

## Development of ZWIPERO, a model forecasting sporulation and infection periods of onion downy mildew based on meteorological data

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### Abstract

The weather-based forecasting model ZWIPERO was developed by the German Weather Service and determines the risk of sporulation and infection of *Peronospora destructor* quantitatively based on actual as well as predicted weather data (temperature, relative humidity, leaf wetness, precipitation). The model allows precise planning of disease monitoring and infection-related application of fungicides. ZWIPERO is a more complex mathematical model than the previously published models for downy mildew. In order to operate ZWIPERO independently of the actual field location and season, the time of sunrise and sunset of the location are exactly determined by a subroutine. Another subroutine provides simulated microclimatic input variables based on local production data as well as actual and hourly predicted (up to 4 days) standard weather data. Starting at the time of 'sunrise + 7 h', ZWIPERO calculates the number of sporangia produced, the time of onset of sporangia release, as well as the number of infections possible and the number of sporangia which may survive the day for each 24-h time step. Field evaluations of sporulation periods of downy mildew showed that the simulated micrometeorological input variables are reliable. As the actual plant development, the susceptibility and the disease incidence in the field are not taken into account, ZWIPERO has to be considered primarily as a decision support system for extension services and growers.

### Introduction

Downy mildew of onion, caused by *Peronospora destructor* (Berk.) Casp. in Berk. occurs in most onion-producing regions throughout the world (Cook, 1932; Yarwood, 1943; Schwartz and Mohan, 1995). The disease can cause serious losses within a short period of time during cool and humid weather conditions (Berry, 1959). In Germany, especially in regions of extensive onion production like the Palatinate in the Southwest, the incidence and the severity of downy mildew has increased in recent years. Several circumstances contribute to this development. The production area of

bunching onions nearly doubled in the last two years. Bunching onions are also grown throughout the year and thus offer a continuous source of sporangia for new infections. Additionally, the new early-ripening high quality varieties of spring sown onions are much more susceptible to downy mildew.

Generally, preventive fungicide sprays are scheduled 7–10 days apart to control downy mildew and to ensure good yields and high crop quality (Palti, 1989; de Visser, 1998). In Germany, in addition to fungicides with protective activity, only the phenylamide fungicide metalaxyl is used, which shows curative activity against downy mildew in onions. However, strains

of *P. destructor* tolerant towards metalaxyl have been detected in Australia (O'Brien, 1992). Several other downy mildews, for instance *P. tabacina* (Wiglesworth et al., 1988; Tuzun et al., 1992) and *P. parasitica* (Vishunavat et al., 1998) show similar tolerance to metalaxyl.

On the other hand, periods of several weeks with unfavourable weather conditions for infection and disease spread occur rather frequently during an onion growing season. Fungicide applications undertaken during these periods are economically and ecologically superfluous. To make infection-related disease control possible, the first forecasting model for downy mildew of onion, DOWNCAST, was developed by Jespersen and Sutton (1987) in Canada. This model was improved by de Visser (1998), who adapted DOWNCAST to the conditions in the Netherlands. Both models determine whether an infection is possible or not according to weather data measured within the canopy (negative prognosis). In contrast, the forecasting model ONIMIL, developed by Battilani et al. (1996) in Italy, provides a quantitative output of the infection risk based on data of a standard weather station in the field. A common feature of these models is, that only actual data are provided and infection risk is determined after an infection has already occurred. As a consequence, only fungicides with curative activity can be applied, enhancing the risk of selecting fungicide-resistant *Peronospora* isolates.

The aim of this work was to develop a mathematical model for *P. destructor* which enables a true sporulation and infection forecast and, thus, a timely use of protectants. This approach is supported by the availability of simulated microclimatic input variables which can be predicted for 4 days. In addition, it should be suitable for different onion production regions and different systems like fall and spring sown onions, as well as bunching onions.

## Materials and methods

### Model input variables and assumptions

The mathematical model ZWIPERO (an acronym for **Z**wiebel-**P**eronospora forecast) was developed by the German Weather Service and provides a quantitative risk assessment for sporulation and infection of *P. destructor* in onions. Input variables of ZWIPERO are hourly values of temperature,

relative humidity (RH), leaf wetness and precipitation as well as the local times of sunrise and sunset. The latter are calculated by a subroutine based on the geographical longitude and latitude, and the day of the year. The temperature, RH and leaf wetness values within the canopy are supplied by the subroutine AMBETI (Agrarmeteorologisches Modell zur Berechnung von Evaporation, Transpiration und Interzeption) (Braden, 1995) of the German agrometeorological forecast system AMBER (AgrarMeteorologisches Beratungsprogramm) (Löpmeier and Friesland, 1998). In order to retrospectively as well as prognostically calculate the microclimatic variables, AMBETI requires actual and hourly predicted (up to 4 days) standard weather data measured in 2 m height above the ground, as well as local production data, like soil type, emergence date, plant density and irrigation.

As a measure for air humidity, the vapour pressure deficit (VPD) is used in ZWIPERO instead of the widely adopted RH. RH provides only information on the percentage of water vapour saturation of the air. In contrast, VPD describes the potential evaporation from surfaces of living tissue and the possible drought stress by itself (Stevens, 1916; Anderson, 1936; Delp, 1954). Therefore, it is better suited to characterize the influence of atmospheric humidity on organisms than RH. ZWIPERO calculates the VPD from the RH and temperature data of AMBETI.

