Characterization of the Virus × Temperature Interaction in Secondarily Infected Potato Plants Using EPIVIT

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ABSTRACT

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The model EPIVIT, designed for contact- and aphid-transmitted viruses of tuber crops, simulates the percentage of infected tubers harvested from a potato field. It includes a module for tuber infection of plants with a tuberborne (secondary) infection (efficiency of autoinfection). This module postulates a monomolecular function for the relation between the efficiency of autoinfection and developmental heat, providing a theoretical basis for understanding how an infectious, systemic virus and the environment, represented by temperature, are interacting. The module was calibrated with temperature and autoinfection data obtained with the modern potato cultivar Yungay (*Solanum tuberosum* ssp. *tuberosum* × *S. tuberosum* ssp. *andigena*) in five contrasting environments in Peru. Model estimates for potato X potexvirus (PVX), Andean potato mottle comovirus (APMV), potato Y potyvirus (PVY), or potato leafroll luteovirus (PLRV) were obtained. They were more accurate when temperature-sensitive growth rates were used for heat accumulation than with constant accumulation rates. The bell-shaped relationships obtained between heat accumulation rates and apparent temperature differed for each virus, with optimum heat accumulation rates at 28°C for PVY, and between 18 and 28°C, 20 and 25°C, and 23 and 28°C for PLRV, PVX, and APMV, respectively. With PLRV and PVY data, high precision levels ($P < 0.05$) were only obtained when the parameter trigger developmental heat was included. This parameter represents a threshold amount of developmental heat accumulated any time temperature fluctuates into the range between developmental cardinal temperatures, before heat becomes effective for the efficiency of autoinfection. This calibration supports EPIVIT's assumptions regarding the influence of temperature on virus behavior in the host plant. With complete verification of this model component, validation is still needed for final confirmation of the model, as well as an elucidation of the biological mechanisms that underlie efficiency of autoinfection and virus behavior at different temperatures by analytical research.

Additional keywords: beta-function, epidemiology, G × E interaction, model parametrization, model tuning.

The model EPIVIT simulates seed potato degeneration by a contact- or an aphid-transmitted virus (2), where degeneration is defined as the increase of virus-infected tubers in a tuber lot used for seed selection in consecutive seasons. The model simulates the percentage of virus-infected tubers in the harvest of the simulated plot (harvest infection). EPIVIT was developed as a biologically meaningful, explanatory simulation model applicable across agroecological conditions, plant genotypes, and viruses. The model's inputs are daily minimum and maximum temperatures and weekly catches of winged aphids from an appropriate insect trap (e.g., yellow water trap). The state variables are the efficiency of autoinfection (the percentage of infected tubers among those produced by a plant with a tuberborne, i.e., secondary infection), the primary infection of plants, and the tuber infection of primarily infected, infectious plants.

The sensitivity of the model to changes in structure and parameter values has been evaluated (2). In order to clarify whether a model may reproduce reality, complete model evaluation is required. Model evaluation may be divided into verification and validation. Verification comprises sensitivity analysis and parametrization (12), the latter also called calibration or tuning (5). Calibration means adjustment of the model's parameters in order to make the model optimally represent the real system. Subsequently, validation consists, once the model is verified, in the quantitative comparison of model outputs with the real system, i.e., with historical data that are completely independent from those used for model verification. If model verification is successful in the sense that parameter values can be found for accurately simulating real-world data, a first indication is provided of whether real-world data can be reproduced based on the model's assumptions, but not whether ultimately these assumptions are correct. EPIVIT's sensitivity has been evaluated (2), but calibration and validation are still lacking.

Temperature sensitivity of virus behavior was suggested (1) by the variability of the efficiency of autoinfection and the extreme differences in daily temperature fluctuation observed in contrasting agroecozones of Peru. According to the data reported (1), some tubers escape infection or at least build up only very low, undetectable virus titers, most likely resulting from suboptimal conditions for virus replication and transport inside the plant. Temperature was assumed to be the principal climatic variable influencing interactions of the virus with its host plant. EPIVIT uses temperature-sensitive growth rates to compute aging of the potato plant and several types of developmental heat sums for the simulation of state variables. Heat accumulation starts with 50% emergence and ends with 100% senescence of the potato crop. The model uses the bell-shaped beta-function for weighting apparent temperatures for their relevance to virus replication and systemic transport inside the plant.

