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Multiplication of Erwinia amylovora in fruit-trees. 1. A simulation study on limitations imposed by temperature and water, weather and soil

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Abstract

Temperature and water may limit multiplication of the fire blight causing bacterium *Erwinia amylovora* in shoots of fruit-trees. To gain insight into these limitation under field conditions, two simulation models were designed: a short-term model for immediate effects of weather and soil water potential, and a long-term model for effects of rain and soil profiles on the limitations imposed by temperature and water on bacterial multiplication.

In the Netherlands, in the month June, if the soil is moist and the weather 'average', water hardly limits *E. amylovora* multiplication in shoots but, according to the short-term model, temperature reduces then the multiplication by about 60 %. When the soil is dry and the potential transpiration rate of the trees high, water may limit *E. amylovora* multiplication in shoots considerably. According to the long-term model, rain has a delayed effect on multiplication. The effect of rain was simulated for three soil profiles representing three typical fruit growing areas in the Netherlands.

Additional keywords: fire blight, relative multiplication rate, water potential, rain, soil profile.

Introduction

Fire blight is a quarantine disease in the Netherlands. Dutch regulations prescribe that plants with fire blight (*Erwinia amylovora* (Burrill) Winslow et al.) have to be removed and destroyed (Anonymous, 1983, clause 8). This implies that no fire blight experiments can be done in the field. Only an inventory of host plants found to be diseased in spite of the regulations (Schouten, 1991a) was made in some parts of the Netherlands and analyzed statistically. The only trial field, isolated in the South-Western part of the Netherlands, where experiments on fire blight are allowed (Van der Scheer, 1984), was not well suited for pathophysiological experiments. An alternative is to simulate fire blight development by means of computer models, although validation of these models remains difficult.

The present models were designed to gain insight into the effect of temperature and water on the multiplication of *E. amylovora* in shoots of fruit-trees. The effects of

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temperature and water were simulated for different weather conditions, values of soil water potential, and soil profiles. The input parameters of the simulation models were meteorological variables as usually measured in weather stations, and commonly used soil entities and characteristics.

Two models were built: one short-term model for immediate effects of the environment, and one long-term model for delayed effects. The simulated period was 24 h in the short-term model and 40 days in the long-term model. In the short-term model, the water potential of the soil was assumed to be constant during the 24 hours' period, but in the long-term model the moisture profile of the soil was simulated dynamically.

Two models

The short-term model

Effect of water potential on the relative multiplication rate. As before (Schouten, 1991b), it is assumed that water potential, ψ, affects the relative multiplication rate, r, of *E. amylovora* according to Schouten (1988). This relationship is derived from in vitro and in vivo experiments by Shaw (1935).

$$r_\psi = r_{\max} \times f_\psi \tag{1}$$

with

$$0 \leq f_\psi \leq 1 \tag{2}$$

where: r = relative multiplication rate (hour^{-1}), the number of daughter bacteria per mother bacterium per hour. The subscript ψ denotes that r is affected by water potential; $r_{\max}$ = maximum value of r; f_ψ = variable relating r_ψ and $r_{\max}$.

Under humid conditions, when ψ approaches 0, r_ψ attains its maximum value, so that f_ψ approaches 1. Under dry conditions, when $\psi < -5$ MPa, the bacteria do not multiply, and f_ψ equals 0.

Effect of temperature on the relative multiplication rate. The relationship between temperature (T) and f_T ($= r_T / r_{\max}$) is derived from in vitro experiments (Billing, 1974) following Schouten (1987b).

$$f_T = \sin(4.2 \times 10^{-4} \times T^{2.46} \tag{3}$$

with

$$0 \leq f_T \leq 1 \tag{4}$$

The argument of the sine function is expressed in radians, and temperature in °C. At optimal temperature (T = 28 °C) f_T equals 1.

Regression analysis by Schouten (1987a) showed that temperature and rainfall affected the development rate of fire blight multiplicatively, hence:

$$r_{\psi,T} = r_{\max} \times f_\psi \times f_T \tag{5}$$

Output variables. The objective was to simulate the effect of water and temperature on the relative multiplication rate of *E. amylovora* in the intercellular space of a shoot of a fruit-tree. The output variables of the short-term model were $f_{\psi,T}$ *and* $\bar{f}_{\psi,T}$ ($= f_{\psi,T}$ averaged over a 24 hours' period).

$$f_{\psi,T} = f_\psi \times f_T \tag{6}$$

$$\bar{f}_{\psi,T} = \frac{1}{24} \int_0^{24} f_{\psi,T} \times \mathrm{d}t \tag{7}$$

where t = solar time (h).
Note that $f_{\psi,T}$ neither accounts for nutrition effects in intercellular spaces, nor for bacterial pressure and softness of host tissue, which can also affect the relative multiplication rate of *E. amylovora* in shoots (Schouten, 1991b).

Simulation of daily course of water potential. The daily course of water potential was simulated over a 24 hours' period for the calculation of f_ψ. The course of water potential in a shoot of a fruit-tree was simulated by means of a module derived from Powell and Thorpe (1977). This module, on water flows and water potentials in a tree, required the following inputs 1) water potential of the soil, and 2) actual daily transpiration of the tree. The water potential of the soil was assumed to be constant during the simulated 24 hours' period, and to equal the water potential of the shoot at night. The actual daily transpiration of the tree was assumed to equal the potential daily transpiration of the tree, which was derived from the potential daily evapotranspiration of an orchard (Table 1). For estimation of the potential daily evapotranspiration

Table 1. Methods and parameter values, used to estimate the actual daily transpiration per fruit-tree.