The model calculation is based on the assumption that infectious leaf area is present and stays constant. Starting from the time of 'sunrise + 7 h', ZWIPERO calculates (a) if sporangia are produced, (b) the number of sporangia formed, (c) the time of onset of sporangia release, (d) how many infections are meteorologically possible, and (e) the number of sporangia surviving each day (Figure 1). Since all these are relative values, they provide information on the effect of the prevailing meteorological conditions on the pathosystem irrespective of the actual disease situation in the field. The 24-h time step of the model, starting and ending with the time of 'sunrise + 7 h', was chosen to recognize infections established at the same wetness period as sporulation occurred; meaning, with continuous leaf wetness, that *P. destructor* sporangia dispersed at dawn may infect onion leaves during the same wetness period (Hildebrand and Sutton, 1982; Sutton and Hildebrand, 1985). At around noon, dew is usually evaporated and the probability of leaf wetness necessary for infection is very low.

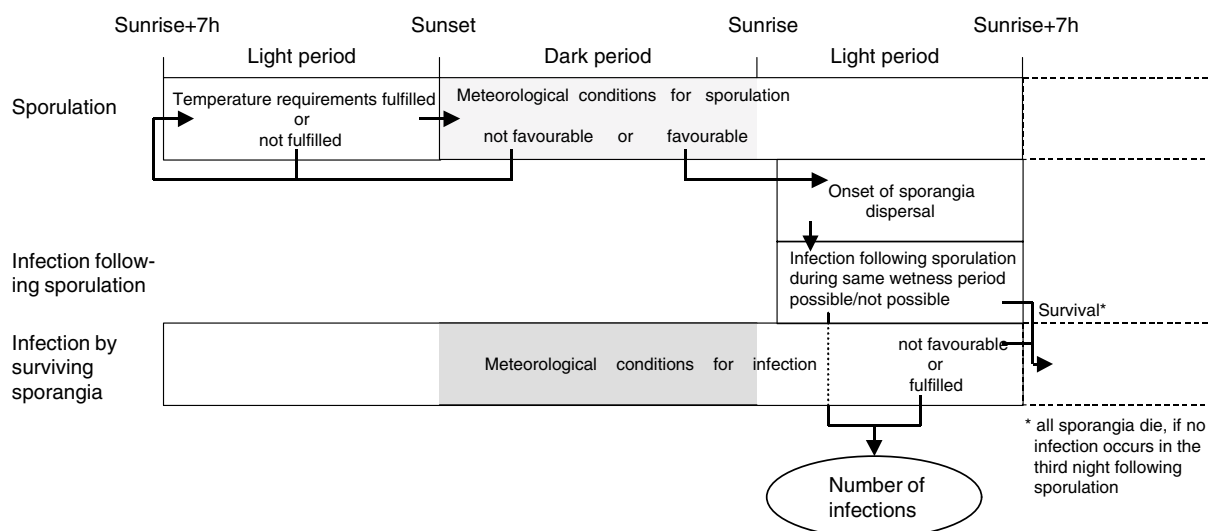


Figure 1. Flow chart of ZWIPERO. For every 24-h time step of the model, starting and ending 7 h after sunrise, the meteorologically possible number of sporangia formed and infections established are calculated.

#### Calculation of sporulation and sporangia discharge

In the following sections, the parameter values of all functions, unless stated otherwise, were fitted to the literature data by eye.

Analogous to Jespersen and Sutton (1987), high canopy temperatures of  $\geq 29$ ,  $\geq 31$  or  $\geq 33$  °C during daytime for more than 7, 4 or 1 h, respectively, prevent sporulation in the following night. Otherwise, starting at sunset (Hildebrand and Sutton, 1982; Jespersen and Sutton, 1987), ZWIPERO calculates how many sporangia are successively formed depending on the hourly canopy climate, leaf wetness and precipitation data.

The effect of the temperature on the sporulation process is calculated using a bete function (Analytis, 1977). The data of Yarwood (1943) and Hildebrand and Sutton (1984a) are compared by setting the highest sporulation value reached at the respective optimum temperature to 1 (Figure 2). The temperature optimum of the derived bete function is at 13.4 °C. The function agrees with the results of other authors (Cook, 1932; van Doorn, 1959; Johnson and Shaw, 1985).

*P. destructor* requires very high air humidity for sporulation (Yarwood, 1943; de Weille, 1975; Hildebrand and Sutton, 1982), with increasing sporulation intensities as humidity increases (Yarwood, 1943). At least 0.4 mm Hg (0.53 hPa; de Weille, 1975) or 95% RH (Virányi, 1974; Hildebrand and Sutton, 1982),

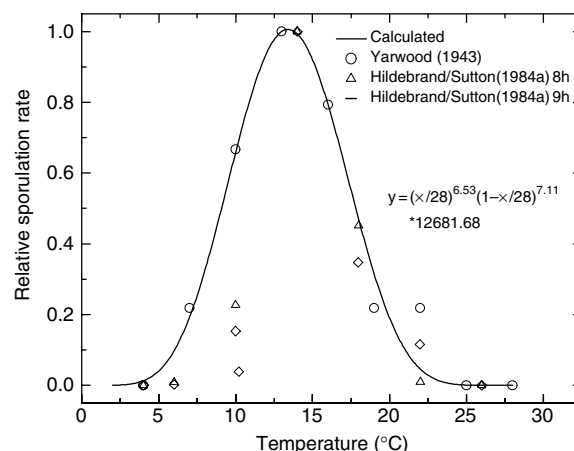


Figure 2. Temperature optimum curve to calculate the effect of temperature on sporangia formation of *P. destructor* (Literature data from Yarwood, 1943, table 8; Hildebrand and Sutton, 1984a, table 1).

