Application of Survival Ratio for Monocyclic Process of *Hemileia vastatrix* in Predicting Coffee Rust Infection Rates

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ABSTRACT

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Apparent infection rates corrected for leaf formation (ρ'') were determined based on proportion of leaves (PLR) and leaf area rusted (PRA) on 60 branches marked among 15 plants on 1 ha of cultivar Mundo Novo coffee in Viçosa, Minas Gerais, Brazil, at 14-day intervals from August 1978 to July 1980. Hourly temperature and leaf wetness were recorded and the data were transformed to infection equivalents for environment (INFEE) and to dissemination equivalents for environment (DISEE). The INFEE was determined by laboratory experiments to be the product of infection equivalents for hours of free water and for temperature, which were calculated from the function of hours of free water and of temperature, respectively, for infection, as determined by laboratory experiments. The functions are $Y = 1 - 1.996 \exp(-0.1089t)$ and $Y' = \sin^2(188.1x - 41.6x^2 - 151.3x^3)$, respectively, in which Y and Y' are the proportions of maximum infection observed (= INFEE), x is the Schrödter's temperature equivalent, and t is hours of free water. DISEE was based on the proportion of rainy and windy days (for 28 days before DP) multiplied by the proportion of leaf density. The monocyclic process equivalents for environment (MPEE) related to the whole monocyclic process was derived from MPEE = DISEE × INFEE. The inoculum was quantified as the proportion of leaf area occupied by visible spores and proportion of spore area index (PSAI). The calculated proportion of spores surviving dissemination and able to cause infection was designated as the proportion of infective spore area index, PISAI = PSAI × DISEE × INFEE. The following regression equations were developed to predict coffee rust infection rates: $Y_1 = 2.0804 + 0.1533X_1 + 0.0852X_2$ ($r^2 = 0.72$), and $Y_2 = 1.393 + 0.1149X_1 + 0.0708X_2$ ($r^2 = 0.49$), in which Y is ρ'' for 28 days after the date of prediction (Y_1 is based on PLR, Y_2 is based on PRA), X_1 is logit PISAI and X_2 is host available for infection, − logit xy when xy is PLR or PRA on the date of prediction corrected for leaf formation during the 28 days after the date of prediction.

Additional key words: *Coffea arabica*, epidemiology, prediction model.

Multiple regression analysis has been used to predict development of coffee rust (1,8,9,17) and other plant diseases (4,6,7). The disadvantages of using multiple regression to predict plant disease development also have been reported (5). In the regression models developed to predict coffee and wheat rusts (1,4,6,7,9,17), the combinations of independent variables have been based on meteorological rather than biological functions. Furthermore, variables relating to a single function have often been repeated, which makes the model less stable. These models are unlikely to describe paths of causation in biological systems because the relationship among variables in multiple regression models is a sum of linear functions and because the independent variables themselves are principally meteorological and thus are not directly related to disease development. However, certain combinations or sequences of meteorological factors at known time intervals may control the progress of various epidemiological processes and thus should relate directly to disease development, especially when paths of pathogen actions are synchronized.

Many simulation models define the functional relationship involved among various subprocesses of a monocyclic process. Zadoks and Schein (20) used principles of ecology to evaluate resistance. They quantified horizontal resistance as survival ratios for successful completion of various subprocesses of a monocyclic process.

In the present study, the environment related to three subprocesses (sporulation, dissemination, and infection) of the monocyclic process of *Hemileia vastatrix* Berk & Br. have been quantified as subprocess equivalents for environment based on the functions of environment for subprocesses developed by laboratory experiments. Meteorological field data have been transformed to subprocess equivalents for environment and survival ratios for monocyclic process using biological field data, which were used in combination with data representing the amount of host tissue available for infection to develop a multiple regression model for predicting coffee rust infection rates. The cause and effect of independent variables for the best-fitting model have been quantified by using path analysis (13).

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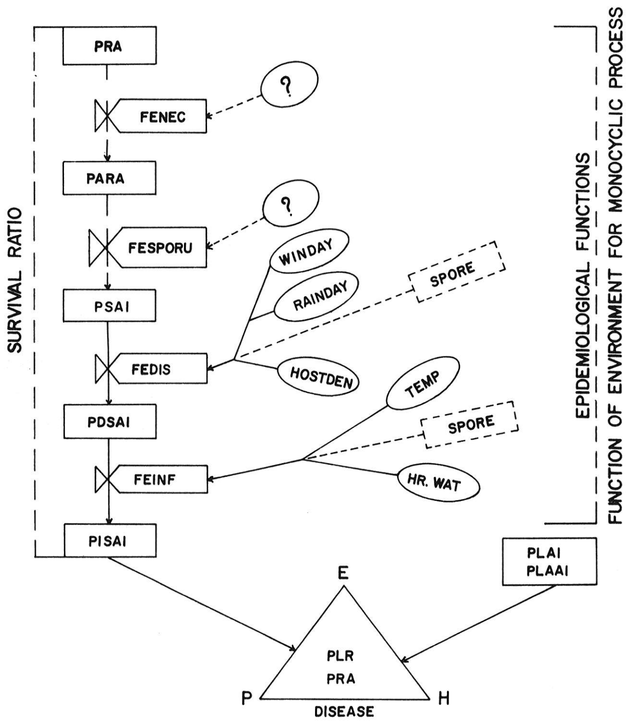
MATERIALS AND METHODS

Laboratory experiments. The influence of temperature and hours of free water on infection were studied under laboratory conditions. Young, completely expanded leaves of 6-mo-old seedlings of *Coffea arabica* L. 'Mundo Novo' were inoculated with a suspension (2 mg/ml) of freshly collected urediniospores of *Hemileia vastatrix* race II in 0.12% Tween-80. The spore suspension was atomized onto the seedlings, and they were placed in a humidity chamber without lights at 21 ± 2 C. The seedlings were removed from the humidity chamber at various time intervals, dried with a fan for 60 min, and then kept in the dark until the longest moisture treatment (48 hr) was completed. Each treatment consisted of five pairs of leaves, one in each of five seedlings or replicates. The experiment was repeated twice. The seedlings were then transferred to a greenhouse and the numbers of lesions formed were counted after 40 days. The mean number of lesions per leaf for each period of free water on the leaves was represented as a proportion of the maximum number of lesions observed, and an exponential fit to the data was estimated by using a computer program SPSS (16). The equations were designated here as functions of environment (for temperature and for hours of free water) for infection, FEINF (acronyms not defined in the text are defined in a footnote to Fig. 1).



