1) = r(A/A) = r. Here,  $x_t$  can be estimated as the proportion of variable host area diseased (3,5,9) and  $y_t$  is calculated by  $Y_t/Y_{max}$ , in which case the host mass  $(Y_t)$  is estimated at time, t. In equation 9, the  $x_ty_t$  increases asymptotically to 1 and, hence, logit  $(x_ty_t)$  can be plotted or regressed against time.

In equation 9 when  $Y_{\text{max}} = Y_2 > Y_1$  then:

$$k'' = \rho'' = \frac{1}{t_2 - t_1} \left[ \ln \frac{x_2}{1 - x_2} - \ln \frac{x_1 y_1}{1 - x_1 y_1} \right]$$
 (10)

Here,  $y_1 = Y_1/Y_2$  as  $Y_{\text{max}} = Y_2$ .

The equation 10 is equivalent to equation 2 in which  $m' = Y_1/Y_2 = y_1$  (When  $Y_{\text{max}} > Y_2$ , if  $\rho''$  is calculated for different intervals within the disease progress curve then each interval is based on  $Y_{\text{max}}$  and thus is an independent curve by itself). When there is no host growth,  $y_1 = y_2 = 1$ , and equations 9 and 10 are equivalent to equation 7.

With the transformation used in equation 9, the transformed equations for other growth models would be (for derivatives see 1,4,5,14):

Exponential:  $\rho' = (\ln x_2 y_2 - \ln x_1 y_1)/(t_2 - t_1)$ .

Monomolecular:  $\rho' = [\ln(1/(1-x_2y_2)) - \ln(1/(1-x_1y_1))]/[t_2-t_1].$ 

Gompertz:  $\rho' = [(-\ln(-\ln x_2y_2)) - (-\ln(-\ln x_1y_1))]/[t_2 - t_1].$ 

Calculation of host growth rate (K). The host growth was determined as proportion of maximum leaves or leaf area formed based on equation 4. The rate of leaf formation was calculated by adopting various growth models using a FORTRAN computer program (6) (see below). The host growth rate was designated as K because the r is apparent infection rate (14).

Calculation of  $\rho$ ,  $\rho'$ , and  $\rho''$ . The parameters  $\rho$  and  $\rho'$  for various intervals within the disease progress curve were calculated by using equations 1 and 9, respectively. In equation 1, Vanderplank's correction for host growth is  $m = y_2/y_1$ , in which y is the host mass (14). In equation 9,  $y_t$  was determined as the proportion of maximum host mass as in equation 4. Since  $y_1 = Y_1/Y_{\text{max}}$  and  $y_2 = Y_2/Y_{\text{max}}$ , the ratios based on mass or proportion are the same  $(Y_2/Y_1 = y_2/y_1)$ .

The infection rates  $\rho''$ , corrected for host growth for various intervals were also calculated based on equation 10 but when  $Y_2 < Y_{\text{max}}$  (when  $Y_2 = Y_{\text{max}}$  equation 2 = equation 10). In such a case, the correction is incomplete because, unlike  $\rho'$ , the value of  $\rho''$  for various intervals is not based on  $Y_{\text{max}}$ , but instead is based on the variable  $Y_2$ . When  $Y_{\text{max}}$  is not known (as in prediction models)  $\rho''$  instead of  $\rho'$  may be calculated.

The parameter o' for the entire disease progress curve was estimated using a FORTRAN program for different growth models (6) (see below) or based on the slope of the regression line in which  $\log_e(xy/(1-xy))$  or the logit (xy) was regressed against time.