which corresponds to 0.5 hPa at 7 °C for example, are necessary for this pathogen to sporulate. Sporulation of *P. parasitica* on cabbage seedlings occurred up to an atmospheric water potential of  $-30$  bar (ca. 0.5 hPa) but not anymore at  $-60$  bar (ca. 1 hPa) (Hartmann et al., 1983). The function used to calculate the influence of the air humidity on sporulation has the general form  $y = C (0.5 + 0.5 \tanh(B(A - x)))$  with  $A$  as the VPD at the inflexion point,  $B$  as the steepness, and  $C$  as a

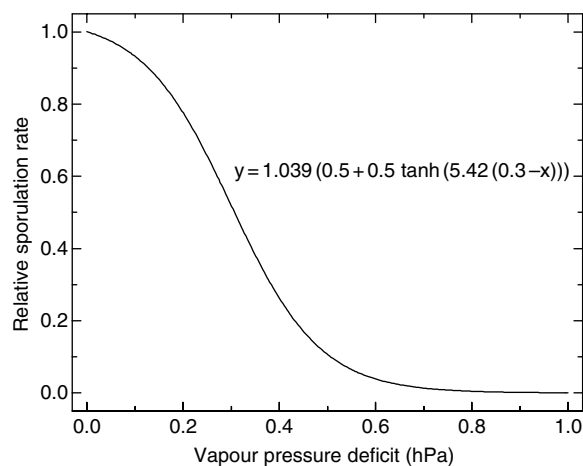


Figure 3. Function used to determine the influence of air humidity on sporulation of *P. destructor*.

scale factor of the curve. With  $C = 1$ , the  $y$ -values always range between 0 and 1. According to the function in Figure 3, most sporangia are formed in a water vapour saturated atmosphere (0 hPa or 100% RH). Sporulation is reduced to 10% of the maximum spore number at 0.5 hPa. At  $\geq 1$  hPa no sporulation occurs.

Leaf wetness was found to strongly stimulate the sporulation compared to a saturated atmosphere alone (van Doorn, 1959; de Weille, 1975). Cook (1932) exposed infected onion plants overnight to high humidity (98–100% RH) without causing visible water on the plant surface and found that in only 2 of 15 cases *P. destructor* sporangia were formed. However, those infected plants which had failed to sporulate were subsequently exposed to high humidity in the presence of visible water, and sporulation occurred. In ZWIPERO, therefore, the presence of leaf wetness has a five times more favourable effect on the number of sporangia formed than a saturated atmosphere alone.

The hourly sporulation rates obtained for the temperature and humidity (Figures 2 and 3) are separately added starting at time of sunset. The thus obtained developmental values are set back to 0, if the saturation deficit rises above 1 hPa before sunrise, because the development of sporophores and sporangia is inhibited by low RH (80–90%) before 04:00 h (Hildebrand and Sutton, 1984a).

Sporophores are also injured by rain after 01:00 h (Hildebrand and Sutton, 1982; Sutton and Hildebrand, 1985). Therefore, precipitation between 'sunset + 5 h' to 'sunrise + 1 h' will reduce the number of sporangia

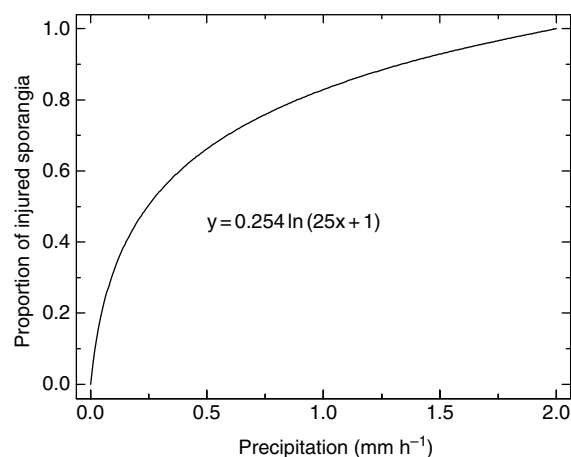


Figure 4. Function for the effect of precipitation on sporangia formation.

formed. The function in Figure 4 was fitted to the spore count results on rainy days of 1993 and 1994 and calculates the proportion of injured sporangia depending on the amount of precipitation. Precipitation of  $\geq 2 \text{ mm h}^{-1}$  during the above mentioned time interval will completely inhibit sporangia formation.

Under optimal conditions at least 4 h are required for the development of mature sporangia (Hildebrand and Sutton, 1984a). Therefore, sporulation of *P. destructor* is calculated whenever a developmental value for the temperature (Figure 2) of  $\geq 4$  is reached.

The number of sporangia produced is interactively affected by the night temperatures and the duration of high humidity (Yarwood, 1943; Hildebrand, 1983; Hildebrand and Sutton, 1984a; Sutton and Hildebrand, 1985). To take this into account, the final number of sporangia formed in a particular night is calculated by multiplying the developmental value for the temperature with that for the humidity.

Discharge of *P. destructor* sporangia is triggered by decreasing RH and red-infrared radiation (Leach et al., 1982); spore dispersal is initiated 1.5 h after sunrise, and peaks between 08:00 and 09:00 h (Hildebrand and Sutton, 1982). Accordingly, sporangia discharge is assumed to be at the earliest 2 h after sunrise and as soon as the VPD within the canopy is  $>0.6$  hPa.

#### Calculation of infection

Following spore dispersal, the number of infections is calculated depending on the meteorological conditions and the number of sporangia formed.