Reference crop evapotranspiration	according to the Makkink formula, which seems to be preferable to Penman's equation and the Penman-Monteith equation (De Bruin, 1987)
Crop factor of fruit orchard in June	1.6 (Feddes, 1987, Table 3)
Daily evaporation of bare soil under tree rows	derived from Ritchie (1972) according to Feddes et al. (1978, Equation (3.31))
Daily transpiration of the trees relative to daily transpiration of grass between the tree rows	4 : 1 (assumption)
Tree density	3200 trees per ha (modern Dutch pear orchard)

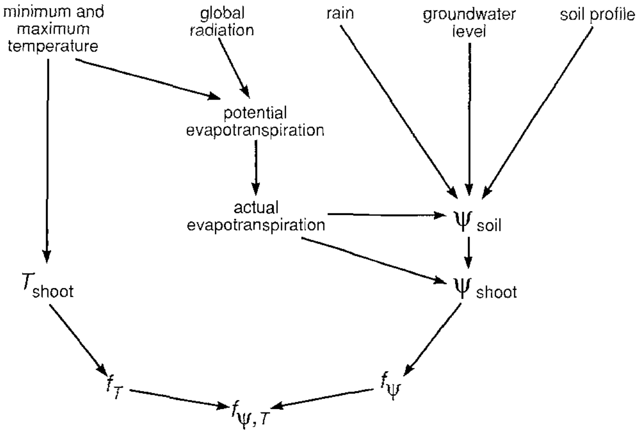


Fig. 1. Relational diagram of the major variables in the long-term model. Omission of the variables rain, ground water level, and soil type gives the relational diagram of the short-term model. T and ψ represent temperature and water potential, respectively, whereas f denotes the standardized relative multiplication rate of *Erwinia amylovora* in a shoot of a fruit tree, limited by T, by ψ, or by T and ψ simultaneously.

of an orchard the temperature course and daily global radiation were required, as shown in Fig. 1.

Simulation of daily course of temperature. The daily course of temperature of the shoot was simulated according to Schouten (1987b, Equations (2) to (5)), using the daily minimum temperature, daily maximum temperature, and day length as input parameters. It was assumed that the temperature of the shoot equalled air temperature, measured in a weather station. The temperature courses were converted into courses of f_T by means of Equation .

Input parameters. The short-term model was used to study the effects of four parameters on the relative multiplication rate of *E. amylovora* by temperature and water: 1) daily minimum temperature (T_{min}), 2) daily maximum temperature (T_{max}), 3) daily global radiation (R), and 4) water potential of the soil (ψ_{soil}). These parameters were used as inputs to the short-term model, as indicated in Fig. 1.

Examples of simulation runs. In order to gain insight into the daily courses of f_ψ, f_T and $f_{\psi,T}$ under different soil and weather conditions, the short-term model was run for 'average' soil water potential in combination with 'average' or sunny weather (Examples 1 and 2) and for a dry soil in combination with average, sunny, or cloudy weather (Examples 3, 4, and 5). The expression 'average' weather refers to the average values of T_{min}, T_{max}, and R measured by a synoptic weather station near Wageningen, the Netherlands, during the second half of June over the years 1974-1988. The exact input values of T_{min}, T_{max}, R and ψ_{soil} are given in Table 2. The daily potential transpiration refers to an orchard, and equals daily reference crop evapotranspiration times crop factor minus daily evaporation of soil (Table 1).

Table 2. Values of daily minimum and maximum temperature (T_{min}, T_{max}), daily global radiation (R), and water potential of the soil (ψ_{soil}), used as inputs to five example runs of the short-term model. The potential transpiration refers to an orchard, and is estimated according to Table 1.

Example	1	2	3	4	5
Weather	average	sunny	average	sunny	cloudy
Soil	moist	moist	dry	dry	dry
T_{min} (°C)	10	10	10	10	5
T_{max} (°C)	20	30	20	30	10
R (J cm^{-2} day^{-1})	1630	2600	1630	2600	260
potential transpiration (mm day^{-1})	4.0	7.0	4.0	7.0	0.5
ψ_{soil} (MPa)	−0.01	−0.01	−1.6*	−1.6	−1.6

* wilting point (J.A. Kipp, Institute for Soil Fertility, Haren, the Netherlands; personal communication).

Effect of water potential of the soil on $\bar{f}_{\psi,T}$. The effect of ψ_{soil} on the average $f_{\psi,T}$ over the simulated 24 hours' period ($\bar{f}_{\psi,T}$) was studied by running the short-term model repeatedly for a range of ψ_{soil} values (-1.6 MPa $< \psi_{soil} <$ 0 MPa), distinguishing the effects of sunny and 'average' weather.

The long-term model

The soil water profile was simulated dynamically by means of the model SWACROP (Feddes et al., 1978). SWACROP is a FORTRAN program for simulation of the water balance of a cropped soil. In the model the soil is divided into compartments of equal size with a nodal point in the centre of each compartment. Variables, calculated for each time step during a run of SWACROP, were a.o. water potentials of the nodal points, water flows from compartments to neighbour compartments, and water uptake from each compartment by plant roots. The rate of water uptake by plant roots was a function of the quotient of the potential transpiration rate and the number of soil compartments with roots, and also a function of the matrix potential of the considered compartment (Feddes et al., 1978; Fig. 7). For each simulated day, the soil moisture profile was converted into a weighted average of the water potentials of the soil compartments, using the rates of water uptake by plant roots from the compartments as weights.

$$\psi_{soil} = \frac{1}{\sum S_z} \times \sum_{z=1}^{L} (\psi_z \times S_z) \qquad (8)$$

where: ψ_{soil} = weighted average of the water potentials of the soil compartments on the considered day (MPa); S_z = rate of water uptake by roots from layer z (mm/day); L = rooting depth, expressed in number of compartments with roots; ψ_z = water potential (MPa) of soil compartment z. The water potential is composed of matrix potential and gravitational potential, ignoring osmotic and pneumatic potential (Feddes et al., 1978). The gravitational potential is assumed to be 0 at the soil surface.

ψ_{soil} was an input parameter of the short-term model, and thus functioned as the link between SWACROP and the short-term model. Calculating ψ_{soil} by means of SWACROP and Equation (8) for a series of days, and running the short-term model for each of these days, gave the long-term course of $f_{\psi,T}$.

