

Mathematical Functions to Describe Disease Progress Curves of Double Sigmoid Pattern

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ABSTRACT

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Ten mathematical functions used to describe disease progress curves of double sigmoid pattern were tested using data from epidemics of sugarcane smut. Four of the functions represent the sum of two simple equations (logistic + logistic, Gompertz + Gompertz, monomolecular + logistic, and monomolecular + Gompertz); the other six functions are generalizations of simple models (logistic, monomolecular, and Gompertz) with four and five parameters. For all the functions, high coefficients of determination ($R^2 > 0.95$) were obtained in the nonlinear

regression analyses of the progress curves of sugarcane smut. To choose the most appropriate function, the coefficients of determination, the residual sums of squares for error, the biological meaning of each parameter, and the accuracy in estimating the upper asymptote were utilized. The generalized monomolecular function and the generalized Gompertz function, each with five parameters, were considered the most useful functions to fit disease progress curves of sugarcane smut.

Some growth processes in nature are characterized by separate and distinct phases, each with a unique growth rate. The growth rates are frequently fast during the first and third phases, while the rate between phases may be rather slow. The growth curves resulting from such processes have a typical double sigmoid pattern, sometimes with a saddle point (a point of inflection with horizontal slope).

Processes with these properties have been observed in different disciplines in agriculture (for example, in the accumulation of sugar in sugar beets [24]). Most examples are related to the growth of tree fruits, e.g., the diameter of apricots (15), the diameter and fresh weight of coffee berries (18), and the fresh weight of sour cherries (7,23). In phytopathology, curves with double sigmoid pattern have been found, e.g., the cumulative spore counts of *Puccinia coronata* (3), the disease progress curves of *Verticicladiella procera* in *Pinus* and other tree species (14), *Fusarium oxysporum* f. sp. *vasinfectum* combined with *Meloidogyne incognita* in cotton (22), *Phytophthora capsici* in pepper (2), *Sclerotinia sclerotiorum* in sunflower (9), *Ustilago scitaminea* in sugarcane (1), *Botrytis cinerea* in grapes (19), and *Puccinia graminis* subsp. *graminicola* on perennial ryegrass (26).

Working with sugarcane smut, Amorim and Bergamin Filho (1) divided the disease progress curves into two parts that were described separately. We will use their data to introduce mathematical functions to approximate the entire progress curves with double sigmoid pattern without splitting the data set. These functions are either sums of two simple functions (the logistic, the monomolecular, and the Gompertz functions) or generalizations of these simple growth functions.

MATERIAL AND METHODS

Disease values. The severity of smut in sugarcane was determined in an experiment begun in February 1985 at the pathology farm of the Copersucar's Technology Centre in Primeiro de Maio, Paraná, Brazil. The experiment consisted of two treatments (inoculated and control) with five cultivars (NA56-79, SP71-799, SP71-1406, SP71-6163, and SP70-1143) and three replicates. A detailed description of the experiment can be found in Amorim and Bergamin Filho (1).

During five consecutive years, beginning 70 days after planting and 30 days after harvesting, biweekly or monthly assessments were made of disease severity, expressed as the number of whips (whiplike sori that arise either from the terminal meristem or from lateral shoots) per hectare. Ten functions used to generate double sigmoid pattern were fitted to all disease progress curves. The severity of sugarcane smut was used as dependent variable y (whips per hectare), and the time, t , measured in days after harvest, was used as the independent variable.

Mathematical analyses. Sum of simple functions. If we assume that double sigmoid curves are the result of two consecutive but overlapping growth processes, then the curves can be approximated by the sum of two simple growth functions. For the logistic equation, the sum is given by

$$y_{LL}(t) = p_{11}/\{1 + \exp[-(p_{12} + p_{13}t)]\} + p_{21}/\{1 + \exp[-(p_{22} + p_{23}t)]\}. \quad (1)$$

This combined equation has six parameters, three for each of the two phases. The parameters p_{11} and p_{21} are the upper asymptotes, p_{12} and p_{22} are related to the initial level of disease, and p_{13} and p_{23} are the rates of the two processes. If the rate parameters p_{13} and p_{23} are both positive, the slope of this function is always greater than zero so that neither extreme values (local minima or maxima) nor a saddle point exist.