Differences in disease progress result from differences among the various host genotypes (G), among viruses (V), and among environmental conditions (E), and also from differential interactions among these three pathosystem components. Differential response of host plant genotypes to different environments has been called G × E interaction (10) and is a major element in determining crop improvement strategies. The differential

response of viruses to various temperatures (V × T interaction) is traditionally lumped into E together with other abiotic and biotic factors that cause G × E. A better understanding of V × T and eventually of G × E would improve overall comprehension of viral pathosystems, leading to applications for better pathosystem management and crop improvement.

The beta-function in EPIVIT's model code provides an analytical model (sensu Jeger, 9), i.e., a theoretical basis for quantitatively characterizing the V × T interaction, achieving the temperature sensitivity of growth rates for the accumulation of developmental heat on which virus behavior depends. A successful application of EPIVIT's module for the efficiency of autoinfection to observed data would contribute to EPIVIT's verification and also allow better understanding of the V × T interaction. The objective of this study was to calibrate this module and complete its verification. A data set collected in Peru between 1987 and 1989 (1) was used. Some, but not all, variables and symbols used by the model are explained. Full documentation of the variables and symbols is found in reference 2.

MATERIALS AND METHODS

Historical data set. The data set used for calibration relates to field studies on the epidemiology of potato viruses conducted in three agroecological zones of Peru (1). The zones represent a range of climatic and agroecological zones from rain-fed tropical highland to irrigated tropical lowland. The epidemiology of the contact-transmitted potato X potexvirus (PVX) and Andean potato mottle comovirus (APMV), and the aphid-transmitted potato Y potyvirus (PVY) and potato leafroll luteovirus (PLRV) were studied with the modern potato cultivar Yungay (*Solanum tuberosum* subsp. *tuberosum* × *S. tuberosum* subsp. *andigena*). In plots with low, intermediate, or high seed infection (approximately 2, 20, and 50%, respectively), plants secondarily infected with one of the viruses mentioned (i.e., plants with a tuberborne infection) were spatially scattered in a uniform, regular (4) way. Seed tubers infected with PVY were coinfected with PVX. Data on efficiency of autoinfection were obtained from the pooled sample of secondarily infected plants situated in experimental plots of one season at a particular location. Three randomly selected tubers of each such plant were analyzed by enzyme-linked immunosorbent assay to determine the percentage of infected tubers obtained from secondarily infected plants (1). Tuber infection and temperature data from three experimental sites were obtained between 1987 and 1989. These data represent six site–season combinations (Table 1), each of which is considered a separate environment (10). Daily temperature data (minimum and maximum) were recorded in five environments, while in Imperial 1987, only monthly average temperature data could be obtained (1).

Calibration strategy. According to EPIVIT's model code (2), the simulation of the efficiency of autoinfection *tsi* requires previous simulation of the physiological time *P-time* with which crop growth advances. Heat accumulation for the simulation of *tsi* and *P-time* was started with temperature data of the five mentioned environments with daily data at 50% crop emergence and ended with 100% senescence. A range of sets of parameter values was tested, and the set that allows for the most accurate simulation was selected according to criteria specified below to represent reality most accurately. The parameters that EPIVIT uses for simulating *tsi* (2) are shown in Table 2. The plant age at which the logistic increase of age resistance begins (*Mri*) and

TABLE 1. Temperature and efficiency of autoinfection data (1) available from experimental sites in contrasting agroecological zones in Peru, representing six environments (10)

Site	Elevation (masl)	Season	Available temperature data	Efficiency of autoinfection (%)[a]			
				PVX	APMV	PVY	PLRV
Imperial	112	1987	Monthly max/min averages	83.3 (193)	84.2 (150)	—[b]	88.2 (76)
		1988	Daily max/min	80.1 (38)	76.8 (59)	83.3 (20)	83.3 (24)
Santa Ana	3,280	1987–88	Daily max/min	75.0 (56)	71.1 (194)	—	32.1 (27)
		1988–89	Daily max/min	71.8 (206)	44.3 (91)	54.4 (117)	33.2 (202)
Chicche	4,000	1987–88	Daily max/min	40.7 (9)	31.5 (18)	—	34.3 (70)
		1988–89	Daily max/min	58.3 (158)	30.3 (44)	58.0 (69)	43.2 (91)

[a] In parentheses, the number of secondarily infected plants involved is given. Three tubers per plant were analyzed by enzyme-linked immunosorbent assay (1).
[b] No data available.

