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Multiplication of Erwinia amylovora in fruit-trees. 2. A simulation study on sensitivity to weather

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Abstract

The sensitivity of an output variable of a model to changes of an input parameter value can be analyzed in various ways. Some methods of sensitivity analysis are described, and applied to a simulation model which has daily minimum and maximum temperatures (T_{min} and T_{max}, respectively), and daily global radiation as input parameters, and standardized relative multiplication rate of *Erwinia amylovora* in shoots in fruit-trees, averaged over a 24 hours' period, as output variable. Values of the input parameters were obtained from a weather station near Wageningen, the Netherlands, and refer to the second half of June, 1974-1988.

According to the model, the output variable was twice as sensitive to T_{max} as to T_{min}. Because of this difference in sensitivity, and because the standard deviation of T_{max} was larger than that of T_{min}, the variation of the output variable due to T_{max} was three times larger than that due to T_{min}. The sensitivity to daily global radiation was negligible when the soil was moist.

Additional keywords: fire blight, temperature, global radiation, water potential, relative multiplication rate, sensitivity analysis.

Introduction

Temperature has a predominant effect on the epidemiological development of fire blight (*Erwinia amylovora* (Burr.) Winslow et al.) in rosaceous plants. Obviously, it affects insect activity and therewith dispersal of fire blight (Free, 1970; De Wael, 1988; Billing, 1990); it influences strongly the epiphytic colonisation of flowers (Zoller and Sisevich, 1979; Van der Zwet et al., 1988), the internal colonization of the host, and the incubation period of fire blight (Billing, 1976). Billing (1976) showed that also water affects the development of fire blight.

To gain more insight into the effects of environment on temperature and water potential within fruit-trees, and thus on the multiplication rate of *E. amylovora* in these fruit-trees, two simulation models were built (Schouten, 1991): a short-term model to investigate immediate effects of weather and soil water potential, and a long-

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term model to study delayed effects of rain and soil. In this paper the short-term model is used. The impact of several weather parameters on multiplication of *E. amylovora* within trees, considering only limitations by temperature and water, was quantified by means of sensitivity analyses.

The model

Sensitivity analyses were applied to a model simulating effects of weather and soil moisture on temperature and water potential in a shoot of a fruit-tree and therewith on multiplication of *E. amylovora* in the intercellular space of that shoot (Schouten, 1991, 'the short-term model'). The output variable of the simulation model was the standardized relative multiplication rate of *E. amylovora* in the shoot, averaged over a 24 hours' period. This standardized relative multiplication rate was obtained by calculating the hourly values of the relative multiplication rate, averaging them over the 24 hours' period, and dividing the average by the relative multiplication rate at optimal temperature and water potential. In the paper in which the simulation model was described (Schouten, 1991), the standardized relative multiplication rate was denoted by $\bar{f}_{\psi,T}$, but in this paper it is represented by the simpler symbol y.

The model required as inputs daily minimum temperature (T_{min}), daily maximum temperature (T_{max}), daily global radiation (R), and water potential of the soil. The sensitivity of the output variable to T_{min}, T_{max}, and R was studied, whereas the water potential of the soil was kept constant (−0.01 MPa) over all simulation runs. During a simulation run T_{min}, T_{max}, and R had constant values, because the simulation period was 24 h, but they varied from run to run.

Sensitivity analyses

Impact of input parameters on the magnitude of the output variable

By running the simulation model repeatedly, with different values of the input parameter x for each run, the effect of changes in the x value on the output variable y was traced. The 'sensitivity' of y to x is:

$$S = \frac{\delta y}{\delta x} \qquad (1)$$

where: S = sensitivity coefficient; δy = the change in y in response to infinitesimal alteration δx in x.

It is common practice to express the alterations δx and δy not in absolute but in relative terms:

$$S = \frac{\delta y}{y} \bigg/ \frac{\delta x}{x} = \frac{\delta \log y}{\delta \log x} \qquad (2)$$

In economics, this coefficient is called elasticity coefficient.

Impact of input parameters on the variance of the output variable

A measure for impact of x on variation in y. To quantify the impact of x on y, not only the sensitivity of y to x was investigated, but also the natural variation in x was taken into account. If y would be equally sensitive to changes in input parameters x_1 and x_2, but x_1 is rather constant whereas x_2 fluctuates strongly, then the variance of y should be attributed to x_2 rather than to x_1.