Selection of growth models. The models and the functions used

TABLE 1. The growth rates, residual sum of squares and coefficients of determination for three growth models<sup>2</sup> for leaf formation and rust progress on cultivar Mundo Novo coffee during 1978–1979 and 1979–1980, in Viçosa, MG, Brazil

Host and disease curves	Logistic			Gompertz			Monomolecular		
	k	RSS	R <sup>2</sup>	k	RSS	R <sup>2</sup>	k	RSS	R <sup>2</sup>
1978-1979									
PLR, x	0.1205	0.0604	91.9†	0.069	0.0783	89.5	0.028	0.1535	79.4
PLR, xy	0.142	0.0369	95.9†	0.083	0.0374	95.8	0.028	0.1333	86.2
PLAR, x	0.119	0.00015	93.4	0.028	0.00012	94.3†	0.001	0.00043	80.6
PLAR, xy	0.127	0.00014	93.9	0.03	0.00011	95.5†	0.001	0.00043	83.6
PL, y	0.244	0.00431	99.4	0.204	0.00368	99.5†	0.167	0.00039	
1979-1980				0.20	0.00500	77.5	0.107	0.0071	99.1
PLR, x	0.116	0.1499	86.3†	0.079	0.1876	82.8	0.048	0.2548	76.6
PLR, xy	0.171	0.03037	98.3†	0.117	0.03051	98.2	0.048	0.2348	92.7
PLAR, x	0.066	0.00024	91.3†	0.017	0.00026	90.7	0.002	0.12807	
PLAR, xy	0.083	0.00017	95.7	0.022	0.00011	97.3†	0.001	0.00046	83.1
PL, y	0.36	0.01222	99.1†	0.275	0.0193	98.6	0.197	0.00017	95.6 96.8

For equations of various growth models see text. The parameter k is used as general indicator of the various growth rate  $(r, \rho', K)$  parameters used in the models; x is the uncorrected proportion of diseased tissue used in calculating r, xy is the proportion corrected for host growth used in calculating p', and  $y_i$  is the proportion of maximum host mass used in calculating K, the rate of host growth. RSS is residual sum of squares,  $R^2$  is coefficient of determination and  $\uparrow$  indicates the model that best fits a given host or disease progress curve based on the highest  $R^*$  and/or lowest RSS. PLR and PLAR are proportion of leaves and leaf area rusted, respectively, and PL is y, proportion of leaves formed (based on  $Y_{max}$ ).

to describe the growth of host (cumulative proportion of maximum leaves formed) and progress of disease (cumulative proportion of leaves or leaf area diseased, not corrected and corrected for leaf formation) were as follows:

Monomolecular:  $x = 1 - b * \exp(-kt)$ 

Logistic:  $x = 1/(1 + b * \exp(-kt))$ 

Gompertz:  $x = \exp(-b * \exp(-kt))$ 

in which, x is the proportion of host area diseased (for details of various parameters consult 1,4,5). The FORTRAN program developed by Kuester and Mize (chapter 6 of ref. 6) was used to estimate the parameters of the functions. The method used here was that of Gauz Newton. The curve fitting was done by least square technique. The model that gave minimum residual sum of square and/or the highest coefficient of determination ( $R^2$ ) was selected as the best.

## APPLICATION OF THE MODEL AND DISCUSSION

**Host growth.** The host growth, quantified as proportion of maximum leaves formed  $(y_i)$  followed a Gompertz function in 1978–1979 and a logistic function in 1979–1980 (Table 1). Both the models explained about 99% ( $R^2 = 0.99$ ) of the variation in host growth in both the years.

The host growth based on proportion of maximum leaf area was highly correlated with proportion of maximum leaves formed; the correlation coefficient was r = 0.98 (for 1978–1979). Hence to correct x for host growth, only the proportion of maximum leaves formed was used.

The host growth data are very useful in calculating  $\rho'$  and  $\rho''$ . The value of  $y_t$  may be obtained directly from observed data or may be calculated from a regression equation, logit  $y_t = \text{logit } y_0 + Kt$ . For example, for 1979–1980, logit  $y_t = -1.468 + 0.18 t$ , in which t is time in weeks from September. The value of  $y_t$  can be calculated from logit  $y_t$ ,  $y_t = ((\exp. (\log it y_t))/(1 + \exp. (\log it y_t)))$ .

