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Effects of temperature on the length of the incubation period of rose powdery mildew (*Sphaerotheca pannosa* var. *rosae*)

Xiang-Ming Xu
Horticulture Research International, East Malling, West Malling, Kent ME19 6BJ, UK
(Fax: 44 (0)1732 849067)

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Abstract

The effect of temperature on the length of the incubation period of rose powdery mildew, caused by *Sphaerotheca pannosa* var. *rosae*, was studied. At constant temperature over the range 8–28 °C, the length of the incubation period ranged from 3 to 10 days; no visible colonies developed at 30 °C after 19 days. The relationship between temperature and the rate of development of mildew colonies within the incubation period under constant temperature was described by two alternative non-linear models (exponential and thermodynamic). The resulting curves were asymmetrically bell-shaped with an optimum temperature of c. 23 °C. The two constant-temperature models predicted the development of powdery mildew under fluctuating temperatures with similar accuracy, even though the exponential model fitted the constant temperature data less well than the thermodynamic model. The thermodynamic model failed to fit the fluctuating-temperature data directly, whereas the exponential model fitted those data directly and the fit was similar to the corresponding model from the constant-temperature data. Fitting the models to the combined (constant and fluctuating temperature) data gave results that were nearly identical to those based on the constant-temperature data alone.

Introduction

Powdery mildew of rose, caused by *Sphaerotheca pannosa* var. *rosae*, is an economically important disease. It can cause serious crop losses to rose producers as a result of reduced plant quality and vigour. Conidia are dispersed in the air with a diurnal periodicity (Pady, 1972; Tammen, 1973; Leu and Kao, 1975). The severity of an epidemic is determined mainly by the number of conidia that successfully infect host tissue, the rate of colony expansion/growth and the length of the latent period, i.e. the time from deposition of conidia on leaves to sporulation.

In the UK, control of rose powdery mildew is achieved mainly by routine fungicide applications, often at intervals of 7, 10 or 14 days because of the rapid production of susceptible tissues (Wheeler, 1978). To adopt a more rational disease management strategy, where the application of disease control techniques is based primarily on the magnitude of disease risk, it is important to understand the relationship between disease development and environmental factors. The growth of the powdery mildew fungus is influenced considerably by temperature, relative humidity and free water (Longree, 1939; Rogers, 1959; Pathak and Chorin, 1969; Price, 1970; Perera, 1972; Leu and Kao, 1975; Sivapalan, 1993a,b). The minimum, optimum and maximum temperatures for the growth of the fungus are 3–5, 21 and 33 °C, respectively (Longree, 1939). Price (1970) showed that conidia can withstand long periods at 0 °C without loss of viability, provided they are incubated in moist conditions. Price further showed that, on detached leaves, the latent period ranges from 4 days at 20 °C to 28 days at 3 °C. On rose leaves, conidial germination is not affected greatly by relative humidity (Rogers, 1959; Pathak and Chorin, 1969) but is reduced significantly by the presence of free water (Sivapalan, 1993b). Mycelial growth on

leaves is apparently not affected by relative humidity (Rogers, 1959) but is affected by temperature (Price, 1970), as has been confirmed recently for apple powdery mildew (Xu and Butt, 1998). However, a more detailed quantitative description of the effects of environmental factors is needed to understand and predict the progress of rose mildew epidemics.

This paper reports the results of experiments conducted to study the effect of temperature on the developmental rate (defined as the inverse of the length of the incubation period) of rose powdery mildew. Non-linear models were fitted to data collected under constant temperatures and were validated subsequently using data obtained under fluctuating temperature regimes.

Materials and methods

Plants

Plants of cv. Rosa 'Renaissance' of a Hybrid Tea type (Large-Flowered Bush type under the new classification) were used. Plants were lifted in December 1995 and 1996, stored at 0 °C, potted up in three batches (April, May and July, 1996 or 1997) and grown in a glasshouse compartment with daily temperature set at c. 23 °C and relative humidity (rh) at c. 70% with a 16 h light/8 h dark daily regime. The plants were checked frequently for signs of powdery mildew. Mildewed leaves were removed and all the plants were then sprayed with bupirimate (Nimrod [Zeneca], at the rate of 250 ml per 100 litre). Plants were only used for experiments when at least 1 week had elapsed since the last spray.