The temperatures favourable for germination of *P. destructor* sporangia range from about 1 °C (Yarwood, 1943; van Doorn, 1959) to 25 °C (Yarwood, 1943) or 28 °C (van Doorn, 1959) with an optimum at 10–11 °C (Cook, 1932; van Doorn, 1959; Hildebrand and Sutton, 1984c). No germination was observed at temperatures >27–28 °C (Cook, 1932; Yarwood, 1943; van Doorn, 1959). Similar values were found for the infection process (Yarwood, 1943; van Doorn, 1959). The optimal range for appressorium formation and infection was 10–14 °C (Hildebrand and Sutton, 1984c). The derived beta function for the effect of temperature on sporangia germination (Cook, 1932) and infection (Hildebrand and Sutton, 1984c) has a temperature optimum of 11.2 °C (Figure 5). Starting from the time of spore dispersal to 'sunrise + 7 h', the hourly developmental rates for temperature are added up as long as the temperature is in the favourable range and leaf wetness, necessary for germination and infection (Yarwood, 1943; Virányi, 1981; Hildebrand and Sutton, 1982; Hildebrand, 1983; Sutton and Hildebrand, 1985), persists.

Because an infection requires 2–3 h of leaf wetness at favourable temperatures (Berry, 1959; Hildebrand, 1983), no infection is calculated if the leaf wetness period ends and the developmental value is <2.3. In this case, the developmental value for infection is set back to 0. The meteorological conditions of the model for infection are fulfilled, if the developmental value

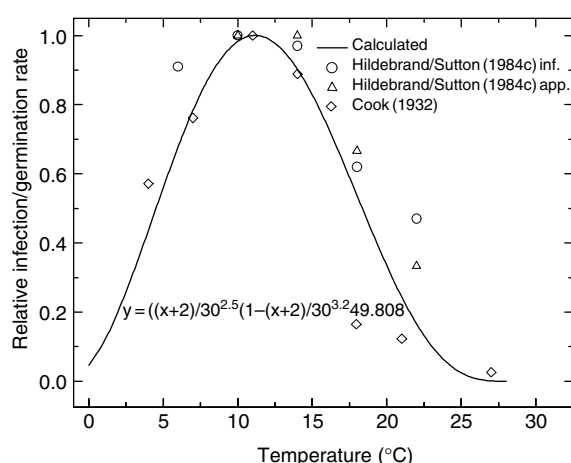


Figure 5. Temperature optimum curve to determine the influence of temperature on sporangia germination and infection of *P. destructor* (Literature data from Hildebrand and Sutton, 1984c, time for appressoria formation and 50% leaf infection rate, respectively; Cook, 1932, figure 7, 40% germination rate).

is  $\geq 2.3$ . This means, for example, that  $\geq 2.3$  h of leaf wetness at optimum temperature or almost 7 h at 20 °C are required for infection.

After a leaf wetness period of, for example, only 3 h at optimum temperature, approximately half of infection values were reached compared to those after longer exposition periods (Berry, 1959; Hildebrand and Sutton, 1984c). According to the derived function (Figure 6), the infection efficiency of the sporangia is calculated: it is 10% of the maximally possible value when a developmental value of 2.3 is reached, and for example, 97% after 6 h at optimum temperature with leaf wetness.

Furthermore, it is assumed that only half of the sporangia formed during one dark period are dispersed early enough to infect the host during the same wetness period, and that only one third of the sporangia formed are deposited on the host. Therefore, the number of meteorologically possible infections following sporulation during the same wetness period is calculated by multiplying one sixth of the number of sporangia formed during that night by the calculated infection efficiency (Figure 6). Irrespective of whether an infection could take place directly following spore dispersal or not, half of the deposited sporangia will survive until the next time step (Figure 1).

Starting from the time of 'sunrise + 7 h' (Figure 1) it is calculated how many of the surviving sporangia are able to infect the host during the following 24-h time step. In principle, the procedure is the same as

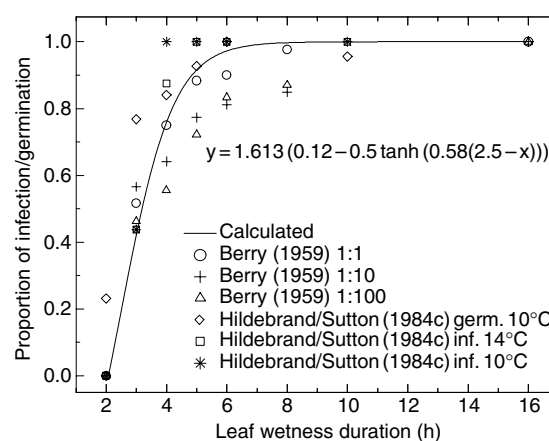


Figure 6. Proportion of germinated sporangia and infection efficiency of *P. destructor* in relation to the leaf wetness duration at optimum temperatures (Literature data from Hildebrand and Sutton, 1984c, figure 2 and table 1; Berry, 1959, figure 1a,b, isolate 2215).

before. However, since the viability of the aged sporangia is reduced (Cook, 1932; Yarwood, 1943; Virányi, 1974; Bashir and Aylor, 1983) and an additional time of leaf wetness necessary for water uptake of the sporangia is assumed, a developmental value of  $\geq 3.3$  is necessary to infect the host. If the developmental value, corresponding to the duration of leaf wetness at the optimum temperature, is  $\geq 3.3$ , the proportion of sporangia able to infect the host is determined according to the function in Figure 6, however with a leaf wetness duration of 3.5 h instead of 2.5 h at the inflexion point. If the developmental value is  $< 3.3$  and the leaf wetness period ends, no infection is possible and the developmental value for infection is set back to 0. Developmental rates (Figure 5) are once again added up as soon as leaf wetness reappears.

The highest developmental value reached during each time step is used to calculate the number of meteorologically possible infections by multiplying the corresponding proportion of infectious sporangia with the number of surviving sporangia. Depending on the number of meteorologically possible infections, four different infection risk groups were assigned (Table 1).