COFFEE RUST PREDICTION MODEL

Fig. 1. Coffee rust prediction model: A schematic flow diagram (arrows indicate the direction) for coffee rust prediction. The acronyms used here and in the text are grouped in five categories, and in each they are arranged according to sequence of pathogen growth or pathogen process.

a. Disease triangle
- P = pathogen
- E = environment
- H = host

b. Functions of environment for process
- FENEC = function of environment for necrosis (function not available)
- FESPORU = function of environment for sporulation (function not available)
- FEDIS = function of environment for dissemination DISEE = $[\Sigma (E_1 + 0.5E_2)]/28 \times E_3$, in which DISEE is dissemination equivalent for environment, E_1 is dissemination equivalent for RAINDAY, E_2 for WINDAY, and E_3 for HOSTDEN (see below)
- FEINF = function of environment for infection, consists of two functions, one is function of temperature for infection (Fig. 3) and the other is function of hours of free water for infection (Fig. 2). (see Fig. 1c)
- RAINDAY = one rainy day, a day when the rainfall is ⩾1 mm (given a value of 1.00)
- WINDAY = one windy day, a day when the rainfall is <1 mm and wind speed ⩾1 m/s (given a value of 0.5, relative to RAINDAY)
- HOSTDEN = host density, proportions of leaves present in a 28-day interval represented as portion of maximum observed in a 2-yr period
- HR.WAT = hours of free water per day based on surface wetness recorder readings
- TEMP = temperature (C) while free water was present, based on thermograph readings

c. Process equivalents for environment
- SPEE = sporulation equivalent for environment (not available)
- DISEE = dissemination equivalent for environment (based on FEDIS)
- INFEE = infection equivalent for environment (INFEE = $\text{INFEE}_t \times \text{INFEE}_{hw}$) in which the subscripts are environment, t is temperature (based on function of temperature for infection Fig. 1b) and hw is hours of free water (based on function of hours of free water for infection, Fig. 1b)
- MPEE = monocyclic process equivalent for environment (= SPEE × DISEE × INFEE); when SPEE = 1.00 or when transformed to survival ratio the MPEE = 1.00 × DISEE × INFEE

d. Survival ratios
- BSR = basic survival ratio (= PRA, PARA), quantified as proportion of leaf area
- SRMP = survival ratio for monocyclic process (SRMP = BSR × MPEE), quantified here as proportion of leaf area (= PISAI)
- PRA = proportion of leaf area rusted
- PARA = proportion of active rust area
- PSAI = proportion of spore area index, proportion of leaf area occupied by visible uredinia with urediniospores (= BSR × SPEE)
- PISAI = proportion of infective spore area index (= PSAI × DISEE × INFEE) or (= BSR × MPEE), (PISAI = SRMP)

e. Host available for infection
- PLAI = proportion of leaves available for infection (= −logit xy)
- PLAAI = proportion of leaf area available for infection (= −logit xy)

Data from Montoya and Chaves (15) on the influence of incubation temperatures for 48 hr on infection were used to develop a trigonometric polynomial function for temperature equivalents as suggested by Shrödter (18). The maximum and minimum temperature limits, which were lacking in the data, were determined. Seedlings inoculated as described above were covered with plastic bags and incubated at 15, 20, or 30 C for 48 hr and then transferred to a greenhouse. Numbers of lesions were counted 40 days later.

Field experiments. Four branches were marked on each of 15 trees selected at random on 1 ha of *C. arabica* in Viçosa, Minas Gerais, and data from individually mapped leaves were collected at 14-day intervals from August 1978 through July 1980. If a marked branch died, a growing tip of a young branch (secondary or tertiary) in the same or a nearby plagiotropic primary branch of the same tree was marked and for the calculation of disease severity the new branch was considered a prolongation of the branch that had died. Data included presence and fall of leaves on given nodes, and presence and absence of rust. Rust severity was estimated by using a diagrammatic scale (9). The numbers of current and fallen leaves with and without rust and the leaf area rusted at each date of reading were calculated by using a computer program LEAFAL (10) from which the apparent infection rate corrected for host growth and the host tissue available for infection were calculated. At each sampling date, 10 leaves were collected from the middle third of the canopy of each of 15 trees selected at random, and the proportion of leaf area rusted (PRA) and proportion of leaf area occupied by visible uredinia (PSAI, proportion of spore area index) were determined as previously described (9).

A surface-wetness recorder, Woelfle type 64 b, and a thermograph (both from R. Fuess Company, Berlin, Germany) were placed in the center of the experimental area 1 m above ground level; the thermograph was in a standard meteorological instrument shelter. The daily rainfall and wind speed data were obtained from a meteorological station situated 100 m from the site of the experiment.

The prediction model. Multiple regression analysis (conducted by using the SPSS computer program [16]) was employed to develop an equation for predicting coffee rust infection rates. Independent variables that did not account for significant ($P = 0.05$) proportions of the variation in the rate of disease development were eliminated by stepwise regression.

The dependent variable was apparent infection rate corrected for host growth (ρ'') for an interval of 28 days from the date of prediction (DP). The independent variables were "survival ratios" and "dissemination, infection, and monocyclic process equivalents" for environment related to the respective subprocesses and monocyclic process (Fig. 1) and the proportion of host tissue available for infection. The independent variables were based on data for 28 days before the DP. The various combinations of independent variables were based on biological relationships, which are depicted diagrammatically in Fig. 1.