In a similar way, a combined equation for two Gompertz functions can be constructed:

$$y_{GG}(t) = p_{11}\exp\{-\exp[-(p_{12} + p_{13}t)]\} + p_{21}\exp\{-\exp[-(p_{22} + p_{23}t)]\}. \quad (2)$$

If the sum of two monomolecular functions is formed, the first function will be zero at $t_{01} = -p_{12}/p_{13}$ and the second at $t_{02} = -p_{22}/p_{23}$ where $t_{02} > t_{01}$. The sum of both functions will be zero at t_{0s} , which cannot be determined directly but which lies between the t_{01} and t_{02} . For $t_{01} < t < t_{0s}$, the combined function will be negative due to the high negative values of the second part, while the first part is positive. For $t_{0s} < t < t_{02}$, the combined function and the first part are greater than zero; the second part is still less than zero. For $t > t_{02}$, both parts and, of course, their sum are positive. It is, however, possible to combine a logistic and a Gompertz function in any sequence or to combine an initial monomolecular function and one of the

two other functions in this sequence. The monomolecular + logistic combination produces

$$y_{ML}(t) = \frac{p_{11}\{1 - \exp[-(p_{12} + p_{13}t)]\}}{p_{21}\{1 + \exp[-(p_{22} + p_{23}t)]\}}, \quad (3)$$

and the monomolecular + Gompertz combination produces

$$y_{MG}(t) = \frac{p_{11}\{1 - \exp[-(p_{12} + p_{13}t)]\}}{p_{21}\{\exp\{-\exp[-(p_{22} + p_{23}t)]\}\}}. \quad (4)$$

Generalization of simple functions. The generalization of simple growth functions will be demonstrated using the logistic function as an example. For the logistic curve, the generalization was proposed by Pearl and Reed (20) and later intensively used by Wingert (27) and Kretschmann and Wingert (13) who applied the function in human and veterinary medicine. The generalized logistic function can be written as $y_L(t) = p_1/\{1 + \exp[-P(t)]\}$ where $P(t)$ is a polynomial of the third degree $P(t) = p_2 + p_3t + p_4t^2 + p_5t^3$. The parameters of the equation are p_1 to p_5 and the independent variable is time t . The parameter p_1 is the upper asymptote, p_2 is related to the initial disease, i.e., $p_2 = \ln\{y_L(0)/[p_1 - y_L(0)]\}$. The usual logistic equation can be deduced by setting p_4 and p_5 to zero, and in this case, p_3 is the usual infection rate.

For processes that increase from a low level and approach the upper asymptotic value p_1 , the parameter value of p_5 must be greater than zero. To determine the extreme values of this function, the first derivative is set to zero. The equation $dy_L(t)/dt = 0$ has the same solution as the quadratic equation $dP(t)/dt = p_3 + 2p_4t + 3p_5t^2 = 0$. Because we are dealing with monotonically increasing curves, the discriminant of the quadratic equation $D = p_4^2 - 3p_3p_5$ has to be less than or equal to zero. If $D < 0$, no local minimum or maximum exists and the slope of the curve is always positive. If $D = 0$, the curve has a point of inflection with a horizontal tangent, i.e., a saddle point, that occurs at time $t_s = -p_4/(3p_5)$. The formula of the discriminant D can be used to set $p_5 = p_4^2/(3p_3)$ if a saddle point is desired. Thus, two generalized logistic functions with four and five parameters can be constructed, respectively, as