According to Jespersen and Sutton (1987), surviving sporangia are presumed to infect during only one infection period. Hildebrand and Sutton (1984b) showed that on pot-grown onion plants inoculated with dry *P. destructor* sporangia, portions of the spore populations could survive for 24 h on 21 of 37 exposure periods and for 48 h in 4 of 8 exposure periods. They also stated that sporangia survived a wide range of weather conditions when exposed on onion leaves during daily dry periods. Accordingly, if infection conditions are not met, half of the sporangia are assumed to survive each 24-h time step irrespective of the meteorological conditions. Analogous to Jespersen and Sutton (1987), it is also assumed that all sporangia die if no infection occurs in the third time step following sporulation. Therefore, sporangia which are able to infect the host under favourable conditions can be from different sporangia generations.

Table 1. Classification of calculated infections into infection risk groups

Number of infections (inf) calculated	Infection risk group
$\text{inf} \leq 10$	Ignorable
$10 < \text{inf} \leq 50$	Low
$50 < \text{inf} \leq 80$	Moderate
$\text{inf} > 80$	High

### Field trials

At the Agrometeorological Research Station of the German Weather Service in Braunschweig, field plots of onion (*Allium cepa* L.) were established on sandy loam soil between 1993 and 1996. On adjacent field plots, plants produced from sets (cv. Stuttgarter Riesen) were planted in mid-March followed by onions (cv. Zittauer Gelbe) sown in the middle of April. The plant density and plot size were 35 plants  $\text{m}^{-2}$  and 100  $\text{m}^2$  for the set-grown onions and 70 plants  $\text{m}^{-2}$  and 200  $\text{m}^2$  for the seeded onions, respectively. Onions were cultured according to the local practice, however, without fungicide applications.

As soon as the first downy mildew symptoms were observed in the set-grown onions, the incidence of airborne sporangia of *P. destructor* was measured continuously with a 7-day Burkard spore trap (Burkard Manufacturing Co. Ltd., Rickmansworth, Hertfordshire, England), positioned near the centre of the plot. The trap sampled air at a rate of 10 L  $\text{min}^{-1}$  at 40 cm above the ground. The sporangia were trapped on a tape coated with a mixture of vaseline-paraffin (8:2, v/v (Strathmann, 1984)). Fourteen days before harvesting the set-grown onions, the trap was moved to the plot with the seed-grown plants. For evaluation, the tapes were mounted on microscope slides and the sporangia were counted at half-hourly intervals at a total magnification of 100 $\times$ . Spore counts were expressed as number of sporangia per 0.04  $\text{m}^3$  of air and hour. The daily spore counts are, therefore, equal to the number of spores per 0.96  $\text{m}^3$  of air. Towards the end of the growing season, the incidence of downy mildew in the seed-grown onion plots was scored from 'no occurrence' to 'highly infected'.

## Results

### Sporangia dispersal during the day

The spore trap counts show a diurnal course in sporangia dispersal. Figure 7 shows the mean time course of sporangia dispersal of 13 representative days (with spore counts of more than 50 sporangia/day) in 1993. The highest sporangia concentrations usually occurred in the morning at 07:00–09:00 h. The numbers decreased rapidly during the course of the day, with numbers near to zero after sunset (in Braunschweig, Germany, at about 20:00 h (CET) during the summer). Initiation of sporangia release occurred in the morning

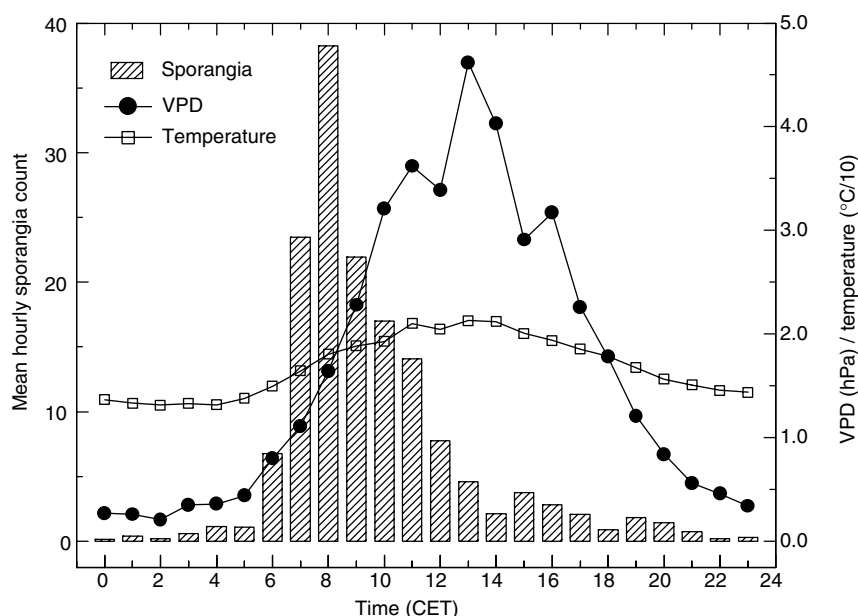


Figure 7. Mean diurnal course of sporangia dispersal, VPD and temperature within the canopy in 1993.

1–2 h after sunrise (in Braunschweig at about 04:00 h (CET) in June and July) and was associated with rising VPDs within the canopy.

#### *Sporangia dispersal monitored and calculated*

At the beginning of the epidemic in 1993, the number of sporangia trapped was very low (Figure 8a). As the disease incidence increased high sporangia counts (200 and above) occurred on 6 occasions. In 1994, the spore trap failed to work between days 196 and 220 of the year. High numbers of sporangia were counted on 4 days (Figure 8b). In 1995, spore catches were too low for evaluation due to a very low disease incidence. In 1996, high numbers of sporangia were assessed on 8 occasions (Figure 9).