TABLE 2. EPIVIT's variables used for simulating the efficiency of autoinfection (2)

Variables	Description	Dimension[a]	Units
Input variable			
T_{min}, T_{max}	Historical minimum and maximum of daily temperature	$[T]$	[°C]
Parameters of the physiological time (*P-time*)		$[DT]$	[*P-days*]
m_p, n_p, dr_p,	Beta-function parameters for the calculation of the rate of physiological	[1]	[–]
$T_{min;p}$, $T_{max;p}$	time advancement with time, $r_p(t)$	$[T]$	[°C]
Parameters of the efficiency of autoinfection (*tsi*)		[1]	$[plant^{-1}]$
m_a, n_a, dr_a,	Beta-function parameters	[1]	[–]
$T_{min;a}$, $T_{max;a}$	Beta-function parameters	$[T]$	[°C]
TH	Trigger developmental heat	$[DT]$	$[bdd_a]$[b]
r_a,	Rate parameter and y-axis intercept of the monomolecular function	$[DT^{-1}]$	$[bdd_a^{-1}]$
tsi_0	representing $tsi = f(DH)$	[1]	[%]
Susceptibility of plants to an infection (Su_{mr})		[1]	[–]
Su_c	Constitutive susceptibility index ranging from 0 to 1.0	[1]	[–]
P_{max}	Physiological age at 100% senescence of the crop	$[DT]$	[*P-days*]
Mri	Physiological age at the initialization of mature plant resistance	$[DT]$	[*P-days*]
r_{mr}	Rate parameter of the logistic function for mature plant resistance	$[DT^{-1}]$	$[P\text{-}days^{-1}]$
Auxiliary variables			
DH	Developmental heat sum	$[DT]$	*bdd*
r_p	Rate of advancement of physiological age with t	$[DT/Ti]$	*P-days*/hour

[a] Dimensions are DT: developmental heat; T: temperature; Ti: time; 1: dimensionless (ratios, proportions, etc.).
[b] Beta-degree-days.

the rate of the logistic increase (r_{mr}) were estimated at 200 *P-days* and 11.0E-3 *P-day*$^{-1}$, respectively, according to empirical observations and experimental evidence (L. Bertschinger, *unpublished*).

Physiological time. Two approaches for simulating *P-time* were tested to identify the more accurate one. They differ in the function with which temperature is weighted for achieving temperature sensitivity of heat accumulation effective for crop development. One set of physiological ages was calculated with the method described by Sands et al. (13; Fig. 1A). Furthermore, several sets of physiological ages were calculated by using the beta-function approach (2) and by a stepwise change of the parameters and cardinal temperatures of this function. The covered range of values for the respective beta parameters (Table 2) was 0.5 to 3.0 for m and n with a step size of 0.5; a delay range (dr) of 0, 5, and 10°C; and cardinal temperatures of 0, 2, 4, and 6°C for the minimum and 30 and 35°C for the maximum. *P-times* were computed with both above-mentioned approaches using the reported phenological and historical temperature data (1) for the five environments for which daily temperature data were available (Table 1). *P-time* was assumed to be a constitutive parameter of the potato cultivar used in the Peruvian studies (1), in the sense that it has to be equal wherever the cultivar is grown. Therefore, the parameter data set and model approach that permits simulating *P-time* most accurately was selected to be the one that yields minimal differences between the computed *P-times* at 100% crop senescence of all five environments considered.