Inoculum

Fresh colonies of rose powdery mildew were maintained on plants grown as described above in a separate glasshouse compartment. These stock plants were supplemented frequently with plants used previously in experiments and carrying fresher mildew colonies. Stock plants were shaken twice each week to ensure that conidia were dispersed to susceptible tissues and also on the day before inoculation to remove old conidia.

Inoculation

Infected leaves with sporulating colonies were collected from the stock plants. On each plant to be inoculated, four young leaves, each with five leaflets, were labelled individually. Each labelled leaf was inoculated by shaking conidia from the collected mildewed leaves onto its surface.

Constant temperature experiments

Experiments were conducted in three controlled environment (CE) cabinets (Sanyo, model SGC170.CFX.J) equipped with mixed fluorescent/tungsten lights and rh/temperature controls. Each cabinet was set for a daily cycle of 16 h light/8 h dark (light intensity c. 300 μmol m^{-2} s^{-1} at plant height) and a constant 80% rh. Twenty-one temperatures were tested ranging from 8 °C to 30 °C in steps of 1 °C except 9 °C and 29 °C. These were allocated randomly to the CE cabinets over time. At each temperature, three plants were inoculated. Plants were moved to the cabinet one day before inoculation. Only one run was conducted for each temperature.

In order to assess the effect of a sequence of high temperatures on the development of powdery mildew, twelve plants were inoculated: six at 20 °C and six at 30 °C. One day after inoculation, two of the plants at 20 °C were exchanged with two of the plants at 30 °C and, two days after inoculation, a further two plants were exchanged in the same way.

Fluctuating temperature experiments

For each inoculation (treatment), three plants were moved to an unheated polythene tunnel or a heated glasshouse with the minimum temperature set to 5 °C and inoculated within an hour. In total, 48 such treatments were carried out during the period June to November (19 in 1996, and 29 in 1997). Temperatures in the polythene tunnel and the glasshouse were recorded at 24 min intervals using a Tinytalk temperature logger ($\pm$ 0.2°C, Orion Components [Chichester] Limited, West Sussex, England), sited c. 0.5 m away from the canopy at plant height inside a Stevenson screen.

Data collection

After inoculation, the leaflets of each inoculated leaf were examined daily for powdery mildew colonies. The numbers of colonies observed on each leaflet were recorded for all inoculated plants. Recording was discontinued either when colonies on more than one third

of leaflets had coalesced, or when the time since inoculation was greater than twice the time from inoculation to the appearance of the first colony. At 30 °C, recording was terminated after 19 days. The total numbers of colonies were collated over all inoculated leaflets of the three plants for each inoculation experiment. The median incubation period (i.e. the numbers of days from inoculation to the day when the median number of colonies was recorded), hereafter referred as the incubation period (IP), was determined for each treatment.

Statistical analysis

The reciprocal of the median incubation period (1/IP) is a measure of the rate of mildew development within leaves. Two non-linear models described the relationship between the developmental rate and temperature. The first model was a critical exponential model (Payne et al., 1993):

$$R(T) = (a_1 + b_1 T)c_1^T. \tag{1}$$

The second was a variant of the thermodynamic model (Wagner et al., 1984):

$$R(T) = \frac{a_2((T + 273.2)/298)}{1 + \exp[c_2(1 - (d_2/(T + 273.2)))]} \times \exp[b_2(1 - (298/(T + 273.2)))]. \tag{2}$$

In the two models, T and $R(T)$ are respectively temperature (°C) and developmental rate (h^{-1}) at temperature T; a_1, b_1, c_1, a_2, b_2, c_2 and d_2 are the parameters to be estimated.

The models derived from the constant temperature experiments (hereafter referred to as 'constant-temperature' models) were validated using the data collected from the fluctuating temperature experiments. Two validation schemes were used and both used rate summation methods (Hau et al., 1985). Firstly, the two models (equations 1 and 2) were fitted directly to fluctuating temperatures (not to mean temperatures, see below); then the resulting models (hereafter referred to as 'fluctuating-temperature' models) were compared with the 'constant-temperature' models using the method described by Gilligan (1990). In this method, significance of the improvement (i.e. reduction in residual variance) of fitting two separate models for the constant and fluctuating temperature data over fitting a common model was tested by an F-test. Secondly, the length of the incubation period under fluctuating temperatures was predicted by integrating the developmental rate from the 'constant-temperature' models.