To gain insight into the influence of the considered input parameter on variation in y, different sources of variation in y have been distinguished:

$\sigma_{y,\omega}$ = standard deviation of y as found in orchards. Variation in y is not only caused by variation in T_{min}, T_{max}, and R, but also by variation in numerous other variables, e.g. soil water potential, leaf area index, and rootstock.

$\sigma_{y,n}$ = standard deviation of y, caused by simultaneous variation in n considered input parameters (T_{min}, T_{max}, and R; $n = 3$). T_{min}, T_{max}, and R vary simultaneously in mutual dependence. Other variables (e.g. soil water potential, leaf are index) are assumed to be constant;

$\sigma_{y,1}$ = standard deviation of y, caused by variation in only one input parameter ($n = 1$).

The impact of x on variation in y was quantified by means of S_σ, defined as:

$$|S_\sigma| = \frac{\sigma_{y,1}}{\sigma_{y,n}} \tag{3}$$

When an increase of x causes a decrease of y, S_σ is negative. Because the right hand term cannot be negative, S_σ is rendered as an absolute value.

The more the value of S_σ deviates from 0, the more the considered input parameter explains variation of the output variable. Note, however, that S_σ is not a measure of the importance of x in determining the magnitude of the output variable y, in contrast to S and $S_{\%}$ according to Equations (1) and (2).

Estimation method 1. It was not possible to estimate the real standard deviation $\sigma_{y,\omega}$ by means of the model. But $\sigma_{y,3}$ could be estimated by varying the parameter values of T_{min}, T_{max}, and R simultaneously, in mutual dependence, as found in reality. This was attained by using meteorological data from a weather station near Wageningen, the Netherlands, from 15 to 29 June of the years 1974-1988. Global radiation measurements were missing on four out of these $15 \times 15 = 225$ days, so that 221 complete daily records remained. For each of the 221 daily records the corresponding response y was calculated, running the simulation model. The standard deviation of these calculated y-values was the estimate of $\sigma_{y,3}$.

To estimate $\sigma_{y,1}$ (a measure of variation in y, caused by variation in one weather parameter), the simulation model was run 221 times, using the 221 measurements of one considered weather parameter as input values, and giving the other two weather parameters constant average values. The standard deviation of the 221 obtained y-values was the estimate of $\sigma_{y,1}$.

Estimation method 2. Rather than estimating $\sigma_{y,1}$ by means of running the simulation model 221 times, this standard deviation can be approximated by means of two runs of the model, using $\bar{x} + \sigma_x$ and $\bar{x} - \sigma_x$ as input values:

$$\sigma_{y,1} \approx \frac{|y_{\bar{x}+\sigma_x} - y_{\bar{x}-\sigma_x}|}{2} \tag{4}$$

where: $\bar{x}$ = the mean of x; σ_x = the standard deviation of x.

This approximation requires that the relationship between x and y is a linear one, which is often not the case in simulation models. Furthermore, for unbiased estimation of $\sigma_{y,1}$ using Equation , the frequency distribution of x has to be approximately symmetric. When both requirements are satisfied, y also has a symmetric distribution.

$\sigma_{y,1}$ can be substituted into Equation , giving

$$S_\sigma \approx \frac{(y_{\bar{x}+\sigma_x} - y_{\bar{x}-\sigma_x})}{2 \times \sigma_{y,3}} \tag{5}$$

Estimation method 3. S_σ can also be estimated by means of regression analysis. Coefficients of a multiple regression equation were estimated, using T_{min}, T_{max}, and R from the 221 weather records as explanatory variables, and the simulated y as dependent variable:

$$y = a + b_1 \times T_{min} + b_2 \times T_{max} + b_3 \times R \tag{6}$$

where: a = an estimate of the intercept; b_1, b_2, b_3 = regression coefficients.

The estimated regression coefficients were used to approximate $\sigma_{y,1}$:

$$\sigma_{y,1} \approx b \times \sigma_x \tag{7}$$

so that

$$S_\sigma \approx \frac{b \times \sigma_x}{\sigma_{y,3}} \tag{8}$$

In statistical a context, $b \times \sigma_x/\sigma_y$ is called standard regression coefficient (Snedecor and Cochran, 1980).