Efficiency of autoinfection. EPIVIT simulates *tsi* according to the monomolecular model as a function of developmental heat measured in beta-degree-days (2). Heat accumulation measured in beta-degree-days requires a beta-function with the parameters m_a, n_a, dr_a, $T_{min;a}$, and $T_{max;a}$, and also an optional parameter called trigger developmental heat (*TH*) (2). The latter represents developmental heat that may be required for initiating effective heat accumulation for *tsi*, always if temperature fluctuates into the range between cardinal temperatures $T_{min;a}$ and $T_{max;a}$ (Table 2). Beta-degree-days were computed with different parameter value sets for all five environments considered. These sets were obtained by stepwise changes in parameters and by building all possible combinations among obtained parameter values. The range of values covered for the beta parameters was 0.5 to 3.0 for m_a and n_a, with a step size of 0.5; for the delay range dr_a, 0, 5, and 10°C; for the cardinal temperatures, 0, 2, and 5°C for the minimum $T_{min;a}$, and 30 and 35°C for the maximum $T_{max;a}$; and 0, 10, and 20 bdd_a for *TH*. Every seasonal total of computed beta-degree-days was paired with *tsi* reported for the respective environment, which was transformed to the linear form of the monomolecular model $\ln[1/(1 - tsi)]$. Linear regressions were fitted through each obtained set of data pairs. The best regression was selected according to the following criteria: 1) highest Student's t value (highest significance level of regression slope being >0), 2) the highest coefficient of determination (r^2), and 3) unbiased residual of back-transformed function plot. The parameters corresponding to the best fit were those that allow for the most accurate simulation of *tsi* related to the data set used. To document the level of simulation precision achieved by using a temperature-sensitive rate for accumulating developmental heat for *tsi*, the obtained best regressions were compared to regressions obtained by using degree-days, accumulated with a constant, temperature-nonsensitive rate, as independent variable.

Statistics. The 95% confidence limits of binomial distribution were computed for the historical efficiencies of autoinfection (n = tuber number from secondarily infected plants used for the determination of *tsi* in the respective environment [Table 1]) and tested for whether the simulated data lay within these limits.

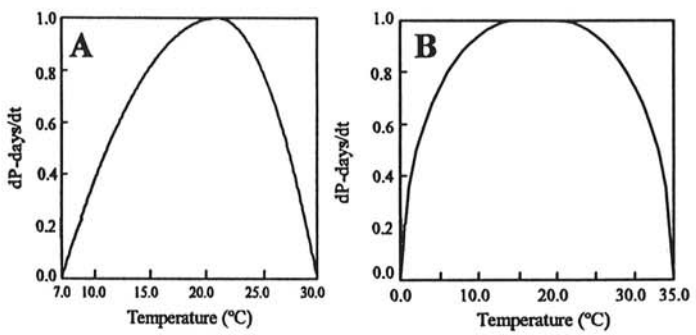

Fig. 1. Functions for the simulation of the rate of advancement of physiological crop age with temperature $T(r_p)$ between 50% emergence and 100% senescence of the potato crop. **A,** Compound continuous functions according to Sands et al. (13). **B,** Beta-function with which EPIVIT simulates most accurately r_p if using phenological data of the modern potato cultivar Yungay (*Solanum tuberosum* subsp. *tuberosum* × *S. tuberosum* subsp. *andigena*) from contrasting environments (10) of Peru.

RESULTS

Physiological time. The smallest difference between physiological ages was obtained by using a beta-function with the parameters $m_p = 0.5$, $n_p = 0.5$, $dr_p = 5.0$, $T_{min;p} = 0$, and $T_{max;p} = 35$ (Fig. 1B). The highest number of *P-days* was 1,047, obtained for an environment of 126 days (50% emergence until senescence). The greatest difference in *P-days* obtained with this parameter set among the five environments considered was 15. Of the 144 parameter combinations tested, all others yielded differences greater than 50, which corresponds to between 5 and 6 days. With the method of Sands et al. (13), the greatest number of 892 *P-days* was obtained for an environment of 104 days. The difference from the environment with the lowest number of *P-days* was 624, which corresponds to 60–70 days.

Efficiency of autoinfection. The monomolecular function provided significant ($P < 0.05$) regressions between degree-days, which were accumulated with a constant, temperature-nonsensitive rate and efficiencies of autoinfection with PVX and APMV, but not with PVY and PLRV. However, with the use of virus