Infection rate (ρ''). The apparent infection rates corrected for host growth (leaf formation) for intervals 28 days after DP were calculated by using Vanderplank's equation for ρ (19) as modified by Kushalappa and Ludwig (11) to obtain ρ''.

$$\rho'' = \ln [x_2 (1 - x_1 y_1)/ x_1 y_1 (1 - x_2)]/(t_2 - t_1),$$

in which x_1 is the proportion of disease (PLR or PRA) present at

DP; x_2 is the cumulative proportion of disease based on leaves present on t_2 and those removed due to leaf fall during the interval 28 days after DP (for equation see [11]); $y_1 = Y_1/Y_2$ in which Y_1 is number of leaves present at DP and Y_2 is the cumulative number of leaves present during the 28-day interval.

Monocyclic process equivalents for environment (MPEE). The daily weather information was transformed into subprocess (dissemination and infection) equivalents for environment related to the respective subprocesses from which the monocyclic process equivalent for environment was calculated (MPEE = SPEE × DISEE × INFEE in which SPEE was eliminated or given a value of 1.00 [Fig. 1]). The daily mean MPEE ranged from zero to one.

The mean INFEE per day was calculated by substituting hours of free water and temperature in the functions for infection, which were determined under laboratory conditions with those based on daily weather data for 28 days before the DP. The daily INFEE was derived from $INFEE = INFEE_{hw} \times INFEE_t$ in which hw is hours of free water and t is temperature (Fig. 1), which were calculated from the functions (or equations) of hours of free water (Fig. 2) and of temperature (Fig. 3), respectively. The total hours of free water were determined from surface-wetness recorder readings and the temperature was recorded on a thermograph. Since the temperature varied during long free-water periods, the daily INFEE was calculated as the mean of the products of infection equivalents for every 6 hr with the infection equivalent for total number of hours of free water on a given day. The continuous free-water hours were treated together and not separated according to days.

The mean DISEE per day for 28 days before DP was calculated from the function of environment for dissemination (FEDIS, Fig. 1): $DISEE = [\Sigma (E_1 + 0.5\,E_2)/28] \times E_3$ in which E_1 is dissemination equivalent for RAINDAY (Fig. 1), a day with rainfall $\geqslant$1 mm; E_2 is dissemination equivalent for WINDAY (Fig. 1), a day with no rainfall or with rainfall <1 mm and with wind speed $\geqslant$1 m/s. Consecutive days of uninterrupted rain, as determined by continuous leaf wetness hours, were considered as one RAINDAY; E_3 is dissemination equivalent for HOSTDEN (Fig. 1) and was based on the average cumulative number of leaves for 28 days before DP, and was represented as a proportion of the maximum observed during the 2-yr study period. The mean DISEE is a proportion of maximum dissemination and ranged from zero to one.

Survival ratio for monocyclic process (SRMP). The SRMP was calculated as SRMP = BSR × MPEE (Fig. 1), in which the basic survival ratio, BSR, is the initial stage of the monocyclic process (= proportion of leaf area rusted). For the purpose of this study the proportion of leaf area occupied by visible uredinia with urediniospores, PSAI (Fig. 1) was considered as the initial stage (PSAI = BSR × SPEE) and was estimated directly in the field, which eliminated the need for SPEE. The PSAI for samples of marked plants were obtained indirectly from those for random samples in order to reduce extensive handling of marked plants. The PSAI, cumulative for 28 days before DP, for samples of marked plants was calculated from an average (on DP and 14 and 28 days before DP) ratio of PSAI: PRA estimated from random samples; the ratio was multiplied by PRA, cumulative for 28 days before DP calculated from marked plants to yield PSAI.

The PSAI surviving after the subprocesses dissemination and infection depending on the environment during a 28-day period before DP were calculated and represented as proportions of leaf area. The probable survival ratio after dissemination was designated as proportion of disseminated spore area index (PDSAI) and that after infection as proportion of infective spore area index (PISAI). Here, the PISAI is the proportion of leaf area occupied by spores that initiate infection. The rate of flow of each subprocess depends on the mean DISEE and INFEE as explained above. The value of SRMP ranged from zero to one (SRMP = PISAI = PSAI × DISEE × INFEE, Fig. 1).

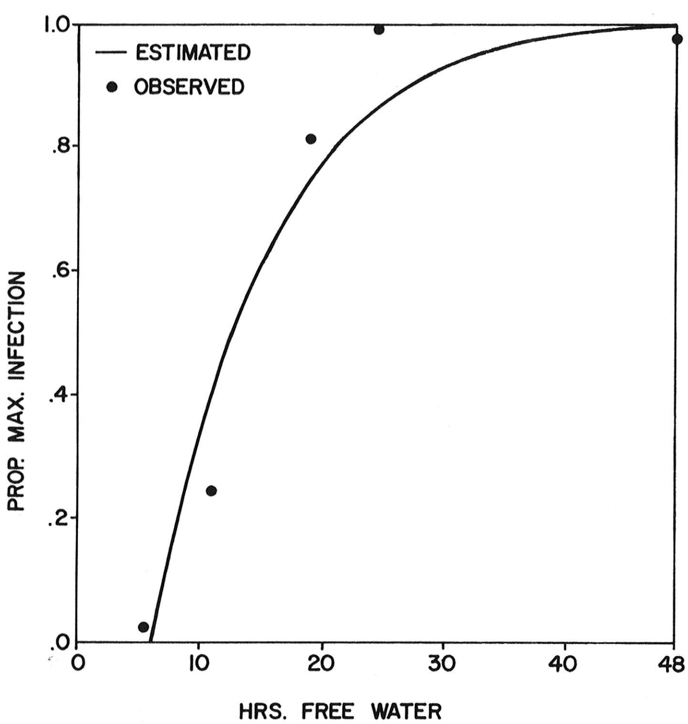


Fig. 2. Function of hours of free water for infection of coffee leaves by urediniospores of *Hemileia vastatrix*: observed values and an exponential fit. The equation is $Y = 1 - 1.996 \exp(-0.1089t)$, ($r^2 = 0.79$), in which Y is the proportion of maximum infections or lesions observed (= infection equivalents for environment), t is the hours of leaf wetness, and r^2 is the coefficient of determination.