An important advantage of the regression method is that S_σ- values could be estimated of interaction terms, e.g. $T_{max} \times R$, and of higher-order terms, e.g. $(T_{max})^2$. One has to be aware, however, that estimations of regression coefficients are based on correlations between x and y, rather than on real cause-effect relations, so that this method may be misleading with respect to causal relationships.

Results

Impact of input parameters on the magnitude of the output variable

Table 1 shows calculated sensitivity coefficients S of y for T_{min}, T_{max}, and R. To calculate an S value, only one input parameter was varied at a time, while the other input parameters were kept constant (*ceteris paribus*). According to the model, y is

Table 1. Sensitivity of y to daily minimum and maximum temperature (T_{min} and T_{max}), and daily global radiation (R), applying the *ceteris paribus* rule. y represents the standardized relative growth rate of *Erwinia amylovora* (see text). S represents the sensitivity coefficient according to Equation , replacing the differential quotient by the corresponding difference quotient ($\Delta x = \pm 0.1 \times \bar{x}$). The values for $\bar{x}$ are based on $n = 221$ observations. The value of y is based on 2 simulation runs.

	Mean	$y_{1.1 \times \bar{x}}$	$y_{0.9 \times \bar{x}}$	Δy	Δx	$S = \Delta y/\Delta x$
T_{min} (°C)	10.1	0.388	0.353	0.035	2.02	0.017
T_{max} (°C)	19.7	0.436	0.306	0.129	3.94	0.033
R (J cm^{-2} day^{-1})	1630	0.367	0.371	−0.0043	326	−1.3E−5

most sensitive to T_{max} (S = 0.033 °C^{-1}; Table 1), and only half as sensitive to T_{min}. The reason for this is that the curve relating relative multiplication rate of *E. amylovora* (vertical axis) to temperature (horizontal axis; Schouten, 1987, Fig. 1) is steeper at the mean T_{max} value than at the mean T_{min} value, so that changes of T_{max} affect the relative multiplication rate of *E. amylovora*, and thus y, more than changes of T_{min} would do. The output variable y is hardly sensitive to global radiation (Table 1): High values of R reduce y only slightly ($S < 0$). Strong radiation increases the transpiration rate of fruit-trees (De Bruin, 1987), and therewith lowers the water potential of the shoot, and y (Schouten, 1991). With a dry soil y would have been more sensitive to R (Schouten, 1991).

The choice for a x of 10 % in Table 1 instead of e.g. 5 % or 25 % was arbitrary. A more complete image is given in Fig. 1, in which the relationships between the input parameters and y are depicted over ranges of input values. These input ranges equal the ranges of the values as measured at the weather station. The sensitivity coefficient S according to Equation (1) and given in Table 1 equals the slope of the straight line between the points ($0.9 \times \bar{x}$; $y_{0.9 \times \bar{x}}$) and ($1.1 \times \bar{x}$; $y_{1.1 \times \bar{x}}$). As expected from the S values in Table 1, this slope is smaller in the T_{min} - y graph (Fig. 1A) than in the T_{max} - y graph (Fig. 1B), and slightly negative in the R - y graph (Fig. 1C). Fig. 1 shows also that the three curves approximate straight lines, except at high values of T_{max}. This implies that S would hardly alter when not 10 % changes in the input parameters were chosen, but e.g. 5 % or 25 % changes.

Impact of input parameters on the variance of the output variable

Estimation method 1. Values of S_σ are given in Table 2, considering not only the sensitivity of y to the input parameters, but considering also the standard deviations of the input parameters. S_σ of T_{max} has the highest value, which means that among the three input parameters, variation in T_{max} has the highest impact on variation in y. According to the model, T_{max} is nearly three times as important as T_{min} in explaining variation in y, because first y is more sensitive to T_{max} than to T_{min} (Table 1), and second the standard deviation of T_{max} is larger than that of T_{min} (Table 2).