Since literature data describing the effect of air humidity and precipitation on sporangia formation are rare, the spore trap records of 1993 and 1994 were also used to adjust the functions of Figures 3 and 4 to the observed values. During the epidemic, the days on which sporangia were trapped and the days for which sporulation was calculated with actual simulated micrometeorological input variables showed good agreement (Figure 8). At the beginning of the epidemic in 1993 on day 192 and 193, however, the calculated numbers were higher than the numbers

of sporangia trapped. In 1994, all sporangia counted are also represented by the number of sporangia calculated.

ZWIPERO was checked with the results obtained in 1995 and 1996. Also in 1996, the days for which high numbers of sporangia were calculated correspond to the observed peaks of the spore catches for the most part of the season (Figure 9). Due to a very low disease incidence in 1995, only single sporangia were trapped during the field season of that year. Similarly, sporulation was calculated by ZWIPERO only on 5 out of 43 days (186–228 day of the year), the corresponding values ranging from 119 to 633 sporangia/day.

#### *Infection calculated and disease incidence*

In the years with moderate to high downy mildew incidence in the seed-grown onions (1993 and 1996), the number of infections calculated with actual weather data from the end of June to the beginning of August was 4–5 times higher than in the years with a very low disease incidence (Table 2). The same was true for the number of days with an infection risk during this period. About 3–5 times more days with an infection risk were detected in the years with a moderate to high disease incidence as compared to the years with a low incidence.

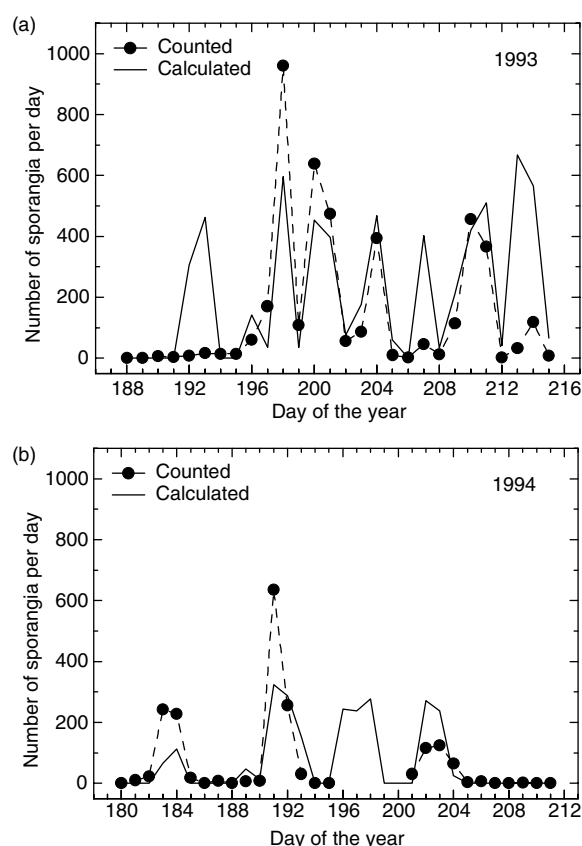


Figure 8. Daily spore counts and calculated numbers of *P. destructor* sporangia in 1993 (a) and 1994 (b). The spore count data of both years were used for the adjustment of the model.

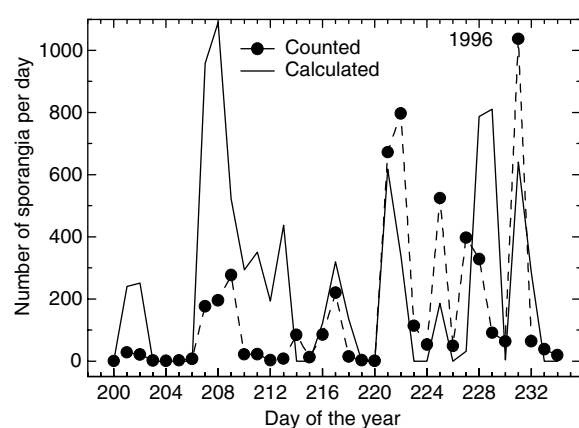


Figure 9. Daily spore counts and calculated numbers of *P. destructor* sporangia in 1996. The independent spore count data display a model validation.

Table 2. Number of infections calculated and days with low, moderate and high infection risk from end of June to beginning of August (178–221 day of the year) in relation to the observed disease incidence in field plots of seed-grown onions 1993–1996

Year	Number of infections calculated	Days with infection risk			Observed disease incidence
		Low	Moderate	High	
1993	1285	10	10	3	Moderate
1994	260	8	1	0	Low
1995	332	3	0	2	Low
1996	1459	15	2	7	Moderate to high

An infection was usually calculated for the night following sporulation. In an overall view of the years, only in one out of ten occasions *P. destructor* sporangia dispersed at dawn were also able to infect onion leaves during the same wetness period in which they had been formed.

## Discussion

For the control of downy mildews, the application of fungicides is presently the common practice. In this situation, the rational use of fungicides is a first step towards integrated control. In order to determine critical periods and, consequently, to allow an infection-related control of *P. destructor*, three weather-based advisory models have been developed. DOWNCAS (Jespersen and Sutton, 1987) and the version refined to the conditions met in the Netherlands (de Visser, 1998) run with rules established by epidemiological studies, which in form of a negative prognosis determine, whether an infection by *P. destructor* is possible or not. ONIMIL (Battilani et al., 1996) as well as ZWIPERO are more complex mathematical models which allow to simulate different phases of the infection cycle with a quantitative output of the meteorologically determined sporulation and infection risk.