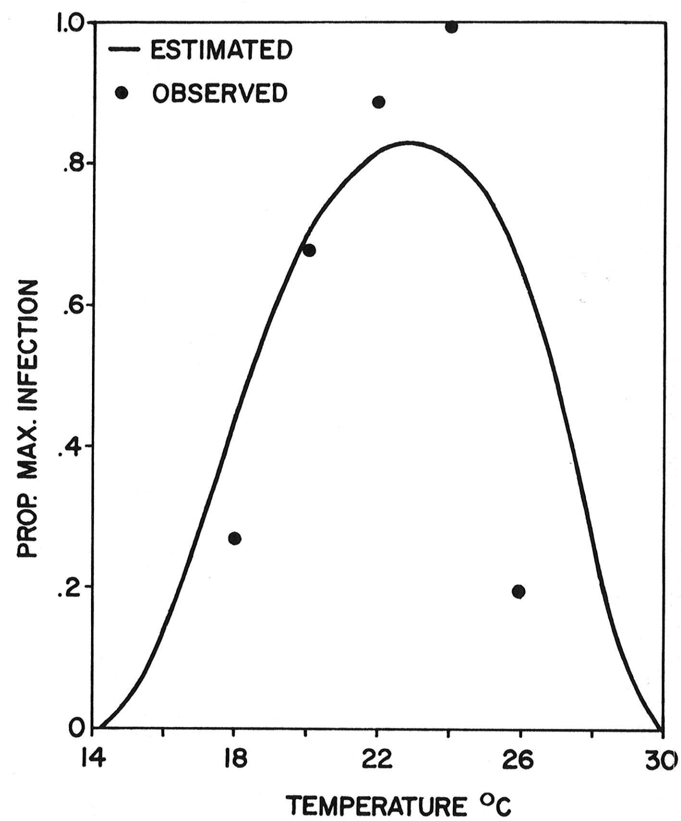


Fig. 3. Function of temperature for infection of coffee leaves by urediniospores of *Hemileia vastatrix*: observed values and a trigonometric polynomial fit. The equation is $Y = \sin^2(188.1x - 41.6x^2 - 151.3x^3)$, ($r^2 = 0.77$), in which Y is the proportion of maximum infections or lesions observed (= infection equivalents for environment) and x is temperature equivalents (18), in which $x = (t_{ob} - t_{min})/(t_{min} - t_{max})$, in which t is temperature in C, observed, and minimum and maximum for activity, and r^2 is the coefficient of determination. For the transformation of weather data, the estimated values were adjusted to a maximum of one.

Host tissue available for infection. The proportion of leaves (PLAI) and leaf area available for infection (PLAAI) during an interval of 28 days preceding DP was calculated based on the formula, $-$logit xy, in which x is PLR or PRA present at DP and $y = Y_1 / Y_2$, where Y_1 is leaves present at DP and Y_2 is cumulative for 28 days after DP (here the amount of host during the prediction interval is considered constant as in the calculation of ρ'').

Path analysis. Path analysis deals with relationships among the standardized variables. The regression coefficient for any standardized variable is called the path coefficient (ρ), thus the latter is a standardized regression coefficient. The path coefficient carries a direction with it and is shown by arrows. The total percentage of the coefficients of determination is the sum of partial determination by each variable ($\rho_{01}^2 + \rho_{02}^2$) and by correlation among variables ($\rho_{01}\, r_{12}\, \rho_{02} + \rho_{02}\, r_{21}\, \rho_{01}$); the rest is unexplained variation (for details see reference 13, pages 113–115).

RESULTS

Function of environment for infection. *Function of free water for infection.* The proportion of the maximum number of lesions per leaf observed at various time intervals of free water and an exponential fit to the data are shown in Fig. 2. The equation was $Y = 1 - 1.996 \exp(-0.1089\, t)$, in which Y is the proportion of the maximum number of lesions per leaf and t is the number of hours of free water; the coefficient of determination (r^2) was 0.79. The hours of free water exposure tested were 6, 12, 18, 24, and 48. At 6 hr free water, the number of lesions produced was 0.03 of the maximum (1.00), which was reached in 24 hr.

Function of temperature for infection. The proportion of the maximum number of lesions per leaf observed at various temperatures and a trigonometric polynomial fit are presented in Fig. 3. The equation was $Y = \sin^2(188.1x - 41.6x^2 - 151.3x^3)$,