The updated version of SWACROP, issued in March 1989, was used. This version has many options for dealing with the ground water table, weather, soil profiles, etc. (Wesseling et al., 1989). The options chosen for the long-term model are given in Table 3.

Table 3. SWACROP options chosen and input parameter values (Feddes et al., 1978; Wesseling et al., 1989) used for dynamic simulation of the soil moisture profile in the long-term model.

Simulated period	from 15 June till 5 August
Potential evapotranspiration	constant over all runs; calculated for 'average' weather (Table 2), using Makkink's equation and a crop factor (Table 1)
Rain	no rain, except on the third simulation day (17 June); no irrigation
Ground water level	input parameter; constant during a run
Initial soil moisture profile	initial matrix potential constant over the rooting depth and under the roots linearly increasing to 0 at ground water level
Thickness of compartments	10 cm each
Water uptake by roots	according to Feddes et al. (1978; Fig. 7), with $\psi_1 = -10^{-5}$ MPa, $\psi_2 = -3 \times 10^{-2}$ MPa, and $\psi_3 = -1.6$ MPa

Input parameters. Input parameters of the long-term model were (Fig. 1) 1. rain on the third simulation day, and no rain during the other days; 2. soil profile. The soils were characterized by means of soil moisture retention and hydraulic conductivity curves of Dutch top- and subsoils according to Wösten et al. (1986); 3. ground water level (Fig. 1).

The long-term model was run for three characteristic soils of Dutch fruit growing areas (Table 4). For T_{min}, T_{max}, and R constant average values were chosen (Table 2, 'average' weather).

Output variable. Simulated was the effect of rain on the course of $\bar{f}_{\psi,T}$. The output variable was $\Delta\bar{f}$, which equals $\bar{f}_{\psi,T}$ when it rains on the third simulation day minus $\bar{f}_{\psi,T}$ when there is no rain during the simulation period.

Table 4. Three characteristic soils of Dutch fruit growing areas (J.A. Kipp, personal communication), used as example soils for runs of the long-term model. The soil codes (B8, O1, and O12) refer to soil moisture retention and hydraulic conductivity curves of Wösten et al. (1986).

Dutch fruit growing area	Betuwe	IJsselmeer polders	Zeeland
Soil type (code)	0 - 200 cm: clay (O12)	0 - 200 cm: sandy loam (B8)	0 - 60 cm: sandy loam (B8) 60 - 200 cm: sand (O1)
Groundwater level (cm)	80 - 100	140 - 180	80 - 160
Rooting depth (cm)	60	120	60

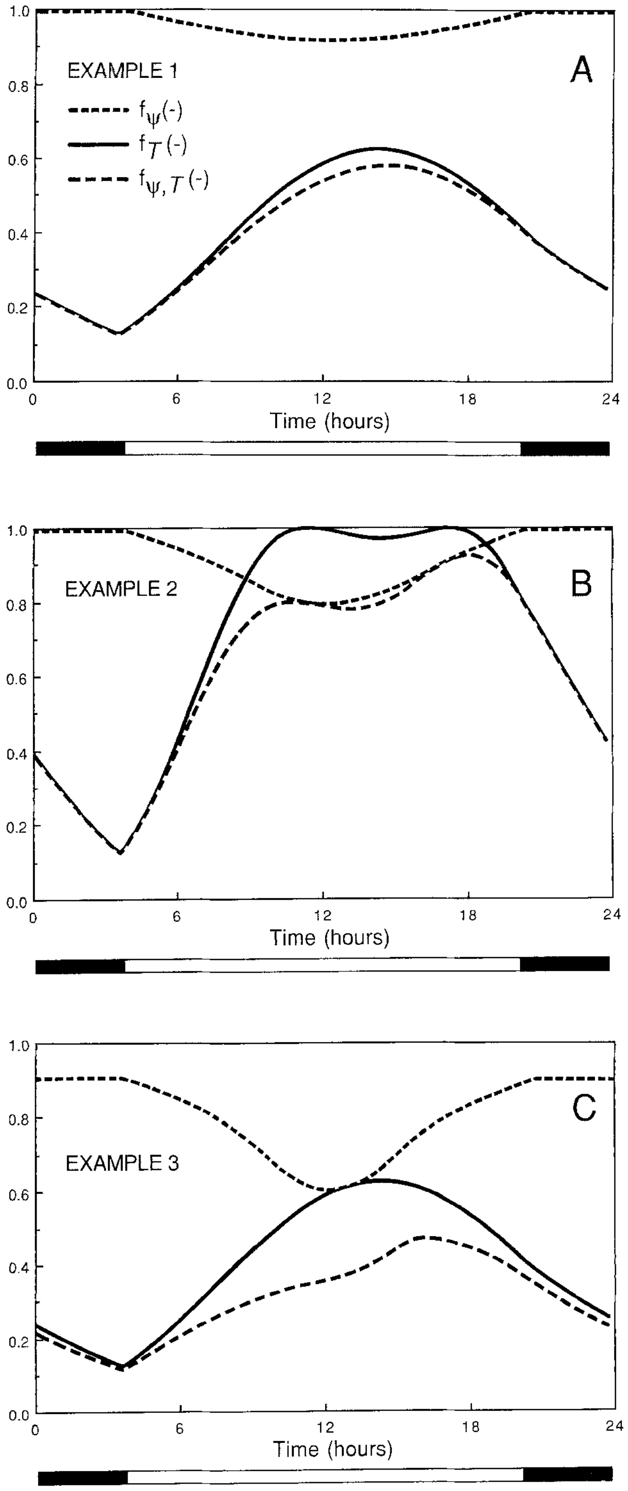
Results

The short-term model

Examples of simulation runs. The simulated courses of the factors f_ψ, f_T, and $f_{\psi,T}$ ($= f_\psi \times f_T$) for 'average' weather and moist soil (Example 1 in Fig. 2A) indicate that at night, when ψ_{shoot} approaches ψ_{soil}, water does not limit multiplication of *E. amylovora*. At noon, the transpiration rate of the tree reaches its maximum value, so that ψ_{shoot} and f_ψ reach their lowest values, but even then water hardly limits multiplication of *E. amylovora* ($f_\psi = 0.91$), because of good water uptake from the soil by the roots. Temperature limits *E. amylovora* multiplication far more, even at noon, so that $f_{\psi,T}$ follows f_T closely in Example 1.