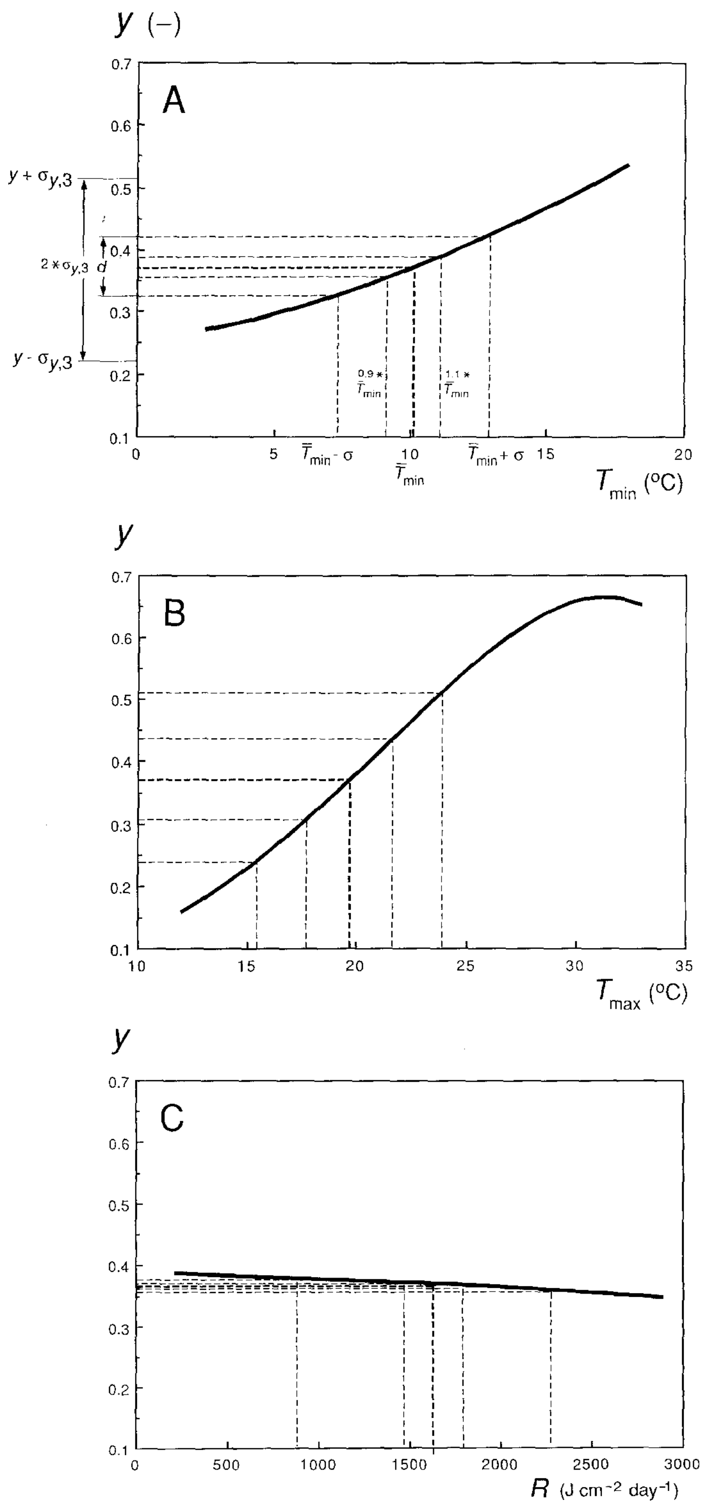
y (–)
A
y + σy,3
2 ∗ σy,3 d
y - σy,3
0.9 ∗ T̄min
1.1 ∗ T̄min
T̄min - σ
T̄min
T̄min + σ
Tmin (°C)
y
B
Tmax (°C)
y
C
R (J cm-2 day-1)

Fig. 1. Relationship between an input parameter and output parameter y, keeping other input parameters constant (*ceteris paribus*). S according to Equation (1) equals the slope of the straight line between the co-ordinate pairs $(0.9 \times \bar{x}\,;\, y_{0.9 \times \bar{x}})$ and $(1.1 \times \bar{x}\,;\, y_{1.1 \times \bar{x}})$. S_σ according to Equation (5) equals $d/(2 \times \sigma_{y,3})$ (Fig. 1A). Fig. 1B and 1C are similar to Fig. 1A. The five x values in each graph equal from left to right $\bar{x} - \sigma$, $0.9 \times \bar{x}$, $\bar{x}$, $1.1 \times \bar{x}$, and $\bar{x} - \sigma$, where σ represents the standard deviation of the input parameter x.