Disease progress. Infection rates for intervals corrected for leaf formation,  $\rho$ ,  $\rho'$ , and  $\rho''$ . The apparent infection rate (r) for intervals of 14 days, and the rates corrected for leaf formation  $\rho$ ,  $\rho'$ , and  $\rho''$  for the coffee rust epidemic of 1978–1979 are in Table 2. The r values for various intervals within the disease progress curve of 1978–1979 were often negative due to host growth. The negative values persisted even after correcting for host growth using Vanderplank's equation for  $\rho$ . However, no negative values were found when the equations for  $\rho'$  and  $\rho''$  were used. The negative r values were due to dilution of disease proportion (x) during periods

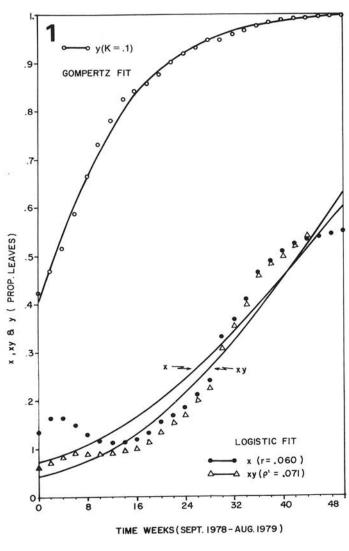
TABLE 2. Apparent infection rates for fortnightly intervals, not corrected and corrected for host growth, for rust on cultivar Mundo Novo coffee plants during the epidemic of 1978–1979 in Viçosa, MG, Brazil

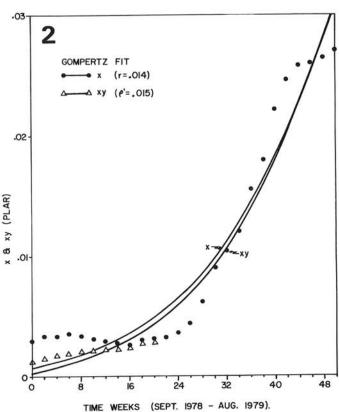
Time interval	Infection rates							
(fortnight)	r	ρ	$\rho'$	ρ"				
1	0.214	0.307	0.285	0.321				
2	-0.006	0.094	0.108	0.113				
3	-0.087	0.039	0.062	0.062				
4	-0.144	-0.020	0.0	0.0				
2 3 4 5	-0.092	0.005	0.013	0.020				
6	-0.070	-0.009	0.0	0.0				
7 8	-0.012	0.048	0.059	0.056				
8	0.067	0.086	0.088	0.088				
9	0.133	0.128	0.122	0.130				
10	0.162	0.188	0.182	0.187				
11	0.103	0.134	0.138	0.140				
12	0.106	0.133	0.139	0.138				
13	0.209	0.216	0.211	0.217				
14	0.127	0.137	0.141	0.140				
15	0.447	0.450	0.439	0.451				
16	0.169	0.188	0.197	0.198				
17	01.68	0.176	0.174	0.181				
18	0.235	0.245	0.250	0.251				
19	0.092	0.097	0.100	0.101				
20	0.094	0.094	0.092	0.094				
21	0.043	0.049	0.056	0.056				
22	0.043	0.046	0.048	0.050				
23	0.019	0.022	0.024	0.025				
24	0.015	0.017	0.020	0.019				
25	0.025	0.025	0.025	0.025				

<sup>&</sup>lt;sup>z</sup>Apparent or logistic infection rates for 14-day intervals, not corrected (r) or corrected for leaf formation  $(\rho, \rho', \rho'')$ . Equations 1, 9, and 10, respectively, (see text) were used to calculate  $\rho$ ,  $\rho'$ , and  $\rho''$ ; the r was based on Vanderplank's equation (14). The rates were calculated for proportion of leaves diseased.

when the formation of new leaves occurred more rapidly than the increase in rusted area or rusted leaves.