For Example 2 (Fig. 2B) the daily courses of f_ψ, f_T, and $f_{\psi,T}$ were simulated for sunny weather and a moist soil. As in the previous example, f_ψ approaches 1 at night time, but at midday water limits *E. amylovora* multiplication indeed, because of the high transpiration rate of the tree. In the afternoon the global radiation decreases, followed by a decrease of temperature, so that the transpiration rate slows down. Consequently, ψ_{shoot} and f_ψ increase. Temperature and f_T are higher than in the previous example during the whole 24 hours' period except at dawn, when temperature has its minimum value (10 °C). At about noon temperature reaches the optimal value for multiplication of *E. amylovora* (28 °C), so that f_T equals 1. At 14:20 hour, temperature equals $T_{\max}$ (30 °C), which is above the optimal temperature. Then, f_T is below 1. Somewhat later, temperature is optimal again, giving rise to a second peak in the f_T course. The daily course of $f_{\psi,T}$ in this example is not only greatly affected by the f_T course, but also by the f_ψ course. Note that temperature strongly affects the transpiration rate (De Bruin, 1987), and thereby f_ψ, so that temperature influences $f_{\psi,T}$ directly via f_T and indirectly via f_ψ.

In Examples 3, 4, and 5 the soil is so dry that the trees are about wilting at noon in case of average weather ($\psi_{\mathrm{soil}} = -1.6$ MPa; J.A. Kipp, personal communication; Feddes et al., 1978). In Example 3 the factors are simulated for average weather (Fig. 2C). The f_T course of Example 3 equals that of Example 1, because of identical temperature courses. The f_ψ course, however, differs greatly from that in Example

1.0
0.8
0.6
0.4
0.2
0.0
EXAMPLE 1
A
$f_{\psi}(-)$
$f_{T}(-)$
$f_{\psi,T}(-)$
0
6
12
18
24
Time (hours)
EXAMPLE 2
B
EXAMPLE 3
C

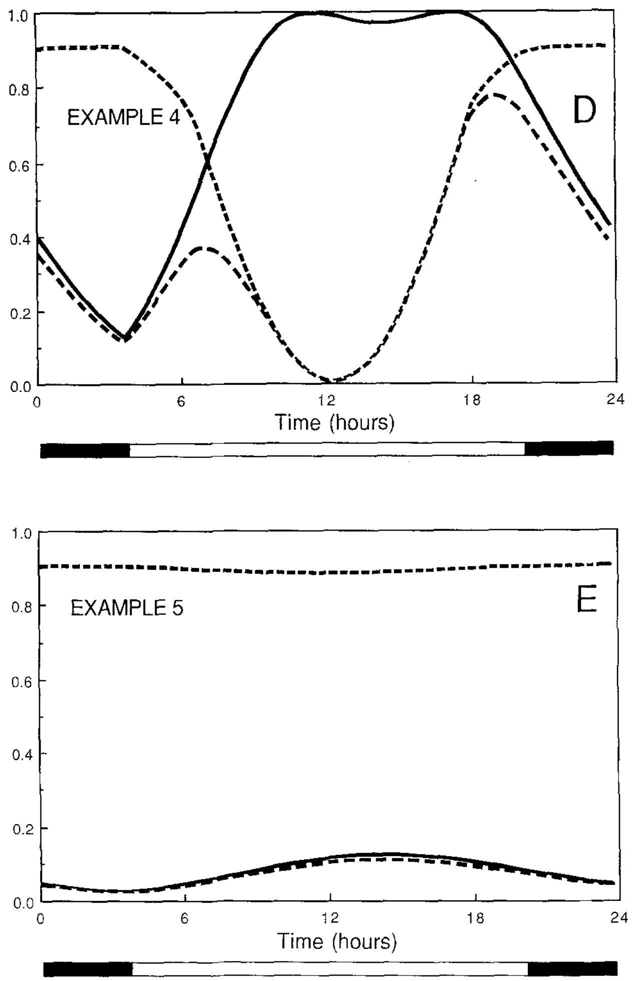


Fig. 2. Five simulated examples, illustrating effects of weather and soil water potential on the daily courses of f_ψ, f_T, and $f_{\psi,T}$. Table 2 gives the input parameter values used in the five examples. The day-night rhythm is displayed by horizontal white-black bars.

1. At night f_ψ does not approach 1, as in Example 1 and 2, because *E. amylovora* multiplication is noticeably reduced at $\psi = -1.6$ MPa, but not at $\psi = -0.01$ MPa (Schouten, 1987b). During daytime, f_ψ has lower values in Example 3 than in Example 1.

The factors at sunny weather and dry soil are simulated in Example 4 (Fig. 2D). f_ψ and thus $f_{\psi,T}$ fall nearly to 0 at about noon. Later, ψ, f_ψ and $f_{\psi,T}$ increase (because of decreasing transpiration rate), $f_{\psi,T}$ reaches a maximum value and decreases again during the evening and night because of decreasing temperature. This example indicates that a dry soil, combined with a high potential transpiration rate, reduces *E. amylovora* multiplication in the tree dramatically.