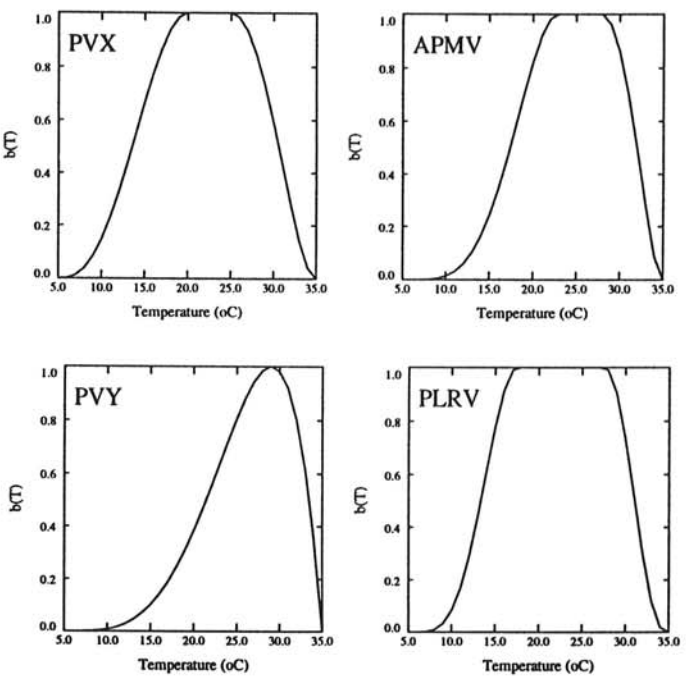

Fig. 2. Beta-functions representing the rate at which heat is accumulated at different temperatures T between 50% emergence and senescence of the modern potato cultivar Yungay (*Solanum tuberosum* subsp. *tuberosum* × *S. tuberosum* subsp. *andigena*), effective for the efficiency of autoinfection with potato X potexvirus (PVX), Andean potato mottle comovirus (APMV), potato Y potyvirus (PVY), and potato leafroll luteovirus (PLRV). Heat accumulated by means of these functions was used as an independent variable for the regressions represented in Figure 3. The parameter values of the beta-functions are, for PVX: $m_a = 2$, $n_a = 3$, $dr_a = 5$, $TH = 0$; for APMV: $m_a = 2$, $n_a = 5$, $dr_a = 5$, $TH = 0$; for PVY: $m_a = 1$, $n_a = 4$, $dr_a = 0$, $TH = 0$; for PLRV: $m_a = 3$, $n_a = 5$, $dr_a = 10$, $TH = 20$.

specific, temperature-sensitive heat accumulation rates (Fig. 2), significant regressions were obtained for all viruses (Table 3). The use of the beta-function resulted in drastic changes of the significance levels of regressions obtained for PVY and PLRV (e.g., error probability reduced from 0.232 to 0.008 in the case of PLRV). Significance of regressions also improved for PVX and APMV (Student's t statistic increased; Table 3), even if to a much lower extent since regressions were already significant when degree-days were used as the independent variable.

All efficiencies of autoinfection predicted by the calibrated model are estimated accurately by the monomolecular model, i.e., they are included in the 95% confidence limits of reported data (Fig. 3) except in one case (PLRV at 4,000 m above sea level in 1988–1989). The use of the discontinuous version of the beta-function (2) for the calculation of beta-degree-days was beneficial except for PVY (Fig. 2), with which the conventional version provided good results (delay ranges of 5°C for PVX and APMV, and of 10°C for PLRV). To obtain satisfactory fits for the aphid-transmitted viruses PVY and PLRV, a developmental heat of 20 beta-degree-days (TH) had to trigger heat accumulation for tsi each time T fluctuated into the range between cardinal temperatures 5 and 35°C. For PVX and APMV, the accumulation of beta-degree-days did not need to be initialized by TH.

DISCUSSION

Physiological time. The shape of the beta-function presented in Figure 1 is different from the functions applied by other authors (8,13), who used skewed bell-shaped functions. The beta-function could represent the growth-temperature relationship of a modern potato cultivar grown in the Andes (*S. t. tuberosum* × *S. t. andigena*), which is likely to be different from a corresponding cultivar grown at higher latitudes (*S. t. tuberosum*). Andean potato cultivars are productive under short days and a very wide range of temperatures (1). The beta-function approach provided more accurate results than the function reported by Sands et al. (13), confirming the adaptability and practicability of the approach used by EPIVIT (2).

Efficiency of autoinfection. Results for PVY are based on three environments only (Table 1), two of which have very similar efficiencies of autoinfection. The regression obtained is therefore driven by basically one point (Fig. 3), which is also true for PLRV, where four environments out of five had similar efficiencies of autoinfection. Even if the beta-function found for PVY is not in disagreement with the limited data on PVY behavior at different temperatures (6,16), the results obtained for PVY and PLRV should be viewed with particular care because of the above reasons. More data should be obtained at intermediate temperature conditions to provide more evidence for the monomolecular relation hypothesized. However, the results of the four viruses investigated appear jointly to support a common principle for virus × temperature interactions. As a whole, the results add support to the assumptions made when developing EPIVIT's module for the simulation of tsi.