To derive a non-linear model directly from fluctuating temperatures, the method described by Xu (1996b), which takes into account non-linear effects, was used. This method is based upon the fact that the accumulated development (S_i, dimensionless and set to zero initially) over the observed incubation period for an inoculation is expected to be 1.0, i.e.

$$1 = S_i + \varepsilon_i = \int_0^{\mathrm{IP}_i} R(T(t);\, \theta)\mathrm{d}t + \varepsilon_i. \tag{3}$$

This is a non-linear regression model in which the dependent variable always takes the value one (i.e. at completion of an observed incubation period) and the independent variable is the observed IP. A vector (θ) of parameters may therefore be estimated by least square. In this study, S_i was approximated by numerical integration, with a temperature increment of 1 °C, after changing the variable of integration in equation 3 from time to temperature. The minimum and maximum temperatures for the development of rose powdery mildew were assumed to be 0.5 °C and 30.5 °C (Wheeler, 1978), respectively; when the temperature was outside this range, $R(T)$ was set to zero.

The Genstat command 'FITNON-LINEAR' was used to estimate the parameters (Payne et al., 1993). This command fits non-linear models by least squares using a modified Gauss-Newton method. The parameter a_2 in the thermodynamic model was estimated as a linear parameter. The two models were fitted to the constant, the fluctuating temperature and the combined data sets, using equation 3.

The 'constant-temperature' models were used to predict the length of the incubation period under fluctuating temperatures by integrating the developmental rate ($R(T)$) over the fluctuating temperature regime (from inoculation to the end of an observed incubation period) at a time step of 24 min, i.e.

$$S = \sum_{i=1}^{n^*\mathrm{IP}} R(T_i)\Delta t \tag{5}$$

where Δt and n are 0.4 and 60 respectively. The closer the accumulated development (S) is to 1.0, the more accurate the prediction. The accuracy of the predictions was tested by a t-test against the expected value of 1.0; correlation between prediction errors ($S_i - 1$) and mean

temperatures of each individual incubation periods was calculated to detect any systematic bias in the model prediction in relation to temperatures.

Results

Constant temperature experiments

The median incubation period was longer at low and high temperatures than at intermediate temperatures (Figure 1). No visible colonies developed at 30 °C 19 days after inoculation. The shortest median incubation period was 3 days at 22 and 24 °C and the longest incubation period recorded was 10 days at 8 °C. The largest numbers of colonies developed at temperatures in the range 18–24 °C and the smallest numbers developed at temperatures above 24 °C.

Plotting the rate of powdery mildew development against temperature (Figure 2) shows that the optimum temperature for development during the incubation period was in the range 22–24 °C. The fitted models are also plotted in Figure 2 with the estimates of model parameters listed in Table 1. The two models, especially the exponential model, underestimated the development rate in the range 22–24 °C. In a t-test against the standard error of observations from the regression analysis, the fitted rates were significantly ($P < 0.05$) less than those observed at 22 and 24 °C for the exponential model. The exponential model accounted for less variation than the thermodynamic model, which is due mostly to larger residual errors at the points 22 and 24 °C (Figure 2). The estimated optimum temperature from the two models was c. 23 °C. Compared to the optimum temperature, the rate of development declined more rapidly at higher temperatures than at lower temperatures.

In the experiments where plants were inoculated at 20 °C and 30 °C and subsequently exchanged between these two temperatures one or two days after inoculation, no colonies were observed on plants moved from 20 °C to 30 °C one day after inoculation and only two colonies per leaf on plants moved from 20 °C to 30 °C two days after inoculation. However, with plants maintained at 20 °C, 42 colonies per leaf were observed. For those plants inoculated at 30 °C, mildew colonies (five per leaf) were recorded only on those plants moved to 20 °C one day after inoculation.