At dry soil and low potential transpiration rate (Example 5, Fig. 2E) f_ψ has high

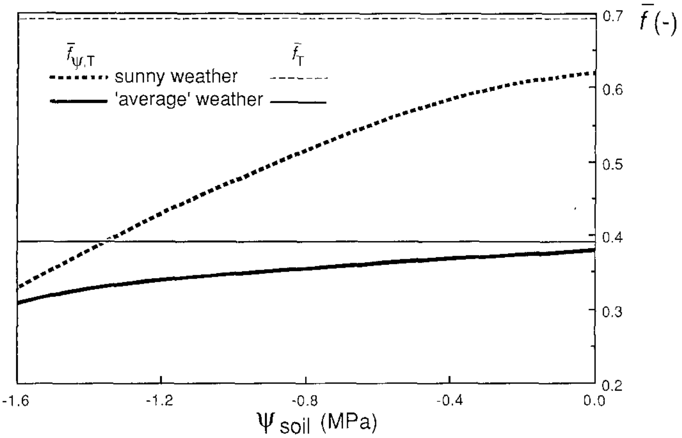


Fig. 3. Standardized relative multiplication rates $\bar{f}_{\psi,T}$ and $\bar{f}_T$ in simulated dependence of water potential of the soil (ψ_{soil}) at sunny weather (T_{min} = 10 °C, T_{max} = 30 °C, R = 2600 J cm^{-2} day^{-1}) and at 'average' weather (T_{min} = 10 °C, T_{max} = 20 °C, R = 1630 J cm^{-2} day^{-1}). $\bar{f}_{\psi,T}$ (heavy lines) and $\bar{f}_T$ (thin lines) represent $f_{\psi,T}$ and f_T, respectively, averaged over a 24 hours' period.

values, but in spite of this the bacterial multiplication may be slow because of low temperatures, which coincide with low potential transpiration rates.

Effect of water potential of the soil on $\bar{f}_{\psi,T}$. Fig. 3 shows the dependence of $\bar{f}_{\psi,T}$ on water potential of the soil (ψ_{soil}) during sunny weather and 'average' weather. $\bar{f}_{\psi,T}$ represents $f_{\psi,T}$, averaged over a 24 hours' period with constant ψ_{soil} over that period. The graph indicates that $\bar{f}_{\psi,T}$ is higher at sunny weather than at 'average' weather, as in Figures 2A and 2B. The high values of $\bar{f}_{\psi,T}$ during sunny weather are caused by the high T_{max} value via a high $\bar{f}_T$ value. The $\bar{f}_T$ values (f_T averaged over a 24 hours' period) at sunny and at average weather are also rendered in Fig. 3 as thin horizontal lines. When ψ_{soil} decreases, $\bar{f}_{\psi,T}$ decreases somewhat at average weather. This decrease is caused by decreasing $\bar{f}_\psi$, as $\bar{f}_T$ is constant. The small decrease of $\bar{f}_{\psi,T}$ indicates that this variable is not very sensitive to ψ_{soil} at average weather. At sunny weather, however, $\bar{f}_{\psi,T}$ decreases strongly at decreasing ψ_{soil}. When the soil is dry, water uptake by the roots is slow, so that ψ_{shoot} is low at high potential transpiration rates. The low f_ψ during the day compensates the high f_T, to give a moderate $\bar{f}_{\psi,T}$.

The two $\bar{f}_{\psi,T}$ curves in Fig. 3 are not parallel, which means that the sensitivity of $\bar{f}_{\psi,T}$ to ψ_{soil} depends on weather. In statistical terms: there is an interaction between ψ_{soil} and weather with respect to the effect on $\bar{f}_{\psi,T}$.

The long-term model

Fig. 4 shows the time course of $\Delta\bar{f}$, the standardized relative multiplication rate of *E. amylovora* when it rains during one day, indicated by an arrow, minus the standardized relative multiplication rate when there is no rain during the simulated period. The graph indicates that for the chosen conditions (clay; ground water level

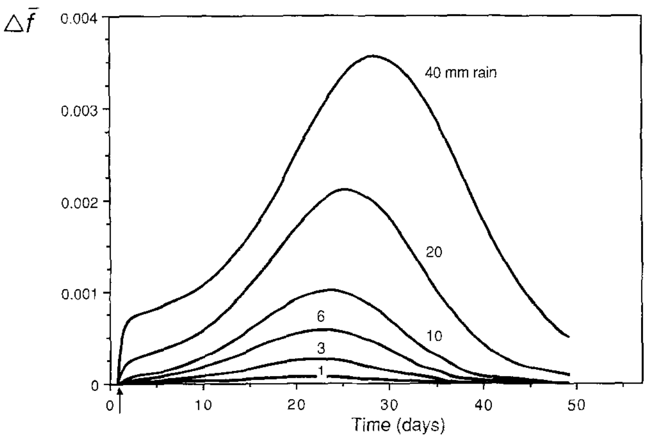


Fig. 4. Simulated effect of a day's rain on $f_{\psi,T}$ in the course of time at 'average' weather. $\Delta\bar{f}$ represents the standardized relative growth rate of *E. amylovora* when it rains during the one day indicated by an arrow, minus the standardized relative growth rate when there is no rain during the simulated period. The different curves refer to different amounts of rain. Soil: clay (see Table 4, fruit growing area Betuwe); Groundwater level = 80 cm; $\psi_{\text{soil}} = -0.04$ MPa on day = 0.

= 80 cm; $\psi_{\text{soil}} = -0.04$ MPa on day = 0; average weather) the effect of rain on $\Delta\bar{f}$ starts immediately, increases gradually in course of time, reaches its maximum from 25 days after a 1 mm rain fall to 30 days after a 40 mm rain fall, and decreases finally. In case of little rain, evapotranspiration exhausts the amount of rain water earlier than in case of much rain, so that the tops of the curves in Fig. 4 move slightly to the right at increasing rain fall.