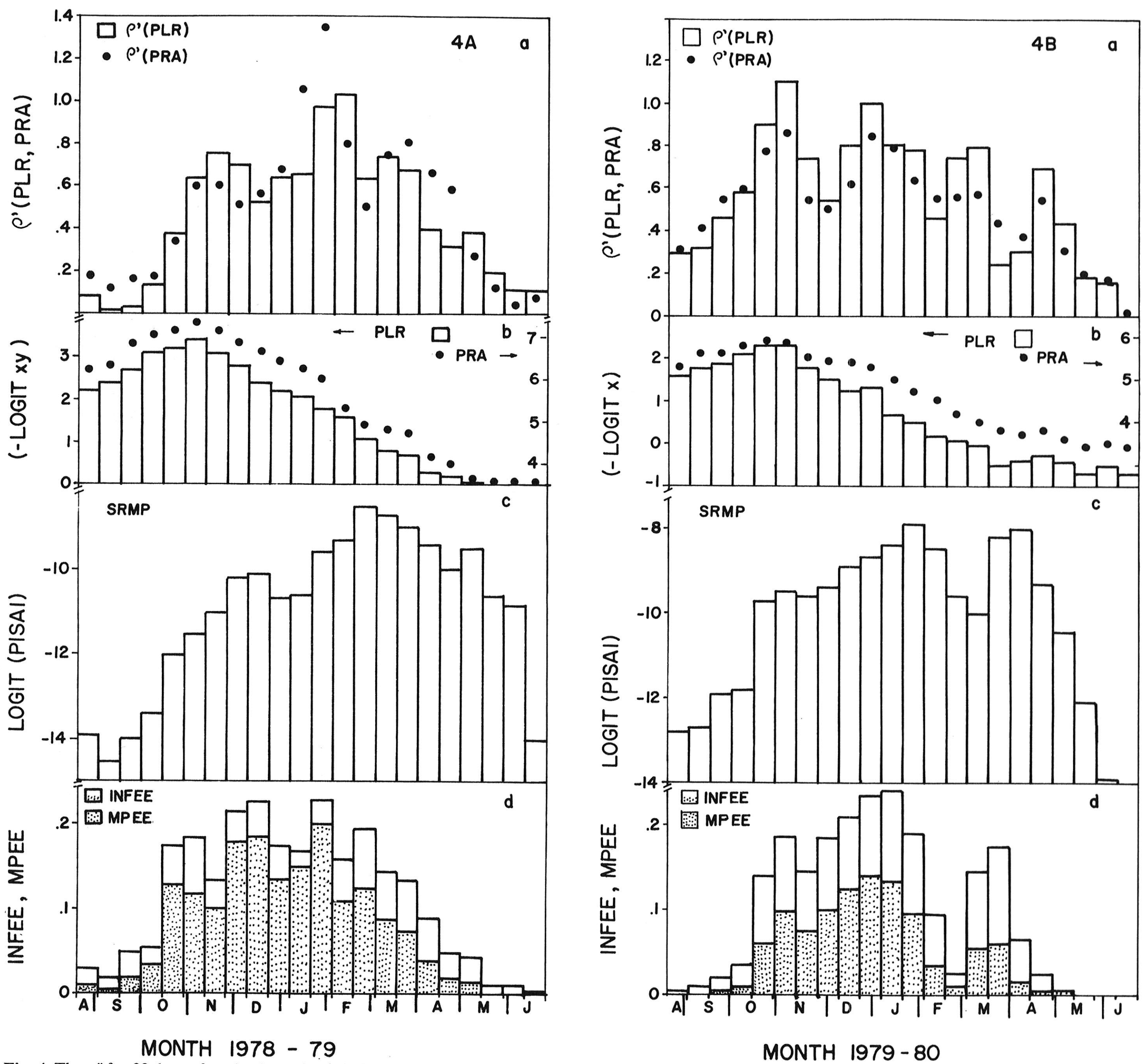


Fig. 4. The ρ'' for 28 days after the date of prediction (DP) for coffee rust (**a**) was superimposed on corresponding $-$logit xy (**b**), logit PISAI (**c**), and MPEE and INFEE (**d**), for 28 days before DP, observed from August 1978 to June 1979 (**4A**) and from August 1979 to June 1980 (**4B**), respectively, at Viçosa, Minas Gerais. The ρ'' is based on proportion of leaves (PLR) and leaf area rusted (PRA); $-$logit xy is host available for infection in which xy is PLR or PRA cumulative for 28 days before DP corrected for leaf formation; logit (PISAI) is logit proportion of infective spore area index (PISAI = SRMP, survival ratio for monocyclic process); MPEE is monocyclic process equivalent for environment and INFEE is infection equivalent for environment.

where Y is the proportion of maximum infection (lesions); x is the temperature equivalent ($x = t_{ob} - t_{min})/(t_{max} - t_{min})$, in which ob indicates observed, min indicates minimum, and max indicates maximum temperature for activity (18). The coefficient of determination (r^2) was 0.77. An average of less than one lesion per leaf appeared at 15 (0.35) and 30 C (0.1); consequently, a minimum of 14 and a maximum of 30 C were chosen as the limits for activity.

Host available for infection. The proportion of leaves and leaf area available for infection (Fig. 4Ab and Bb) increased until November after which they decreased. The proportion of maximum leaves observed (= HOSTDEN) were relatively higher during 1978–1979 (Fig. 5Ac) than during 1979–1980 (Fig. 5Bc); within each growing season, the HOSTDEN was higher from October through March. The new flush of growth of branches and leaves started in September after the winter months of June–August. After March, fewer leaves formed, and the continued leaf fall reduced the amount of foliage, especially after harvest (May).

Disease development. The rate of disease increase (ρ'' for 28 days), based on PLR and PRA, was relatively higher from October to April than from May to September (Fig. 4Aa and Ba). The rate of rust development in general was similar between years, although it varied between corresponding months.

Equations to predict rust infection rate. The coefficients of determination (r^2) for various independent variables are shown in Table 1. Four of the six variables, DISEE, INFEE, MPEE, and logit proportion of infective spore area index independently explained more than 25% of the variation in the rate of rust development. When data from April to July were excluded, because of longer incubation periods, the r^2 significantly increased in logit proportion of spore area index and in logit proportion of infective spore area index, but decreased in other variables. The logit proportion of infective spore area index explained up to 67% of the variation in ρ'' based on PLR.

The weather was favorable for infection of coffee leaves by *H. vastatrix* from the second half of October through March (INFEE, Fig. 4Ad and Bd). However, a higher proportion of infective spore area index (Fig. 4Ac and Bc) was observed after March because of the higher proportion of spore area index, which was due to a higher proportion of disease area (an inverse function of −logit xy, Fig. 4Ab and Bb). Although the proportion of host available for infection (Fig. 4Ab and Bb) and the host density (Fig. 5Ac and Bc) were relatively higher from August through October, the INFEE (Fig. 4Ad and Bd) and logit proportion of infective spore area index (Fig. 4Ac and Bc) were lower, which consequently reduced the infection rate (Figs. 4Aa and Ba, 5Aa and Ba, and 5 Ab and Bb).