Scatter plots of tsi with PVX (2) and APMV (not shown) against degree-days suggested a monomolecular relationship between the two variables when EPIVIT was developed. Such a relationship was confirmed between tsi and beta-degree-days by the obtained significant regressions. The underlying biological principle that gives value to this monomolecular relation remains unclear and has to be studied analytically. The monomolecular equation has frequently proved useful for representing the progress of monocyclic diseases (14,15), i.e., epidemics in which diseased plants or diseased tissue do not contribute to additional disease in the same season. The absolute rate of disease progress is directly proportional to the proportion of healthy plants or tissue. The total amount of available tissue to be infected is the limiting factor from the beginning of the progress, as opposed to the "unlimited" exponential growth at the beginning of the logistic progress representing polycyclic diseases. Although the relationship is hypothetical so far, it appears logical to assume that a monomolecular relationship governs this mechanism; because from the beginning of tuber infection, the number of infectible entities, i.e., tubers per plant, is indeed limited (to approximately 15 to 30).

The monomolecular functions found predict a positive value of tsi at zero beta-degree-days (positive y-axis intercepts, Fig. 3). This means that virus is translocated even if zero beta-degree-days are accumulated. This appears to be biologically significant, because some particles must be transported in vascular bundles even under conditions that are suboptimal for virus multiplication

TABLE 3. Comparison of the regression between efficiencies of autoinfections determined in contrasting environments (10) of Peru for the modern potato cultivar Yungay (*Solanum tuberosum* subsp. *tuberosum* × *S. tuberosum* subsp. *andigena*), and developmental heat accumulated with temperature-sensitive and nonsensitive rates in each environment

Virus	Heat accumulation rate	Regression		
		P	t[a]	r^2
PVX	Temperature nonsensitive[b]	0.009	4.769	0.884
	Temperature sensitive[b]	0.003	6.355	0.931
APMV	Temperature nonsensitive	0.001	8.527	0.960
	Temperature sensitive	0.001	9.268	0.966
PVY	Temperature nonsensitive	0.195	1.922	0.787
	Temperature sensitive	0.005	13.608	0.994
PLRV	Temperature nonsensitive	0.232	1.408	0.398
	Temperature sensitive	0.008	4.873	0.887

[a] Null-hypothesis: slope > 0.

[b] Temperature nonsensitivity is achieved by accumulating degree-days with a constant rate. Sensitivity is achieved by using the beta-functions represented in Figure 2.