$$y_L(t) = p_1/\{1 + \exp[-(p_2 + p_3t + p_4t^2 + p_4^2 t^3/3p_3)]\} \quad (5)$$

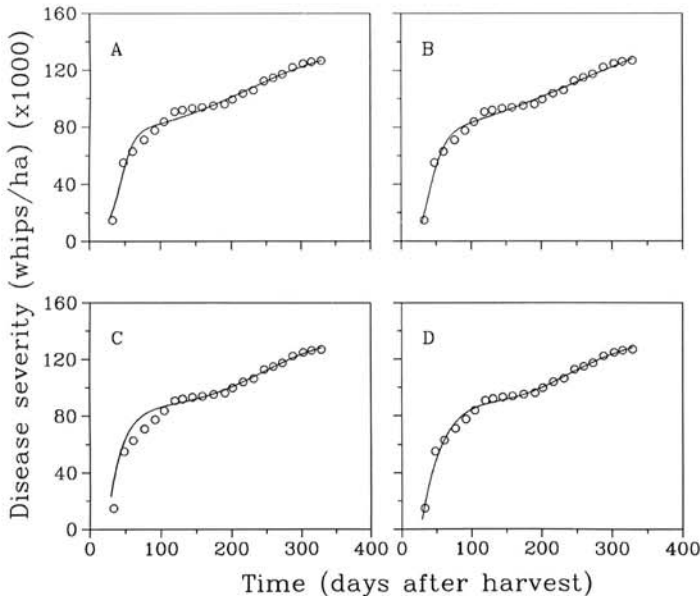


Fig. 1. Observed (circles) and predicted (solid lines) disease progress curves of sugarcane smut (number of whips per hectare $\times 1,000$) in the third raton of the relatively susceptible cultivar NA56-79 in the treatment with inoculation. Curves are calculated by the sum of two simple functions: **A**, logistic + logistic, **B**, Gompertz + Gompertz, **C**, monomolecular + logistic, and **D**, monomolecular + Gompertz.

and

$$y_L(t) = p_1/\{1 + \exp[-(p_2 + p_3t + p_4t^2 + p_5t^3)]\}. \quad (6)$$

In a similar way, the monomolecular and the Gompertz functions can be generalized. The properties outlined for the logistic growth are valid without changes for the two other functions, the generalized monomolecular with four and five parameters,

$$y_M(t) = p_1 \{1 - \exp[-(p_2 + p_3t + p_4t^2 + p_4^2 t^3/3p_3)]\} \quad (7)$$

and

$$y_M(t) = p_1 \{1 - \exp[-(p_2 + p_3t + p_4t^2 + p_5t^3)]\} \quad (8)$$

and the generalized Gompertz function with four and five parameters

$$y_G(t) = p_1 \left\{ \exp\{-\exp[-(p_2 + p_3t + p_4t^2 + p_4^2 t^3/3p_3)]\} \right\} \quad (9)$$

and

$$y_G(t) = p_1 \left\{ \exp\{-\exp[-(p_2 + p_3t + p_4t^2 + p_5t^3)]\} \right\}. \quad (10)$$

Fitting the functions to the temporal increase in severity of sugarcane smut. The fitting of the 10 mathematical functions described above to the progress curves for sugarcane smut was made by nonlinear regression, utilizing Marquardt's compromise procedure. Two statistical software packages were used: PlotIT (Scientific Programming Enterprises Haslett, MI) (6), which includes the generalized monomolecular and logistic functions, and BMDP (5).

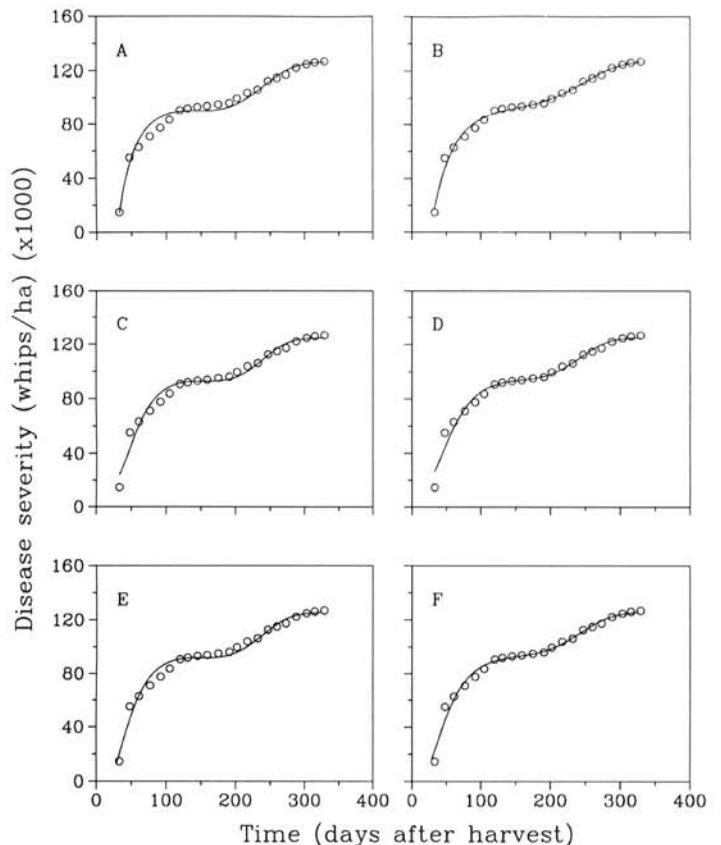


Fig. 2. Observed (circles) and predicted (solid lines) disease progress curves of sugarcane smut (number of whips per hectare $\times 1,000$) in the third raton of the cultivar NA56-79 in the treatment with inoculation. Curves are calculated by generalized functions: monomolecular with **A**, four and **B**, five parameters; logistic with **C**, four and **D**, five parameters; and Gompertz with **E**, four and **F**, five parameters.