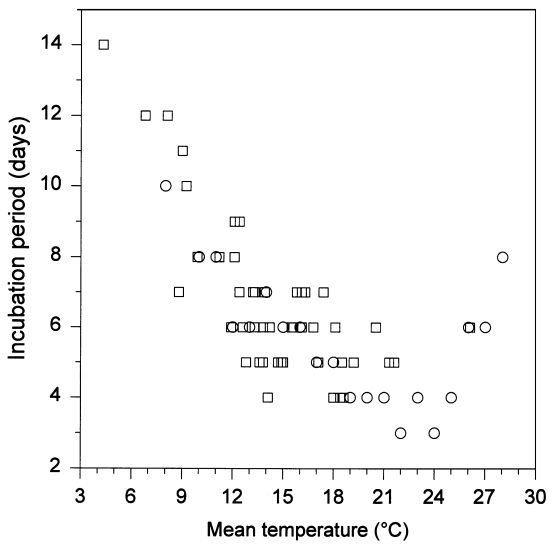

Figure 1. Observed incubation periods (days) of rose apple powdery mildew under constant (○) and fluctuating (□) temperatures. The length of the incubation period for each inoculation was based on the total number of colonies observed on 60 inoculated leaflets of the three plants. Visible colonies did not develop at 30 °C.

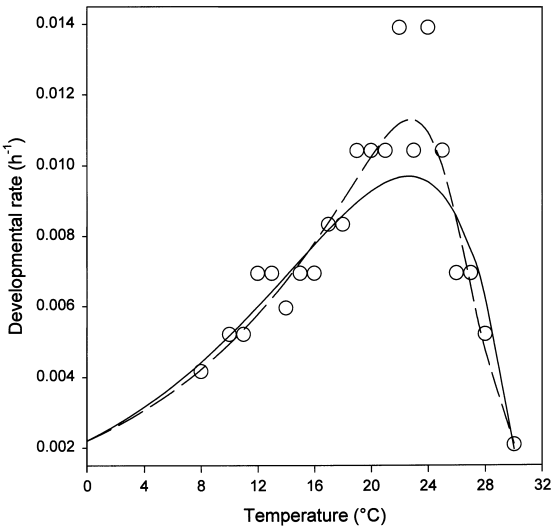

Figure 2. Relationship between temperature and development rate (○) of rose powdery mildew under constant temperature: solid line – exponential model, dashed line – thermodynamic model. The development rate (h^{-1}) is calculated as the reciprocal of the observed median incubation period. In fitting the model, the development rate at 30 °C was set to 0.002 (i.e. the incubation period is 20 days). Parameter estimates of the models are given in Table 1.

Table 1. Parameter estimates of two non-linear models describing the relationship of development rate (reciprocals of the incubation period) of rose powdery mildew to temperature

Data type	Exponential model		Thermodynamic model	
	Parameters[a]	Estimates	Parameters	Estimates
Constant temperature	a_1	0.0022 ± 0.00026[b]	a_2	0.0148 ± 0.0013
	b_1	-0.000072 ± 0.00001	b_2	20.04 ± 2.36
	c_1	1.1328 ± 0.00741	c_2	174.1 ± 16.0
			d_2	299.36 ± 0.44
Fluctuating temperature	a_1	0.0018 ± 0.00034	a_2	
	b_1	-0.000059 ± 0.00001	b_2	Optimisation
	c_1	1.1428 ± 0.0221	c_2	did not converge
			d_2	
Combined data	a_1	0.0020 ± 0.00016	a_2	0.0152 ± 0.0013
	b_1	-0.000065 ± 0.00001	b_2	21.12 ± 2.11
	c_1	1.1392 ± 0.00583	c_2	1707 ± 19.9
			d_2	299.24 ± 0.50

[a] See equations 1 and 2 in text.
[b] The number after the $\pm$ is the standard error of the corresponding parameter estimate.

Fluctuating temperature experiments

In the fluctuating temperature experiments, temperatures recorded at 24 min intervals ranged from $-3.2\,^{\circ}$C to $50.0\,^{\circ}$C (Figure 3) with an average of $13.6\,^{\circ}$C. The daily temperature range (i.e. the difference between daily maximum and minimum temperatures) varied from $2.6\,^{\circ}$C to $38.3\,^{\circ}$C with an average of $14.6\,^{\circ}$C. All experiments had average temperatures in the range of 4–$22\,^{\circ}$C, except one inoculation with an average of $26.1\,^{\circ}$C. Mildew colonies were generally less fluffy and took longer to coalesce than those developing under constant temperatures. Figure 1 shows the length of the incubation period plotted against the mean temperature over the entire incubation period. The shortest incubation period was 4 days and the longest was 14 days.