Equations for various combinations of independent variables are given in Table 2. In general, the r^2 was higher when the dependent variable ρ'' based on PLR was chosen than when ρ'' based on PRA. In all but one case (Table 2, eq. 12) the r^2 increased when the data from April to July were excluded. A maximum of 72% of the variation in ρ'' based on PLR was explained by a combination of logit proportion of infective spore area index, and host available

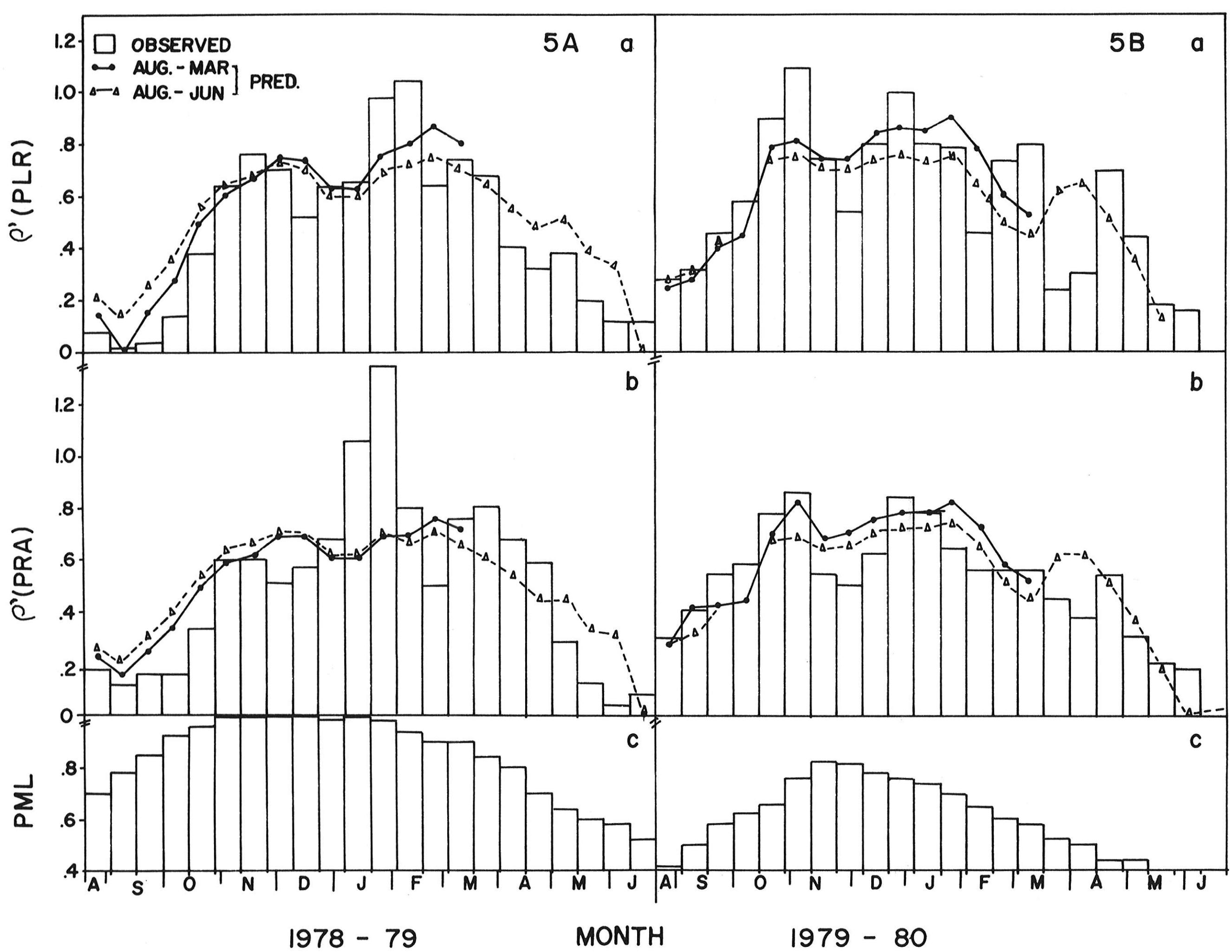


Fig. 5. Apparent infection rate corrected for leaf formation (ρ'') for 28 days after date of prediction, observed and predicted based on the equation 11 (Table 2), and the number of leaves present in an interval of 28 days before DP, represented as proportion of the maximum observed from August 1978 to June 1979 (**5A**) and from August 1979 to June 1980 (**5B**), respectively, at Viçosa, Minas Gerais. PLR, proportion of leaves rusted (**a**); PRA, proportion of leaf area rusted (**b**); PML, proportion of maximum leaves present (**c**).

for infection ($-$logit xy). In none of the four combinations (Table 2) did the independent variable DISEE explain significant variation in infection rate, even though individually it explained significant variation (Table 1). This is because of high multicolinearity between the variables DISEE and INFEE ($r = 0.796$ and 0.759) (Table 3). High multicolinearity among independent variables were also observed between logit PSAI and $-$logit xy.

Path model and multicolinearity. The amount of variation explained by each variable directly and due to multicolinearity (due to correlated causes) among variables, in a combination of independent variables, is described with the aid of path coefficients. The combination that gave highest r^2 value has been chosen for illustration (eq. 11, Table 2). In a stepwise regression, the variable logit proportion of infective spore area index entered first, and it explained 67% of the variation in ρ''. Next entered the logit proportion of leaves available for infection ($-$logit xy), which increased the r^2 to 72%. However, $-$logit xy independently explained 10% of the variation; the reduced contribution with logit PISAI is due to the correlation of $-$logit xy with logit PISAI ($r = -0.589$). Based on path coefficients, the variable logit proportion of infective spore area index in the combination directly explained 96% ($\rho_{01}^2 = 0.96$) and $-$logit xy explained 8% ($\rho_{02}^2 = 0.08$) of the variation in the rate of disease development (ρ''), but the final amount was reduced to 72% because of negative correlation ($r = -0.598$) between the independent variables; the correlation reduced the final r^2 by 32%, 16% from each path [($\rho_{01} r_{12} \rho_{02} = -0.16$) + ($\rho_{02} r_{21} \rho_{01} = -0.16$)]. The correlation between logit PISAI and $-$logit xy is negative because the logit PISAI is based on the proportion of leaf area diseased, while $-$logit xy is logit proportion of leaves that are not diseased (based on PLR).