In Table 2 the infection rates for intervals of 14 days have been calculated to demonstrate Vanderplank's  $(\rho)$  and improved  $(\rho'$  and  $\rho'')$  correction for host growth. The intervals, however, can vary depending on the information sought. The  $\rho''$ , corrected rate, can be very useful in prediction models, because the increase in disease for certain intervals can be related to factors influencing infection, etc. When necessary,  $x_1$  may be based on current host area diseased (not cumulative) and  $x_2$  may be cumulative for that interval. However, the predicted  $x_1$  for various intervals within a disease progress curve can not be plotted against time, because the denominator, the host area is variable over time ( $Y_1 < Y_{\text{max}}$ ).





Figs. 1 and 2. Host growth and progress of rust, caused by *Hemileia vastatrix*, on Mundo Novo coffee plants during 1978–1979 in Viçosa, MG, Brazil. Disease progress is based on 1, proportion of leaves rusted (PLR) and 2, proportion of leaf area rusted (PLAR), both uncorrected (x) and corrected for leaf formation (xy). Host growth is based on the proportion of the maximum number of leaves formed (y). The observed values and those estimated (line) from the best fit (of three growth models tested: logistic, Gompertz, and monomolecular) are plotted against time. Here K is host growth rate, r is apparent infection rate, and  $\rho'$  is the infection rate corrected for host growth (based on equation 9, see text); the rates are in units per week.

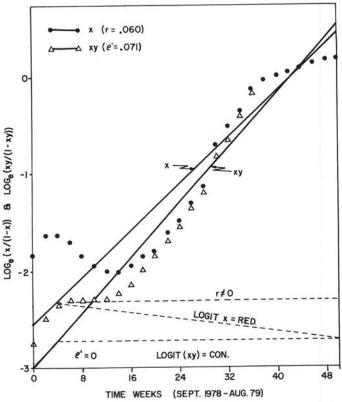


Fig. 3. Progress of rust, caused by Hemileia vastatrix on cultivar Mundo Novo coffee plants during 1978–1979, in Viçosa, MG, Brazil. Here x is proportion of leaves rusted (PLR) and xy is the proportion of rusted leaves corrected for leaf formation. The dots and the triangles are the observed values and the line is the logistic fit (see growth models in text). The broken lines indicate calculated logit x,  $(\log_e(x/(1-x)))$ , or  $\log_e(xy/(1-xy))$ ) when weather was assumed to be unfavorable for rust development after the 4th wk; the value of  $x_i$  was reduced while  $xy_i$  stayed constant. The parameter r is apparent infection rate and  $\rho'$  is the infection rate corrected for host growth (units per week).

The approach to correct for host growth and to determine cumulative disease for the interval in which infection rate is sought, is based on the 'ceteris paribus' hypothesis (15, p. 40) that in a model all the parameters are constant except the one or two variables (X or Y and t) chosen for evaluation.

The cryptic error in estimating x based on current amount of host mass has been reported (8). The current disease proportion can decrease due to disease removal from leaf fall or increase due to fall of nondiseased leaves. Here, a similar error, dilution of x from host growth, has been demonstrated.

The parameters r and  $\rho'$  over the entire disease progress curve (growth models). The residual sum of squares and/or coefficient of determination used to evaluate the suitability of growth models for coffee rust progress during 1978–1979 and 1979–1980 are given in Table 1. The disease progress curve not corrected for host growth fitted best to the logistic model in both the years when quantified as PLR, and to the Gompertz in 1978–1979 and to logistic in

1979-1980 when quantified as PLAR, whereas the disease progress curves corrected for leaf formation fitted best to the logistic model when quantified as PLR and to the Gompertz model when quantified as PLAR. The monomolecular model was not suitable for any curve.