The effect of rain on $\bar{f}$ looks small ($\Delta\bar{f} < 0.004$ in Fig. 4). This agrees with Fig. 3 where an increase of ψ_{soil} from -0.04 MPa to nearly 0 MPa hardly raises $\bar{f}$. Moreover, the increase of ψ_{soil} after a rain shower is often small, because the amount of water from a rain shower is usually small compared to the water holding capacity of soil integrated over the rooting depth. But because the effect of a rain shower lasts for a long period (more than 40 days), the total effect of a short rain fall is significant. In Fig. 4, the area under the curve of the 40 mm rain fall equals 0.1 day, which represents the accumulated effect on $\bar{f}$. At sunny weather the accumulated effect would be stronger (Fig. 3).

Obviously, the effect of rain has a strong delay. This is mainly caused by the hydraulic conductivity of the soil, which is small for a clay soil (Fig. 5A), so that it takes a long time before rain water is spread over all rooted layers, and water uptake by the tree reaches its maximum.

Fig. 6A depicts time courses of $\Delta\bar{f}$ at different initial soil moisture contents when a fixed amount of water is added to the soil (30 mm). Three phenomena in Fig. 6A draw attention: 1. The dryer the soil, the higher the top of the curve; 2. the dryer the soil, the earlier $\Delta\bar{f}$ reaches its maximum; 3. the areas under the three curves are approximately equal. The reason for the first phenomenon (the dryer the soil, the higher the top) is that the matrix potential of the soil, and by that ψ_{soil} and $\bar{f}_{\psi,T}$, raises

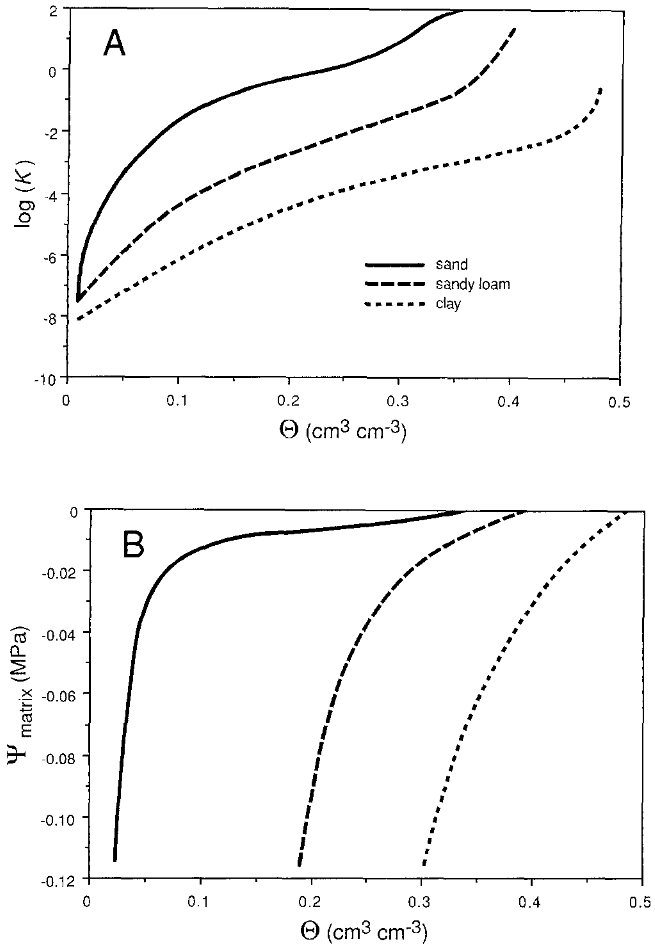


Fig. 5. Hydraulic conductivity (K in cm day^{-1}) and matrix potential (ψ_{matrix}) of the soil, in relation to soil water content (θ) (from Wösten et al., 1986).

more in case of a dry soil than in case of a moist soil: the curve which relates soil water content to matrix potential of the soil is steeper at low than at high soil moisture contents (Fig. 5B). The explanation for the second phenomenon (the dryer the soil, the earlier $\Delta\bar{f}$ reaches its maximum) is that the plant roots absorb from a moistened soil not only water which comes from the 30 mm rain fall, but also water which was present before the rain. Moreover, the roots absorb water ascending from the ground water table by capillary suction. The moist soil had a higher ground water level than the dryer soils. The uptake of rain water is then less fast, and so the rain has a longer effect. The third phenomenon (the areas under the curves are approximately equal) indicates that an isolated precipitation of 30 mm in a continuum of dry weather has the same effect on $\Delta\bar{f}$, integrated over time ($\int\Delta\bar{f}\mathrm{d}t \approx 0.08$ days), over a wide range of soil moisture contents.