DISCUSSION

In the regression model suggested here to predict coffee rust infection rates (Fig. 1), the functional relationships among independent variables (biological and meteorological) that influence increase in disease have been more adequately defined than in earlier models (1,8,9,17) by transforming meteorological information to monocyclic process equivalents for the environment related to the three subprocesses of a monocyclic process and further by deriving the survival ratio for monocyclic process, proportion of infective spore area index from proportion of spore area index. The multiple regression analysis explains the response in the dependent variable as a sum of linear functions of independent variables and not through paths of action as illustrated in Fig. 1. The nontransformed meteorological variables explain variation in disease development since in certain combination they determine the monocyclic process equivalents that are directly related to disease development.

Zadoks and Schein (20, page 51) used 'survival ratios' to quantify horizontal resistance. A reduced proportion of survival from spore to pustule development (infection efficiency) is an indication of resistance. A similar principle has been adopted here to quantify the monocyclic process of *H. vastatrix*, and to predict infection rate. The various functions of environment, designated as epidemiological functions (Fig. 1), have been determined under

TABLE 1. Coefficients of determination (r^2) for various independent variables that were used in formulating a multiple regression equation to predict coffee rust infection rate in Viçosa, Minas Gerais, Brazil, during August 1978–June 1980

		Coefficient of determination for independent variables[z]					
Period	Dependent variable[y]	Logit PSAI	DISEE	INFEE	MPEE	Logit PISAI	$-$Logit xy
August–June	ρ'' (PLR)	0.0001	0.269	0.473	0.411	0.450	0.057
	ρ'' (PRA)	0.0086	0.372	0.477	0.469	0.384	0.082
August–March	ρ'' (PLR)	0.267	0.084	0.397	0.287	0.666	0.097
	ρ'' (PRA)	0.123	0.185	0.364	0.367	0.452	0.051

[y] ρ'' is apparent infection rate based on proportion of leaves rusted (PLR) or leaf area rusted (PRA) for 28 days after the date of prediction (DP), corrected for leaf formation (11).

[z] Variables are for 28 days before DP: proportion of spore area index (PSAI), dissemination equivalents for environment (DISEE), infection equivalents for environment (INFEE), monocyclic process equivalent for environment (MPEE), proportion of infective spore area index (PISAI), and host available for infection ($-$logit xy), in which x is PLR or PRA and y is the correction for leaf formation (see text).

TABLE 2. Constant values, partial regression coefficients, and coefficients of determination (r^2) for various combinations of independent variables for model equations that explained significant variation in the coffee rust infection rate in Viçosa, Minas Gerais, Brazil, during August 1978–June 1980

				Partial regression coefficients for independent variables[y]						
Period	Eq. no.	Dependent variable[y]	Constants	Logit PSAI	DISEE	INFEE	MPEE	Logit PISAI	$-$Logit xy	r^2
August–June	1	ρ'' (PLR)	1.4690	0.2168	—[z]	2.1894			0.2609	0.673
	2	ρ'' (PRA)	0.2507	—	—	2.3695			—	0.478
	3	ρ'' (PLR)	1.6554	0.2403			3.1238		0.2686	0.670
	4	ρ'' (PRA)	1.6892	0.1400			3.0068		0.1542	0.558
	5	ρ'' (PLR)	1.5892					.1225	0.1058	0.626
	6	ρ'' (PRA)	1.1009					.1052	0.1016	0.568
August–March	7	ρ'' (PLR)	1.4617	0.1877	—	2.1242			0.1605	0.711
	8	ρ'' (PRA)	0.7802	0.0600	—	1.9691			—	0.481
	9	ρ'' (PLR)	1.6584	0.2099			2.8121		0.1675	0.711
	10	ρ'' (PRA)	0.9355	0.0788			2.9002		—	0.565
	11	ρ'' (PLR)	2.0804					0.1533	0.0852	0.715
	12	ρ'' (PRA)	1.3930					0.1149	0.0708	0.490

[y] ρ'' is apparent infection rate based on proportion of leaves rusted (PLR) or leaf area rusted (PRA) for 28 days after the date of prediction (DP), corrected for leaf formation (11). Independent variables are for 28 days before DP: proportion of spore area index (PSAI), dissemination equivalent for environment (DISEE), infection equivalent for environment (INFEE) and monocyclic process equivalent for environment (MPEE), proportion of infective spore area index (PISAI), and host available for infection ($-$logit xy), in which x is PLR or PRA, and y is the correction for leaf formation (see text).

[z] Indicates variable that did not account for a significant ($P = 0.05$) proportion of the variation in ρ''. When all variables were included, the r^2 values were 0.690, 0.596, 0.723, 0.560, and 0.570, respectively, for equations 1, 2, 7, 8, and 10.

laboratory conditions or approximated from data in the literature. Hourly microclimatic and macroclimatic data have been transformed to subprocess equivalents and, further, to monocyclic process equivalents for environment. Each subprocess equivalent for environment has been quantified as a proportion of maximum survival, the ratio between the initial and the final stage of a subprocess. We have attempted to follow the path of action; however, this model does not explain the complete biological relationship.