The disease progress curves, based on PLR and PLAR, not corrected (x) and corrected (xy) for leaf formation and those estimated from suitable growth models, for 1978–1979, are illustrated in Figs. 1 and 2. The difference (in space) between the curves for x and xy (Figs. 1 and 2) indicate the dilution of x due to leaf formation. From 2–14 wk x decreased in spite of the increase in xy. The dilution from host growth is accounted for by evidence that from 4 to 14 wk the environment was not favorable for disease increase (Fig. 3). During that time the corrected value, xy, remained constant ( $\rho' = 0$ ) whereas x decreased. When disease proportion is not corrected for host growth the rate of disease increase relative to that of host growth is masked by host growth.

Any host growth reduced or diluted x. The amount of dilution was not very high in the 1978-1979 epidemic as the initial proportion of host tissue  $(y_0)$  was substantial. The magnitude of such a dilution from host growth is demonstrated in a bean rust epidemic (Fig. 4) (D. P. Santos and A. C. Kushalappa, unpublished). The infection rate increased from r = 0.136 to  $\rho' = 0.184$  when corrected for host growth.

Zadoks (Fig. 6.24 in ref. 15) has demonstrated by computer simulation that the intrinsic growth rate of disease area becomes

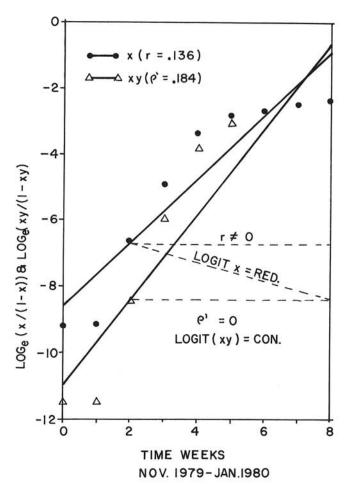


Fig. 4. Progress of rust, caused by *Uromyces phaseoli* var. typica on plants of *Phaseolus vulgaris* 'Rico 23,' in Viçosa, MG, Brazil. Here x is proportion of leaf area rusted (PLAR) and xy is the proportion of leaf area rusted corrected for leaf formation. Dots and triangles are observed values and lines are based on regression of logit x or logit xy over time. Broken lines are logit x or logit xy when weather was assumed to be unfavorable after the 2nd wk; the value of  $x_t$  was reduced, whereas  $xy_t$  remained constant. The parameter r is apparent infection rate and p' is the infection rate corrected for host growth (units per day).

zero  $(r=0 \text{ when } X_t = \text{constant})$  when weather is assumed to be not favorable for disease development, at any stage during the epidemic. If the same disease progress is represented as proportion of variable host then  $x_t$  decreases whereas  $xy_t$  stays constant while the weather is unfavorable; consequently r is negative and  $\rho' = 0$ .

All of the growth models used to characterize disease increase, including the logistic, have a basic requirement that the maximum host area that can be infected, the asymptote, is  $A/Y_{\rm max}=1$  (see equation 7 and 9, when  $A=Y_{\rm max}$ ) and considered to be constant throughout the epidemic.

Turner et al (13) have described a growth model for cases where the asymptote itself is a function of time. They described a function in which both the asymptote and the  $X_i$  are growing logistically:

$$X_i = \frac{K}{((1 + k^m x_0^{-m} - 1) e^{-mt})^{1/m}}$$

in which

$$k = k(t) = \frac{K}{(1 + ae^{-mt})^{1/m}}$$

Here k, the asymptote is a function of time. However, this formula is not only quite complex to be adopted to monitor disease progress but also the host may or may not grow logistically. Jowett et al (4, page 128) commented that "the integrated form of the equation is particularly complex which severely limits its analytical usefulness." The model described here in equation 9 appears to be quite satisfactory to calculate  $\rho'$ , either for any interval within a disease progress curve or for the entire curve. The latter may be calculated based on slope of the regression line. The correction of r for latent period (R) and further for removals due to necrosis and leaf fall (Rc) as described by Vanderplank (14) is not discussed here.

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