RESULTS

Disease progress curves. The progress curves, i.e., cumulative number of whips, of the more resistant cultivars SP71-799 and SP70-1143 were sigmoidal. In contrast, disease progress curves were of double sigmoid pattern for the three cultivars NA56-79, SP71-1406, and SP71-6163 from the first to the fourth ratoon. ("Ratoon" refers to a shoot rising from a sugarcane crown after harvesting, the first ratoon being the sprout after first harvest). For the 24 progress curves of double sigmoid pattern (3 cultivars \times 4 ratoons \times 2 treatments, i.e., inoculated and control treatments), all 10 functions had good fits to the data. As an example, consider the disease progress curve for cultivar NA56-79 in the third ratoon for the inoculated treatment (Figs. 1 and 2). Predicted curves using the sum of two simple functions (Fig. 1) as well as those calculated from the generalized functions (Fig. 2) described the observed data equally well. Little variation was found in the values of the coefficients of determination (R^2) and in the residual sums of squares obtained for the 10 different functions (Table 1).

Results of the analyses carried out with the other cultivars were similar to those found for NA56-79. For cultivar SP71-1406, the R^2 values varied from 0.977 to 0.999 for the treatment with inoculation and from 0.954 to 0.999 for the control treatment, with data from the first to the fourth ratoon. For cultivar SP71-6163, the range for R^2 was 0.959–0.999 (inoculated) and 0.971–0.999 (control). Also, residual sums of squares, obtained for the different functions, were similar for each curve analyzed.

Estimated values of the upper asymptotes, however, sometimes differed markedly from the observed maximum values (Table 2). Asymptotic values estimated for the sum of two simple functions were, in most cases, higher than the observed values, while for the generalized functions, the asymptotes were lower (Table 2).

To compare generalized functions with five parameters with those functions consisting of the sum of two simple functions, the different number of parameters should be taken into consideration. For instance, it was possible to reduce the number of parameters from six to five for the sum of two functions by

assuming that both growth processes have the same rate, i.e., $p_{13} = p_{23}$.

Rate curves. The infection rate is usually given by the slope of the disease progress curve after a suitable transformation. As an example of this approach, we chose the generalized Gompertz function and the sum of two Gompertz functions with the same rates, i.e., $p_{13} = p_{23}$. Observed and predicted values were transformed with a Gompertz transformation in which the last field observation was used as the maximum disease level to create relative figures. The goodness-of-fit of both functions, each with five parameters, were similar (Fig. 3A). The infection rate was variable in time due to the nonlinear shape of the curves (Fig. 3B). In addition, the data and the curves reflect a graph that can be generated by a polynomial of a third degree, which is used in the generalized functions. The rates in dependence on time for both functions can be determined under the assumption that a Gompertz function with variable rate $r(t)$ is given. From the differential equation for the Gompertz function with the maximum disease level y_{\max} , the rate function can be calculated as $r(t) = (dy/dt)/\{y[\ln(y_{\max}) - \ln(y)]\}$. For the generalized Gompertz function, y is replaced by y_G and y_{\max} by p_1 . The rate is then given by $r(t) = dP(t)/dt = p_3 + 2p_4t + 3p_5t^2$, which is a parabolic function of time. By setting y to y_{GG} and y_{\max} to $p_{11} + p_{21}$, the rate function for the sum of two Gompertz functions can be determined. However, $r(t)$ in this case is a rather long mathematical expression and is difficult to interpret. The representation of $r(t)$ for the observed data and for the two functions analyzed can be seen in Figure 3B. The points represent the rate values calculated between two consecutive observations. The generalized Gompertz function with the rate function given by the parabola showed better agreement with the rates calculated from actual data than the sum of two Gompertz functions. The graphs of both functions were similar from day 50 to day 150 but were distinct at the beginning and at the end of the epidemic (Fig. 3B). While the rate function of y_G was a parabola and rates were unlimited in the early and the late phases of the epidemic, the rate of y_{GG} approached asymptotic values in both phases. Both asymptotic values were identical and corresponded to the one