Whereas Fig. 6A refers to clay and rather undeep rooting (60 cm), Fig. 6B refers

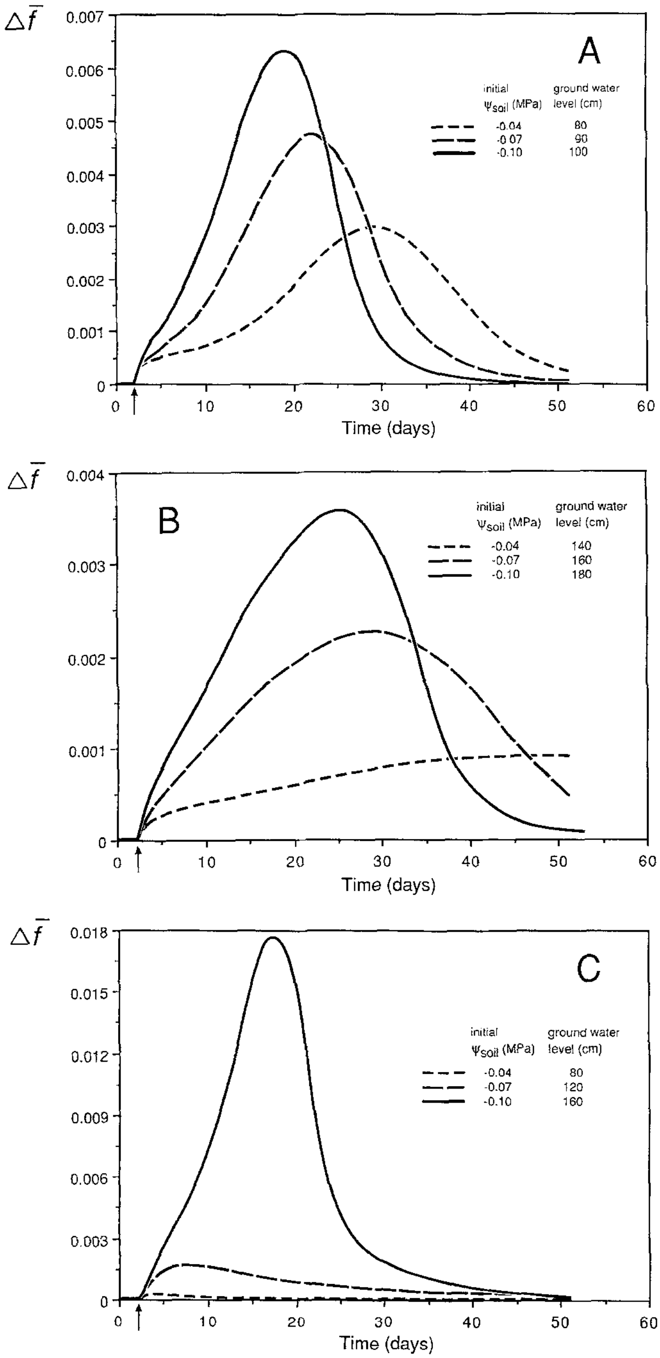


Fig. 6. Simulated time courses of $\Delta\bar{f}$ for a 30 mm rainfall on the day indicated by an arrow. T_{min}, T_{max}, and R have average values continuously (T_{min} = 10 °C, T_{max} = 20 °C, R = 1630 J cm^{-2} day^{-1}). Fruit growing areas: A. Betuwe; B. IJsselmeer polders; C. Zeeland (see Table 4).

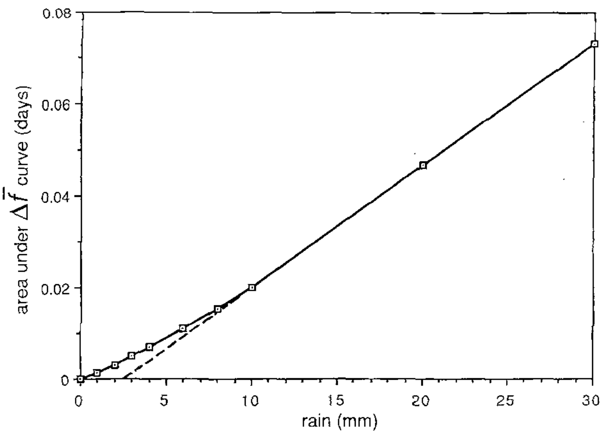


Fig. 7. Effect of the amount of rain on $\Delta\bar{f}$, integrated over the simulation period. Environmental conditions as in Fig. 4.

to sandy loam and deep rooting (120 cm). The stronger delay of the rain effect is caused by the deeper rooting. A part of the delay by deeper rooting is compensated by higher hydraulic conductivity of sandy loam as compared to clay (Fig. 5A). The areas under the curves are virtually equal again (the curve which refers to an initial ψ_{soil} of -0.04 MPa is not complete for reasons of scale), and approximately equal the areas under the curves of Fig. 6A.

Fig. 6C, which refers to a profile with sandy loam as topsoil and sand as subsoil, differs strongly from Figures 6A and B. The first phenomenon (the dryer the soil, the higher the top) holds even more convincingly, but the other two phenomena do not hold at all. The top soil of Fig. 6C with an initial ψ_{soil} of -0.1 MPa has a low hydraulic conductivity. Moreover, the dry top soil has a large water holding capacity (Fig. 5B), so that the rain water barely flows into the subsoil, but remains in the topsoil where it can be optimally absorbed by the roots. The area under the curve equals 0.25 days, whereas the areas under the curves in Figures 6B and B equalled about 0.08 days.

The hydraulic conductivity of the moister soil in Fig. 6C (initial $\psi_{\text{soil}} = -0.04$ MPa) is high, so that rain water sinks fast through the thin root layer into the sand, where no roots are present (Table 4). Therefore, rain has only a short-lasting and small effect.

Fig. 7 shows an example of the simulated effect of amount of rain on $\bar{f}$. The curve is approximately linear, which means that an increase from 0 to 1 mm rain raises $\bar{f}_{\psi,T}$ about as much as an increase from 20 to 21 mm rain, a counter-intuitive result. A close look to the graph reveals that at small amounts of rain the curve is even less steep than at high amounts of rain. This is caused by interception of rain by leaves, so that only a part of the rain reaches the soil. The maximum interception rate by the leaves equals about 2 mm rain per day (Feddes et al., 1978, Fig. 32).

Discussion

The short-term and long-term models were designed to simulate effects of temperature and water on multiplication of *E. amylovora* in shoots. Temperature and water affect *E. amylovora* in shoots not only directly but also indirectly via the growth rate of the host (Barlow, 1975). Fast growing, succulent tissue is more susceptible to fire blight than tough tissue (Van der Zwet and Keil, 1979). Effects of temperature and water on growth rate, succulence, and softness of host tissue, and therewith on multiplication rate of *E. amylovora* in the intercellular space of that tissue, were not incorporated in the model. Differences in tree nutrition from the different soils were not taken into account.

Debatable in both short-term and long-term models is the assumption that the actual transpiration rate equals the potential transpiration rate. Especially at dry soils, the actual transpiration may be slower than the potential transpiration, because of closing of the leaf stomata. For that reason the simulated water potential of the shoot may be lower than actual water potentials of shoots. This would lead to underestimation of f_ψ when the soil is dry and the potential transpiration rate high. On the other hand f_ψ may be overestimated in case of dry soils, because a dry soil reduces the growth rate of shoots (tissues less succulent), and so decreases the relative multiplication rate of *E. amylovora* in the shoots. These over- and underestimations may partly compensate each other.