Table 2. The impact of T_{min}, T_{max}, and R on variation in y. $|S_\sigma|$ represents the standard deviation of y when one x varies ($\sigma_{y,1}$), divided by $\sigma_{y,3}$, the standard deviation of y when the three input parameters vary simultaneously in mutual dependence ($\sigma_{y,3} = 0.146$).

	σ_x	$\lvert S_\sigma \rvert$ Equation (3)	Approximation of S_σ Equation (5)
T_{min} (°C)	2.8	0.335	0.335
T_{max} (°C)	4.3	0.862	0.933
R (J cm^{-2} day^{-1})	641	0.062	−0.059*

* The minus sign indicates that increase of R leads to decrease of y.

Estimation method 2. Unbiased estimation of S_σ using Equations (4) and (5) demands a linear relationship between x and y, and a symmetric distribution of x. T_{min} and R satisfy those requirements (Figures 1 and 2), so that their approximations of S_σ according to Equation (5) were fairly close to the $|S_\sigma|$-values according to Equation , neglecting the minus sign of S_σ of R. T_{max}, however, does not fulfil the two conditions (Figures 1B and 2B). Therefore, the approximation of S_σ according to Equation (5) deviates somewhat from $|S_\sigma|$ according to Equation (3). The skewness of the T_{max} distribution is reflected in the distribution of y (Fig. 3).

$|S_\sigma|$ can be visualized in Fig. 1. $|S_\sigma|$ resembles $d/(2 \times \sigma_{y,3})$ in Fig. 1A when calculated according to Equation . Note that d has different values in Figures 1A, 1B and 1C, whereas $2 \times \sigma_{y,3}$ is constant.

Estimation method 3. Table 3 shows standard regression coefficients, estimated by means of multiple regression analysis. These standard regression coefficients are

Table 3. Regression coefficients of input parameters, selected by means of multiple regression analysis with stepwise backward variable selection (F-to-enter and F-to-remove equalled 40), explaining y ($R^2 = 0.99$, $n = 221$). The initial set of input parameters consisted of T_{min}, T_{max}, R, and their interaction terms. Only T_{min} and T_{max} were selected for the final set of input parameters. The standard regression coefficient equals S_σ according to Equation (8).

	Regression coefficient	Standard regression coefficient
T_{min} (°C)	0.017	0.32
T_{max} (°C)	0.027	0.80