TABLE 1. Coefficients of determination (R^2) and residual sum of squares (SS) of 10 functions fitted to the disease progress data of sugarcane smut (number of whips per hectare) in four ratoons on the cultivar NA56-79 in the treatment with inoculation

Function	Ratoon 1		Ratoon 2		Ratoon 3		Ratoon 4	
	R^2	SS	R^2	SS	R^2	SS	R^2	SS
Logistic + logistic	0.990	88.5	0.997	18.4	0.982	286.0	0.999	3.1
Gompertz + Gompertz	0.995	45.9	0.997	16.1	0.987	191.0	0.999	1.2
Monomolecular + logistic	0.998	15.8	0.997	19.3	0.992	125.0	0.999	4.0
Monomolecular + Gompertz	0.998	13.8	0.997	15.9	0.991	139.0	0.999	0.7
Generalized logistic (4 parameters)	0.981	174.0	0.987	75.2	0.976	370.0	0.991	54.4
Generalized logistic (5 parameters)	0.985	134.0	0.988	69.2	0.979	324.0	0.998	13.6
Generalized monomolecular (4 parameters)	0.998	20.4	0.995	26.4	0.980	310.0	0.990	58.2
Generalized monomolecular (5 parameters)	0.998	16.7	0.995	25.0	0.992	122.0	0.999	6.9
Generalized Gompertz (4 parameters)	0.991	72.2	0.992	48.8	0.979	311.0	0.991	53.9
Generalized Gompertz (5 parameters)	0.993	59.5	0.992	42.9	0.985	228.0	0.999	6.1

TABLE 2. Observed and estimated upper asymptotes of the disease progress data of sugarcane smut (number of whips per hectare \times 1,000) in four ratoons on the cultivar NA56-79 in the treatment with inoculation

Function	Estimated upper asymptote			
	Ratoon 1	Ratoon 2	Ratoon 3	Ratoon 4
Logistic + logistic	82.2	105.5	139.0	95.1
Gompertz + Gompertz	83.8	108.1	169.9	96.7
Monomolecular + logistic	78.5	102.5	136.9	94.7
Monomolecular + Gompertz	80.3	105.7	138.7	96.3
Generalized logistic (4 parameters)	74.8	97.4	124.8	91.0
Generalized logistic (5 parameters)	75.4	97.2	125.2	92.5
Generalized monomolecular (4 parameters)	78.7	99.2	126.6	92.5
Generalized monomolecular (5 parameters)	78.4	99.3	127.8	94.6
Generalized Gompertz (4 parameters)	75.9	98.0	126.0	93.3
Generalized Gompertz (5 parameters)	76.3	98.0	125.4	91.6
Observed	78.5	100.6	126.8	94.4

infection rate estimated for both parts of the disease-progress curves. Obviously, the actual values of $r(t)$ at the beginning and the end of the epidemic have only little effect on the growth curves, because both predicted curves were quite similar although their rates differ. This was due to the fact that in the beginning there was no disease, and in the end the maximum disease level was nearly reached.

It can be shown that for all of the generalized functions with five parameters, the rate function is given as $r(t) = p_3 + 2p_4t + 3p_5t^2$. Following the same reasoning, $r(t) = p_3 + 2p_4t + (p_4^2/p_3)t^2$ for the generalized functions with four parameters. The graphs of $r(t)$ obtained with the generalized monomolecular function (Fig. 4A) and Gompertz function (Fig. 4B) with five parameters for cultivar NA56-79 in the first to fourth ratoon were similar. The infection rates were high in the beginning, declined with time until they reached minimum values (equal or close to zero) at approximately 150 days, and thereafter they started increasing again.

DISCUSSION

Sum of simple functions. When dealing with two consecutive growth processes, it is natural to build the sum of two simple growth functions to describe the whole development mathematically. For each subprocess, a growth function with three parameters can be determined that can have biological meanings, i.e., asymptotic value, initial condition, and rate parameter. Thus, six parameters can be estimated from the observed data, and