Regression analysis, using observed incubation periods of fire blight, and temperature and rain data from weather stations as inputs (Schouten, 1987a), revealed that both temperature and rain fall were positively correlated with development rate of fire blight in hosts. Temperature was more important than rain fall in explaining variation in the development rate. These regression results do not contradict the results in this paper, though the delay in the effect of rain comes as a surprise. The near-linear relationship between amount of rain and $\bar{f}$ demonstrated by simulation, may provide a refinement of the classical rainfall classification (rainfall = 0; < 2.5 mm; ≥ 2.5 mm; Billing, 1976).

When the soil is dry (water potential of the soil below -1 MPa), limitations by water are important, so that progress of the disease through the host tissue may cease more often. Particularly in the Mediterranean area, where fire blight invaded several countries recently (Zutra et al., 1986; Psallidas, 1990), soils are often dry, but temperatures are high compared to Dutch circumstances. In those countries it might be useful to reduce irrigation in orchards with fire blight, so that 1) the multiplication rate of and pressure by *E. amylovora* in intercellular spaces of hosts is reduced (Schouten, 1991b), and 2) host tissues becomes tougher. Then, the diseased tissues can be effectively sealed off by the host plants, reducing oozing of the pathogen and damage to infected trees.

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References

Anonymous, 1983. Besluit bestrijding bacterievuur 1983. Staatsbladen van het Koninkrijk der Nederlanden: 641.

Barlow, H.W.B., 1975. Effects of temperature on apple shoot growth. In: Pereira, H.C. (Ed.), Climate and the orchard. Effects of climatic factors on fruit tree growth and cropping in south-eastern England. Commonwealth Agricultural Bureaux, Slough, England. p. 41-50.

Billing, E., 1974. The effect of temperature on the growth of the fireblight pathogen, *Erwinia amylovora*. Journal of Applied Bacteriology 37: 643-648.

Billing, E., 1976. Weather and fireblight in England. Annals of Applied Biology 82: 259-266.

De Bruin, H.A.R., 1987. From Penman to Makkink. In: Hooghart, J.C. (Ed.), Evaporation and weather. Proceedings and Information No. 39, TNO Committee on Hydrological Research. CHO, the Hague. p. 5-31.

Feddes, R.A., 1987. Crop factors in relation to Makkink reference- crop evaporation. In: Hooghart, J.C. (Ed.), Evaporation and weather. Proceedings and Information No. 39, TNO Committee on Hydrological Research. CHO, the Hague. p. 33-45.

Feddes, R.A., Kowalik, P.J. & Zaradny, H., 1978. Simulation of field water use and crop yield. Simulation Monographs. Pudoc, Wageningen, the Netherlands. 189 pp.

Powell, D.B.B. & Thorpe, M.R., 1977. Dynamic aspects of plant-water relations. In: Landsberg, J.J. & Cutting, C.V. (Eds), Environmental effects on crop physiology. Academic Press, London. p. 259-279.

Psallidas, P.G., 1990. Fire blight of pomaceous trees in Greece. Evolution of the disease and characteristics of the pathogen *Erwinia amylovora*. Acta Horticulturae 273: 25-32.

Ritchie, J.T., 1972. Model for predicting evaporation from a row crop with incomplete cover. Water Resources Research 8: 1204-1213.

Schouten, H.J., 1987a. Confidence intervals for the estimation of the incubation period of fire blight following Billing's prediction system 1. Netherlands Journal of Plant Pathology 94: 49-53.

Schouten, H.J., 1987b. A revision of Billing's potential doublings table for fire blight prediction. Netherlands Journal of Plant Pathology 93: 55-60.

Schouten, H.J., 1988. Notes on the role of water potential in the pathogenesis of fire blight, caused by *Erwinia amylovora*. Netherlands Journal of Plant Pathology 94: 213-220.

Schouten, H.J., 1991a. Simulation of pressure caused by multiplication and swelling of *Erwinia amylovora* in intercellular space of host tissue. Netherlands Journal of Plant Pathology 97: 139-149.

Schouten, H.J., 1991b. The effectiveness of flowering prevention of hawthorns to control fire blight in pear orchards. Submitted to Netherlands Journal of Plant Pathology.

Shaw, L., 1935. Intercellular humidity in relation to fire-blight susceptibility in apple and pear. Cornell University Agricultural Experiment Station, Ithaca, New York. nr. 181, 40 pp.

Van der Scheer, H.A.Th., 1984. The experimental garden for research on fire blight at Ouwerkerk, the Netherlands. Acta Horticulturae 151: 291-292.

Van der Zwet, T. & Keil, H.L., 1979. Fire blight. A bacterial disease of rosaceous plants. Agriculture handbook nr. 510. Washington: United States Department of Agriculture. 200 pp.

Wesseling, J.G., Kabat, P., Van den Broek, B.J., & Feddes, R.A., 1989. SWACROP. Simulation model of the waterbalance of a cropped soil with different types of boundary conditions including the possibility of drainage and irrigation and the calculation of crop yield. Instructions for input. The Winand Staring Centre for Integrated Land, Soil, and Water Research, Wageningen, the Netherlands. 30 pp.

Wösten, J.H.M., Bannink, M.H., & Beuving, J., 1986. Waterretentie- en doorlatendheidskarakteristieken van boven- en ondergronden in Nederland: de Staringreeks. Herziene versie. ICW-rapport 18, STIBOKA-rapport 1932, Wageningen, the Netherlands. 75 pp.

Zutra, D., Shabi, E., & Lazarovits, G., 1986. Fire blight on pear, a new disease in Israel. Plant Disease 70: 1071-173.