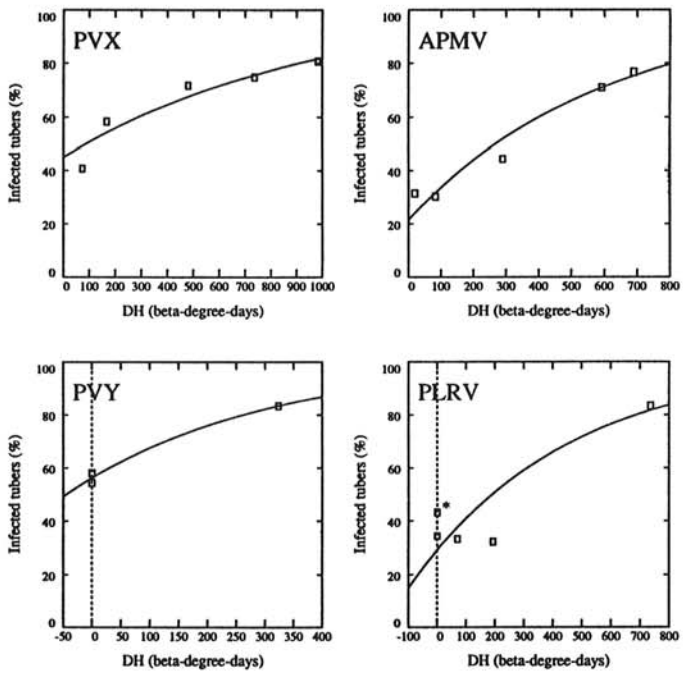

Fig. 3. Monomolecular functions fitted through data pairs of reported efficiencies of autoinfection and beta-degree-days which were accumulated in the respective environment. Historical data of the efficiencies of autoinfection are presented in Table 1. The beta functions which were used for the calculation of beta-degree-days (bdd_a) are presented in Figure 2. The monomolecular model is $tsi(t_{max}) = 1 - \{(1 - tsi_0)\exp[-r_a\, DH_a(t_{max})]\}$ with t_{max} = date at 100% crop senescence. The parameters of the monomolecular fits are, for potato X potexvirus (PVX): tsi_0 = 44.84, r_a = 11.17E-4 bdd_a^{-1}; for Andean potato mottle comovirus (APMV): tsi_0 = 21.40, r_a = 16.87E-4 bdd_a^{-1}; for potato Y potyvirus (PVY): tsi_0 = 56.21, r_a = 29.88E-4 bdd_a^{-1}; for potato leafroll luteovirus (PLRV): tsi_0 = 29.11, r_a = 18.44E-4 bdd_a^{-1}. The coefficient of determination (r^2) obtained with the linearized monomolecular model is, for PVX, 0.931; for APMV, 0.966; for PVY, 0.994; for PLRV, 0.887 (Table 3). * The confidence limits ($P < 0.05$) of the binomial distribution for the indicated historical data do not include the simulated data at the respective DH.

and transport. As long as the plant is alive and synthesis of nucleic acids and proteins in the plant's cells occurs, it is expected that the viral genome is transcribed and eventually viral products are accumulated. Therefore, the simulated mechanism represents the number of virus particles produced and transported in addition to those transported under suboptimal temperature conditions.

If a specific virus interacts with a specific plant genotype at a determined temperature, the beta-function characterizes what relative, quantitative virus multiplication and transportation rates result from this interaction compared to other temperatures. A tentative discussion of the likely epidemiological significance of *TH* required for both aphid-transmitted viruses has been presented elsewhere (2).

Future application of the verified model component. Virus replication and transportation rates have not been studied explicitly under the temperature range covered by the beta-functions. The accuracy of the obtained model outputs does not ultimately prove the correctness of the assumptions made for developing the module for *tsi* (2), even if it offers strong support to these assumptions. Therefore, analytical research and complete model validation with independent data sets are critical for future application of the model. Data sets should also be generated with other cultivars, which would allow for the characterization of the G × V × T interaction and eventually contribute to the understanding of the G × E interaction. Independent data can be obtained with limited additional input by planting secondarily infected tubers of the selected cultivars in contrasting environments and analyzing the tuber progenies obtained using tuber-indexing procedures.

Confirmation of the postulated V × T relationship and its simulation is also needed, since the chosen model approach might have additional relevance to the prediction and understanding of other mechanisms involved in G × E interactions. Tuber infection of primarily infected plants is governed most likely by the same principles (as assumed by EPIVIT; 2). Furthermore, the biological principles of the efficiency of autoinfection may have a genetic basis, as suggested by data obtained by epidemiological studies with African cassava mosaic geminivirus (ACMV). Partial systemic infection of vegetatively produced cuttings from ACMV infected mother cuttings, which has been called reversion (7), and variation of this phenomenon among different genotypes has been observed (7,11). If it can be confirmed that this mechanism has a genetic basis, and if its principles are better understood, it may be exploited for host plant improvement.

Further efforts have to be directed to the validation of EPIVIT's module for the efficiency of autoinfection and the clarification of this mechanism, which was recognized as a significant pathosystem variable only recently (1,7). The impact of the efficiency of autoinfection on virus epidemics is particularly evident for polyethic epidemics (epidemics that develop over successive generations of planting material, because infected harvest materials are used for propagation, becoming the inoculum of the next season's plantings). Such pathosystems exist, for example, in the Andes with potato viruses and in sub-Saharan Africa with ACMV. According to the equilibrium concept (7), epidemics in such pathosystems may stabilize at a virus incidence level below 100% as a result of the combined effects of the efficiency of autoinfection, primary spread of the pathogen, roguing practices, plant propagation techniques, the differences in vigor of infected and noninfected plants, and other factors. Practical observations support this concept. For instance, it was observed that virus incidence in potato seed tuber lots in the Andes was not 100% (3) without the input of virus-free seed. Exemplary runs of EPIVIT have reproduced equilibrium progress patterns resulting in such an equilibrium as a result of the efficiency of autoinfection (2).

Once EPIVIT is entirely validated, it may find practical application in pathosystem management. For example, it may be used to help determine, in pathosystems with polyethic epidemics, the beneficial and economically sustainable frequency of introduction of virus-free propagation material in production systems where input of this expensive resource cannot be afforded by the farmer every year.

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