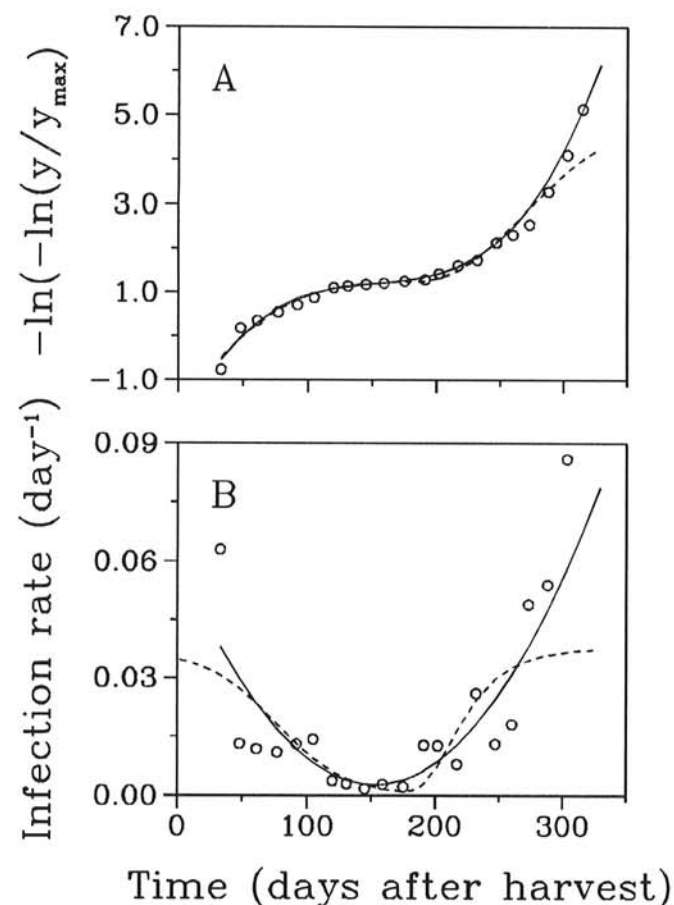


Fig. 3. A, Observed (circles) and predicted disease progress curves of sugarcane smut in the third ratoon of cultivar NA56-79 in the treatment with inoculation using the generalized Gompertz function (—) and the sum of two Gompertz functions (---). The smut data (number of whips per hectare $\times 1,000$) were divided by the last field observation as maximum disease level (y_{\max}) and then transformed with $-\ln[-\ln(y/y_{\max})]$. B, Observed (circles) and predicted infection rates for the same data set using the generalized Gompertz function (—) and the sum of two Gompertz functions (---).

accordingly, a good fit to the data can be expected. Although the sum of simple functions produced the best fit to the observed data, the estimated asymptotes sometimes differed markedly from the observed values and had only a low precision (Table 2). Therefore, the combined process was described very well, but the interpretation of each subprocess was completely misleading. In addition, in this type of function a high correlation can be observed between the two parameters p_{i2} , containing the information on the initial condition, and p_{i3} , the rate parameter. This means that alterations of the infection rate can be compensated for by changes of the initial disease and vice versa, without causing significant deviations in the goodness-of-fit. In fact, when the logistic + logistic function was fitted to the data of cultivar NA56-79 (first ratoon) by using fixed rates of 0.07, 0.08, 0.09, 0.10, and 0.11 per day for both parts, all resulting functions showed good fit to the data ($R^2 = 0.981, 0.984, 0.985, 0.984, \text{ and } 0.982$, respectively). The consequence of this high intercorrelation with respect to data interpretation cannot be overlooked (16,17). For instance, the infection rates calculated for this type of function may not represent an adequate component for the comparison of cultivars, since their estimated values are related to the parameter p_{i2} that represents $y(0)$.

Generalized functions. Generalized functions of the monomolecular, logistic, and Gompertz functions generated curves of similar shape (Fig. 2). The similarity among the generalized functions can be shown by introducing the same parameter values in the generalized equations. The resulting curves (Fig. 5) were different only at the beginning of the epidemic. Over time, the

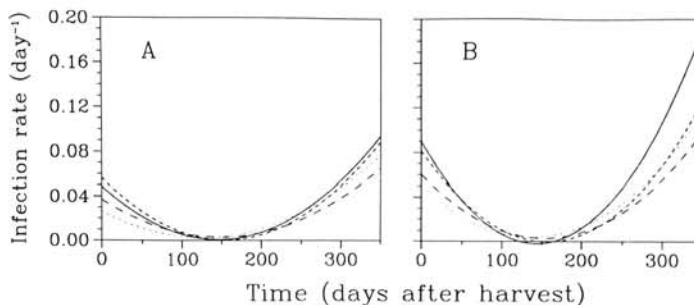


Fig. 4. Dependence on time of the infection rates calculated with the generalized A, monomolecular function and B, Gompertz function, each with five parameters, for sugarcane smut progress of cultivar NA56-79 in the treatment with inoculation in the first (—), second (---), third (-.-), and fourth (···) ratoons.