Of the two models, only the exponential model fitted the fluctuating temperature data (Table 1). The parameter estimates were similar for the 'constant-temperature' and 'fluctuating-temperature' exponential models and an F-test showed there were no significant differences between the two models, although the 'fluctuating-temperature' model gave greater rates for temperatures above $21\,^{\circ}$C (Figure 4a). The two models that fitted the combined (constant + fluctuating temperature) data were all nearly identical to the corresponding 'constant-temperature' models (Table 1, Figure 4). In a t-test using the standard error of the observations from the regression analysis, predicted development times deviated significantly

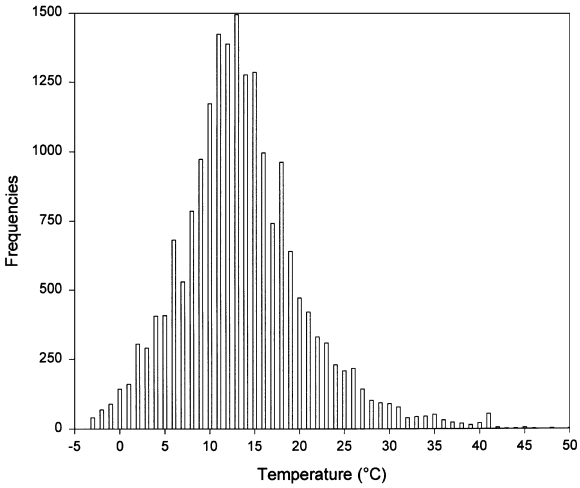

Figure 3. Frequency distribution of temperature recorded at 24-min intervals over all 48 fluctuating temperature regimes.

($P < 0.05$) from those observed at only three points for the 'combined' thermodynamic models, and at two points for the 'combined' exponential model.

The 'constant-temperature' models were used to predict the development under fluctuating temperatures. Figure 5 shows the predicted development for each fluctuating period. The accumulated development predicted by the two models is close to 1.0, except in a few instances where the predictions deviate more than 0.25 from 1.0, and the two models gave very similar predictions. The average predicted development was 0.98 and

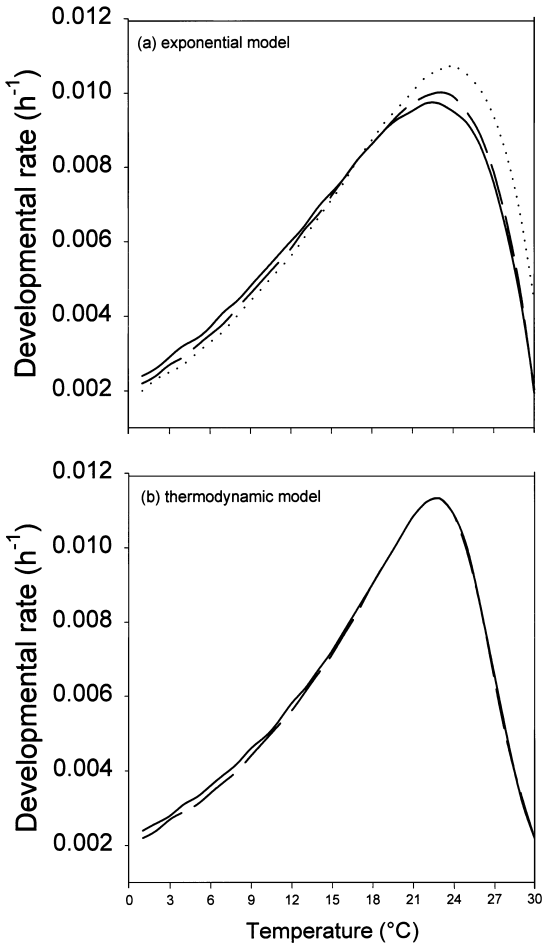

Figure 4. Relationship between temperature and development rate of rose powdery mildew: solid line – 'constant-temperature' model, dashed line – 'combined' model, dotted line – 'fluctuating-temperature' model. The thermodynamic model could not be fitted successfully to the fluctuating temperature data. Parameter estimates of all the models are listed in Table 1.