Various combinations of independent variables in addition to that in the final functional model eq. 5, 6, 11, and 12 were tested to evaluate variation and to compare them in terms of the relationships that they represented. Although the variables in equations 1–4 and 7–10 are functional, the relationships among them are additive, whereas in equations 5, 6, 11, and 12 the relationships involve proportion of survival (thus a functional model), except for −logit *xy*, which is additive. In the equation 11 (similarly in eq. 5, 6, and 12) the cause and effect relationship is explained by path analysis. In equation 1 a combination of four variables explained 67% of the variation whereas the same variables explained only 63% when the relationship was based on survival ratio (eq. 5). Thus, a nonbiological relation may falsely increase r^2 values. A similar false increase is also possible with repetition of variables (overlapping meteorological variables) for a single function; such relations reduce model stability.

Since no function was available for DISEE, an approximation was made. In eq. 5 (Table 2) when WINDAY and HOSTDEN were excluded from DISEE, the r^2 decreased from 63 to 53%. At higher host density levels the disease has been reported to increase faster (1). Though spores have been trapped in the air (2,3,17) and certain days with maximum wind speed were associated with maximum spore catch (3), no significant increase in number of spores was observed at wind speeds of more than 4 km/hr (14). Spores have been found to be disseminated in drippings from leaves in rains of up to 1.6 mm; an increase in the amount of rain was not associated with either an increase or a decrease in spore dissemination (2). Instead, the relationship was irregular.

The incubation period (the period from inoculation until 50% of the maximum number of lesions appeared) estimated from an equation developed in earlier studies (12) varied from 25 to 40 days for the months included in the model, for September through April and up to 60 days during the winter months, June–August. The prediction interval of 28 days allows an incubation period of 28 to 56 days depending on how many days before DP the infection had occurred. Consequently some overlapping of monocyclic process is possible; the infections initiated earlier than 28 days before DP might develop lesions during the prediction interval and infections initiated a few days before DP might not appear at all during the prediction interval. Such false addition and exclusion of lesions would be predominant during the cooler months after April. A correction for incubation period should increase r^2. When data from April were excluded, the r^2 increased from 63 to 72% (Table 2, eq. 5, 11).

When calculating host available for infection (−logit *xy*) a correction for leaf formation was made as in calculating infection rate (ρ''); the host cumulative until 28 days after DP was considered constant during the predictive period. Future host growth, when needed, may be approximated based on the equation developed (11) (absence of correction may result in little difference in predicted rate).

The model suggested here appears to explain more adequately the variation in rust incidence (PLR) than in rust severity (PRA). This is because rust severity increases due to enlargement of lesions with time, which is not considered in the model since the increase is not part of the infection process. Also the factors associated with spore dissemination within and between plants and/or leaves may differentially influence disease development that is based either on PLR or on PRA.

In the model developed here, we used ρ'' as a dependent variable. From the predicted value of ρ'', the logit x_t (t = 28 days) can be calculated based on an equation similar to that for apparent infection rate (19).

TABLE 3. Correlation coefficients (r) among independent variables that were used in formulating multiple regression equations to predict coffee rust infection rate in Viçosa, Minas Gerais, Brazil, during August 1978–June 1980

Period	Independent variables[z]	r for independent variables INFEE	Logit PSAI	−Logit xy (PLR)	−Logit xy (PRA)
August–June	Logit PSAI			−0.918	−0.930
	DISEE	0.796	−0.655	0.696	0.739
	INFEE		−0.273	0.378	0.443
	MPEE		−0.414	0.494	0.555
	Logit PISAI			−0.250	−0.213
August–March	Logit PSAI			−0.889	−0.923
	DISEE	0.759	−0.449	0.431	0.518
	INFEE		0.013	0.058	0.126
	MPEE		−0.147	0.192	0.275
	Logit PISAI			−0.598	−0.574

[z] Independent variables are for 28 days before the date of prediction (DP): proportion of spore area index (PSAI), dissemination equivalent for environment (DISEE), infection equivalent for environment (INFEE) and monocyclic process equivalent for environment (MPEE); proportion of infective spore area index (PISAI), and proportion of host available for infection based on proportion of leaves (PLR) and leaf area rusted (PRA). Logit $x = \log_e (x/1 - x)$, in which x = PLR, PRA, PISAI, or PSAI; y in −logit xy is the correction for leaf formation (see text).

$$\text{logit } x_t = \text{logit } x_0 + rt$$

$$\textit{logit } x_t = \text{logit } x_0 y_0 + \rho'' \, t$$

in which $y_0 = Y_0 / Y_t$ and t is time, 28 days after DP.

Based on the factors influencing infection, a cropping period can be grouped into three infection periods. The first is 'period of low-initial infection' from beginning of September through mid-October, when the PSAI (inoculum) as well as the MPEE are low but the HOSTDEN and host available for infection are relatively higher. The second is 'period of highest infection' from mid-October to mid-April when the values for PSAI, MPEE, HOSTDEN, and host available for infection are the highest. The third is 'period of declining infection,' from mid-April to the end of August when the value for PSAI is relatively higher but values for MPEE, HOSTDEN, and host available for infection are the lowest; the PSAI reaches its lowest level during July and September. The inoculum in the beginning of the first period, surviving from the preceding winter months, plays a major role in the further development of disease.

Various parameters such as INFEE, PSAI, and PISAI could be used to make decisions on timing of fungicidal applications. Based on MPEE in this study, applications of fungicide may be started during October if the amount of initial inoculum in September is comparatively higher, or during December if the amount of inoculum is lower. Generally, the cumulative number of leaves produced until December is substantial (11). In the State of Minas Gerais fungicides are usually applied three to four times a year. Also, if the season is relatively less favorable (based on MPEE) or if host density and amount of inoculum are lower, the interval between applications can be extended and, consequently, the total number of applications reduced.

The model developed here is flexible, and can be adopted for other host-pathogen systems. The calculation of proportion of infective spore area index should consider the stage of the pathogen observed and the subsequent environmental functions appropriate from the model (Fig. 1). The r^2 values in the model can be increased by improving the functions for subprocesses.

The equations developed here are preliminary. A similar model based on data from more locations and seasons is necessary before it can be recommended for prediction.

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