Sporulation of *P. destructor* is controlled by a circadian rhythm and primarily occurs at night (Yarwood, 1943; Hildebrand and Sutton, 1984a; Sutton and Hildebrand, 1985). In DOWNCAS and in its refined version (de Visser, 1998) as well as in ONIMIL, it is assumed that sunrise and sunset take place at a fixed hour. In ZWIPERO, sunrise and sunset are calculated by a subroutine with the geographical longitude and latitude and the date as input variables. This presumably enables ZWIPERO to be operated at a wide range of seasons and locations.



ZWIPERO involves functions to predict more detailed onion downy mildew sporulation and infection periods than the models previously published. Only in ZWIPERO the proportion of injured sporangia in relation to the amount of precipitation as well as the time of sporangia discharge are calculated; the latter is important to determine infections during the same wetness period the sporangia were formed. In contrast to the cited models working with actual meteorological field data, ZWIPERO uses simulated microclimatic input variables which can also be predicted for 4 days. In principle, all models could also be run with predicted, meteorological input variables in addition to actual data, if they would be available. However, ZWIPERO is specifically adjusted to the calculated microclimatic input data provided by AMBETI of the German agrometeorological forecast system. For example, the canopy temperatures calculated by AMBETI (Braden, 1995) were somewhat higher on sunny days than the measured values; therefore, the canopy temperatures during daytime which are assumed to prevent sporulation in the following night, are set 2–4 °C higher than in DOWNCAST and ONIMIL.

Despite simulated micrometeorological input variables, the results obtained by ZWIPERO, at least those relating to sporangia formation, agree well with the measurements. In the summer periods under consideration, only in one of 10 occasions an infection was calculated for the same wetness period in which sporangia had been formed. These results are in accordance with the observations that two humid nights are usually necessary for completing one sporulation–infection–cycle of *P. destructor* (Yarwood, 1943; Sutton and Hildebrand, 1985).

As in the previously published models the infectious leaf area is assumed to stay constant in ZWIPERO. The model output is, so to speak, a relative number that describes how favourable the meteorological conditions are for sporulation and infection. Besides the meteorological conditions, the number of sporangia and infections strongly depends on the actually infectious leaf area. For example in 1993 on 2 days, the high calculated sporangia numbers do not agree with the low number of spores trapped (Figure 8a). The diseased leaf area was very low at the beginning of the presented period in 1993. Thus despite of favourable meteorological conditions for sporulation, as calculated by ZWIPERO, the number of sporangia formed was probably too low to be detected by the spore trap. During a season with very favourable conditions for sporulation and infection, the infectious leaf

area will exponentially increase due to very high infection numbers. On the other hand, no or only a very low number of infections will occur when downy mildew was not yet detected in the field despite meteorological conditions very favourable for the pathogen with a high risk for (primary) infection as output.

The forecasting model will be centrally operated with actual and predicted data from different weather stations of the German Weather Service as part of the agrometeorological counselling software AMBER. The advantage of this set-up is that microclimatic data can be calculated for any location and that no additional equipment is necessary in the field. With the availability of predicted, meteorological input variables in addition to actual data, ZWIPERO provides – and in principle all cited models could provide – a true sporulation and infection forecast.

ZWIPERO is considered as a decision support system to undertake the right measures in accordance with the knowledge about plant development, possible occurrence of primary inoculum or infection and threshold values. It enables growers and extension service, firstly, to check for disease incidence on days sporulation is predicted and disease symptoms are easily detected and, secondly, to know in advance when fungicides with protective activity will be most effectively applied.

If a refinement of ZWIPERO is found to be necessary, there will be a need for further specific studies on the considered pathogen system. For instance, data are lacking dealing with the effects of weather conditions on washing and blowing off sporangia from the plant surface. Both processes were found to be very important for the survival probability of powdery mildew conidia settled on the host surface (Friedrich, 1994; Friedrich and Boyle, 1997). Also no data for modelling are available which describe the survival of sporangia on the leaves and the infection efficiency of sporangia of different age. The same is true for the effect of a leaf wetness period too short for infection. There are still problems in monitoring leaf wetness, which can be easily observed and described, but a correct assessment of sensor data and simulated values relating to the dew deposition rate and the amount of dew is almost impossible. Even the effect of high leaf temperatures damaging, or even killing latently occurring mycelium is dealt with rather indirectly by the mathematical models.

Currently, ZWIPERO is being validated at the State Research Institute for Agriculture, Viticulture and Horticulture in Neustadt/WeinstraÙe (Germany). Trap plants are exposed for short periods in onion

fields and the correspondence of observed and calculated infection with actual as well as calculated and predicted weather data is analysed. In addition, the close co-operation of research and extension service will be used for test runs in different onion growing regions to put this forecasting model finally into practice.