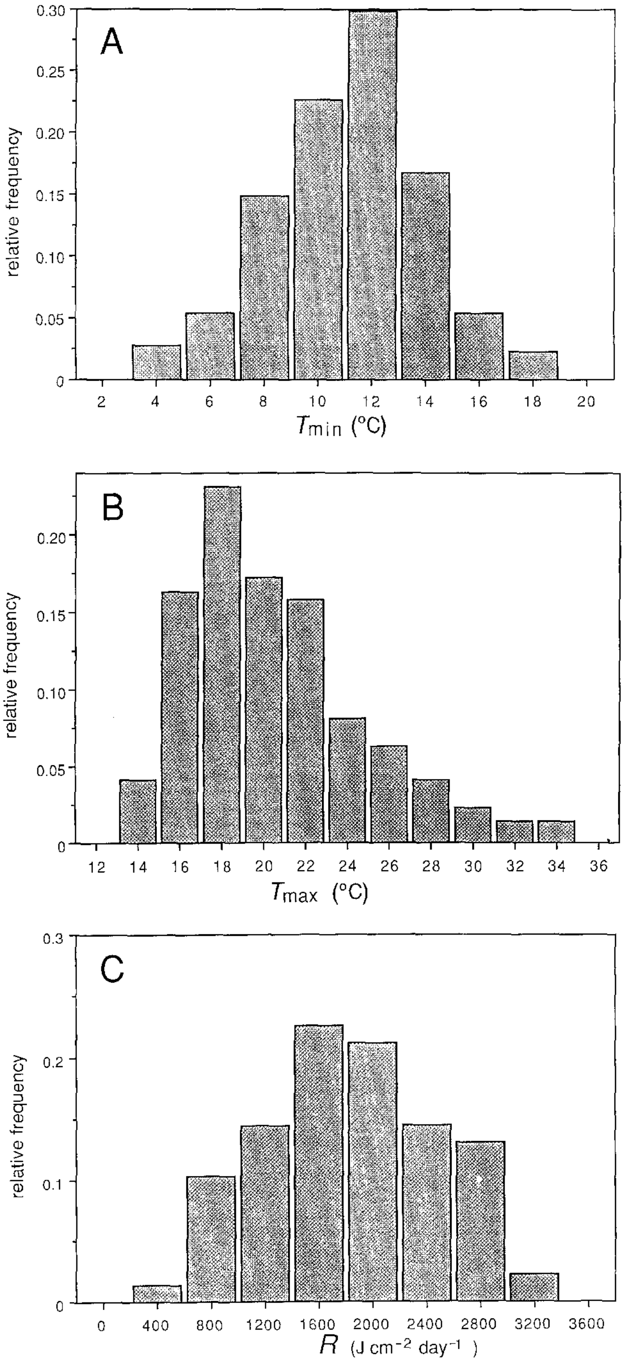

Fig. 2. The distributions of T_{min}, T_{max}, and R. The values on the horizontal axes equal the upper limits of the intervals. The daily records were obtained from a weather station near Wageningen, the Netherlands, and refer to the period 15 to 29 June of the years 1974-1988 (n = 221).

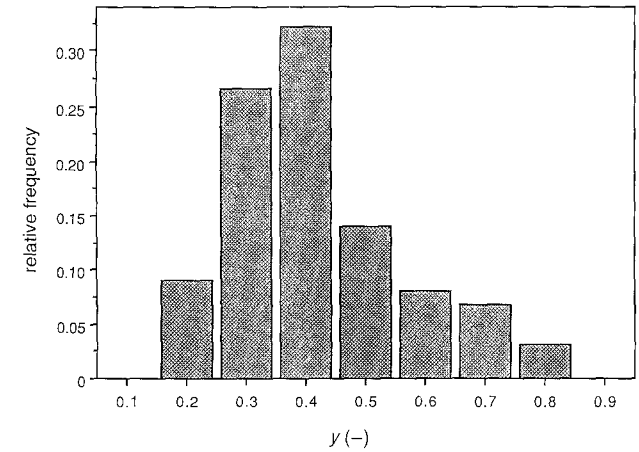

Fig. 3. The distribution of y when T_{min}, T_{max}, and R varied simultaneously in mutual dependence (n = 221).

approximations of S_σ. The initial set of input parameters consisted of simultaneously varying T_{min}, T_{max}, R, and their interaction terms ($T_{min} \times R$, $T_{max} \times R$, $T_{min} \times T_{max} \times R$). By means of multiple regression analysis with stepwise backward variable selection a final set was obtained, containing only input parameters which had high explanatory values simultaneously. The final set consists of only two input parameters, T_{min} and T_{max}. Daily global radiation (R) and the interaction terms were eliminated. The values of the regression coefficients and standard regression coefficients echo the values of S in Table 1 and of S_σ in Table 2. This implies that multiple regression analysis with stepwise variable selection revealed the causal relationships.

Discussion

One assumption of the model is that air temperature equals shoot temperature. Possible deviations from air temperature, because of e.g. heating by solar radiation at day-time, cooling by transpiration, and cooling by long wave radiation at night were not incorporated in the model. The effects of temperature and radiation on succulence and softness of the host (Barlow, 1975) were not simulated either, although Van der Zwet and Keil (1979) showed that succulent and soft tissue is more susceptible to fire blight than tough tissue.

The sensitivity of the standardized relative multiplication rate of *E. amylovora* to soil water potential was studied by means of a simulation model (Schouten, 1991). In this paper the water potential of the soil is assumed to equal −0.01 MPa constantly, which represents a moist soil. When the soil is moist, the water potential in shoots of fruit-trees is continuously high, and thus limits y only to a small extent (Schouten, 1991). For that reason, daily global radiation, which affects the transpiration rate of fruit-trees, and therewith the water potential of shoots, has a negligible effect on y in this paper. Limitations of y by temperature dominate limitations by water, when the soil is moist.

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