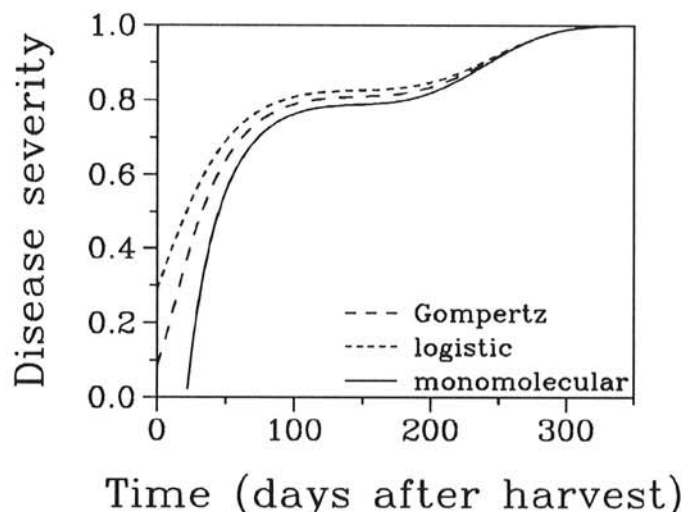


Fig. 5. Disease progress curves simulated with the generalized monomolecular, logistic, and Gompertz functions using the same parameter values: $p_1 = 1, p_2 = -0.9, p_3 = 0.04878, p_4 = -0.0003286, \text{ and } p_5 = 0.0000007497$. The negative values calculated with the monomolecular function are omitted.

calculated function values came closer together and finally converged at the same upper asymptote (Fig. 5). We always analyzed progress curves for sugarcane smut starting from the appearance of the first symptoms. The initial phase with the distinct behavior of the functions was disregarded.

Generalized functions can be considered as simple functions with variable infection rates without inferring the biological nature of the pathosystem from the fitted functions (4,10,21). Variable infection rates have been discussed by Waggoner (25), Jeger (10), and Campbell and Madden (4) to explain irregular growth curves in monocyclic as well as in polycyclic diseases. In polycyclic diseases, the infection rate may vary with host susceptibility and also with environment (8,12,25). However, the variations of the infection rate due to inoculum, environment, and host variability seem to be more important for monocyclic diseases (4). In theoretical analyses of epidemics caused by root pathogens, Jeger (10) used different functions, e.g., linear and exponential, to describe the infection rate as a function of time. In our case, the infection rates were parabolic functions of time.

For sugarcane smut, the changes of the infection rates during epidemics may be related to variations either of the inoculum present in the soil or of the rate of tiller emergence. In the initial phase of the crop, the soil inoculum declines with teliospore germination, which may or may not result in successful infections. Starting from the appearance of the first whips and pathogen sporulation, the inoculum increases again, which may raise the infection rate. However, another aspect should be considered. Since the progress curves for smut obtained in different years and with different cultivars were similar (1), the host growth habit may be related to disease progress. Thus, variations in the infection rate might also be explained by changes in the tillering of the sugarcane as the crop cycle proceeds. In fact, in the initial phase of each crop cycle, the tiller number increases exponentially. Peak population is reached at the end of this phase, which is followed by the second phase when death predominates. After this phase is completed, a more or less stable population survives until harvest (11). The effect of sugarcane tillering on the infection rate has not been investigated in this pathosystem.

By using the generalized functions, the transition time between the first and the second wave of the disease progress curve (saddle point) can be estimated by the expression $-p_4/(3p_5)$, which corresponds to the time when the rate is at its minimum. Sometimes, however, when the functions fit data that do not reflect two sigmoid curves, the second wave is generated outside the observed time range and has no biological meaning. Therefore, the time of the transition should be interpreted with caution when disease progress curves are compared.

The generalized functions with the polynomials in the exponents are difficult to explain from a biological point of view. However, if they are treated as simple functions with parabolic infection rates over time, they may provide important information in order to understand and compare curves in the *Ustilago scitaminea*-sugarcane pathosystem. Therefore, we suggest application of either the generalized monomolecular or the generalized Gompertz function in the more flexible form with five parameters in analyses of progress curves for sugarcane smut.

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