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## References

- Analytis S (1977) Über die Relation zwischen biologischer Entwicklung und Temperatur bei phytopathogenen Pilzen. *Phytopathologische Zeitschrift* 90: 64–76
- Anderson DB (1936) Relative humidity or vapor pressure deficit. *Ecology* 17: 277–282
- Bashi E and Aylor DE (1983) Survival of detached sporangia of *Peronospora destructor* and *Peronospora tabacina*. *Phytopathology* 73: 1135–1139
- Battilani P, Rossi V, Racca P and Giosuè S (1996) ONIMIL, a forecaster for primary infection of downy mildew of onion. *Bulletin OEPP/EPPO* 26: 567–576
- Berry SZ (1959) Resistance of onion to downy mildew. *Phytopathology* 49: 486–496
- Braden H (1995) The model AMBETI. A detailed description of a soil–plant–atmosphere model. *Berichte des Deutschen Wetterdienstes, Offenbach/M.* Nr. 195
- Cook HT (1932) Studies on the downy mildew of onions, and the causal organism, *Peronospora destructor* (Berk.) Caspary. New York, Agricultural Experiment Station, Ithaca (Mem. 143)
- Delp CJ (1954) Effect of temperature and humidity on the grape powdery mildew fungus. *Phytopathology* 44: 615–626
- de Visser CLM (1998) Development of a downy mildew advisory model based on downcast. *European Journal of Plant Pathology* 104: 933–943
- de Weille GA (1975) An approach to the possibilities of forecasting downy mildew infection in onion crops. Koninklijk Nederlands Meteorologisch Instituut, Mededelingen en Verhandelingen No. 97
- Friedrich S (1994) Prognose der Infektionswahrscheinlichkeit durch Echten Mehltau an Winterweizen (*Erysiphe graminis* DC. f. sp. *tritici*) anhand meteorologischer Eingangsparameter. Ph.D. Thesis, Technical University Braunschweig, Germany. Verlag Mainz, Aachen, Germany
- Friedrich S and Boyle C (1997) Simulation of infection probability of powdery mildew in winter wheat. In: Munack A and Tantau HJ (eds) *Mathematical and Control Applications in Agriculture and Horticulture* (pp 243–248) Pergamon Press, Oxford, England
- Hartmann H, Sutton JC and Procter R (1983) Effects of atmospheric water potentials, free water, and temperature on production and germination of sporangia in *Peronospora parasitica*. *Canadian Journal of Plant Pathology* 5: 70–74
- Hildebrand PD (1983) Effects of environmental variables on the infection cycle and epidemiology of *Peronospora destructor* (Berk.) Casp. in onion. Ph.D. Thesis, University of Guelph, Canada
- Hildebrand PD and Sutton JC (1982) Weather variables in relation to an epidemic of onion downy mildew. *Phytopathology* 72: 219–224
- Hildebrand PD and Sutton JC (1984a) Interactive effects of the dark period, humid period, temperature, and light on sporulation of *Peronospora destructor*. *Phytopathology* 74: 1444–1449
- Hildebrand PD and Sutton JC (1984b) Effects of weather variables on spore survival and infection of onion leaves by *Peronospora destructor*. *Canadian Journal of Plant Pathology* 6: 119–126
- Hildebrand PD and Sutton JC (1984c) Relationships of temperature, moisture, and inoculum density to the infection cycle of *Peronospora destructor*. *Canadian Journal of Plant Pathology* 6: 127–134
- Jespersen GD and Sutton JC (1987) Evaluation of a forecaster for downy mildew of onion (*Allium cepa* L.). *Crop Protection* 6: 95–103
- Johnson DA and Shaw CG (1985) Downy mildew of onion. Washington State University, Pullman Washington, Extension Bulletin 1310
- Leach CM, Hildebrand PD and Sutton JC (1982) Sporangium discharge by *Peronospora destructor*: Influence of humidity, red-infrared radiation, and vibration. *Phytopathology* 72: 1052–1056
- Löpmeier FJ and Friesland H (1998) The German agrometeorological forecast system 'AMBER'. In: Dalezios NR (ed) *International Symposium on Applied Agrometeorology and Agrometeorology*. COST 77,79,711 (pp 371–376) Office for Official Publications of the European Communities, Luxembourg
- O'Brien RG (1992) Control of onion downy mildew in the presence of phenylamide-resistant strains of *Peronospora destructor* (Berk.) Caspary. *Australian Journal of Experimental Agriculture* 32: 669–674
- Palti J (1989) Epidemiology, prediction and control of onion downy mildew caused by *Peronospora destructor*. *Phytoparasitica* 17: 31–48
- Stevens NE (1916) A method for studying the humidity relations of fungi in culture. *Phytopathology* 6: 428–432
- Schwartz HF and Mohan SK (eds) (1995) *Compendium of Onion and Garlic Diseases*. APS Press, St. Paul, MN, USA
- Strathmann S (1984) Zum Sporenflug getreidepathogener Pilze – Befallsentwicklung und Ertragsgestaltung in Sortenmischungen des Weizens. Ph.D. Thesis, University of Goettingen, Germany
- Sutton JC and Hildebrand PD (1985) Environmental water in relation to *Peronospora destructor* and related pathogens. *Canadian Journal of Plant Pathology* 7: 323–330

- Tuzun S, Juarez J, Nesmith, WC and Kuc J (1992) Induction of systemic resistance in tobacco against metalaxyl-tolerant strain of *Peronospora tabacina* and the natural occurrence of the phenomenon in Mexico. *Phytopathology* 82: 425–429
- van Doorn AM (1959) Investigations on the occurrence and the control of downy mildew (*Peronospora destructor*) in onions. *Tijdschrift voor Plantenziekten* 65: 193–255
- Virányi F (1974) Studies on the biology and ecology of onion downy mildew (*Peronospora destructor* (Berk.) Fries) in Hungary. II. Factors influencing sporulation and conidium germination. *Acta Phytopathologica Academiae Scientiarum Hungaricae* 9: 315–318
- Virányi F (1981) Downy mildew of onion. In: Spencer DM (ed) *The Downy Mildews* (pp 461–472) Academic Press, London
- Vishunavat K, Nashaat NI, Heran A and Kolte SJ (1998) Sensitivity to the racemic mixture and isomeric forms of metalaxyl in Indian and European homothallic and heterothallic isolates of *Peronospora parasitica* in *Brassica* species. *Crop Protection* 17: 543–546
- Wiglesworth MD, Reuveni M, Nesmith WC, Siegel MR, Kuc J, Juarez J (1988) Resistance of *Peronospora tabacina* to metalaxyl in Texas, USA, and Mexico. *Plant Disease* 72: 964–967
- Yarwood CE (1943) Onion downy mildew. *Hilgardia* 14: 595–691