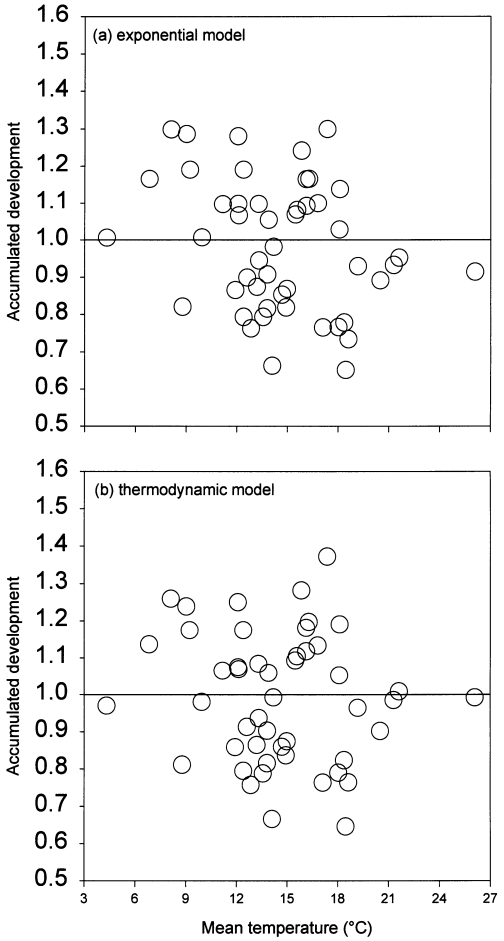

Figure 5. The accumulated development of rose powdery mildew under fluctuating temperature regimes predicted by integrating the development rate calculated from the two constant-temperature models at time steps of 24 min (○).

0.99 for the exponential and the thermodynamic models, respectively; both were not significantly different from 1.0. Only for two inoculations for each model was the predicted development significantly ($P < 0.05$) different from 1.0. Deviations of the predicted development from 1.0 were not significantly correlated with mean temperature.

Discussion

The observed relationship between the rate of development and temperature during the incubation period of rose powdery mildew was consistent with published reports on the effects of temperature on disease development in other pathogens (Eversmeyer et al., 1980; Beresford and Royle, 1988; Shaw, 1990; Wadia and Butler, 1994; Xu, 1996a). Development was slower at temperatures above and below the optimum with the response curve skewed to the lower temperatures. As well as lower rate of development, supra-optimal temperatures are likely to result in higher mortality of spores and a faster rate at which leaves become resistant due to faster host growth than lower temperatures; this is the most likely explanation for the results obtained from inoculated plants exchanged between 20 °C and 30 °C. Temperature affects three aspects of rose mildew dynamics. It influences the numbers of successful

infections (in terms of the numbers and size of visible colonies), the rate of colony growth/expansion (in terms of the length of incubation and latent periods), and sporulation (in terms of the numbers of spores produced by a lesion over its lifetime). At supra-optimal temperatures for the pathogen, the mortality is greater, the rate of development is slower and the growth of the host is faster, hence becoming more resistant to mildew (Rogers, 1959; Mence and Hildebrandt, 1966; Pathak and Chorin, 1969; Perera, 1972) than at sub-optimal temperatures. A period of temperatures above the optimum would be expected to have a more harmful effect on mildew epidemics than a period of the same length at temperatures below the optimum.

In this study, the dose of inoculum was not controlled. To inoculate leaves with a consistent conidial dose for all treatments requires a spore suspension with the inoculum dose adjusted on the basis of counts of conidia using a haemocytomer. However, the development of powdery mildews, as a group of diseases, is generally affected adversely by the presence of free water during the initial infection stage (Butt, 1978; Sivapalan, 1993b). Although a settling tower could have been used to inoculate plants, inoculum dose would be still only approximate in addition to its inconvenience. This study was concerned only with the effects of temperature on the length of the incubation period. The results were unlikely to be affected by variable inoculum dose, provided that the developmental rate of individual spores did not depend on the numbers of spores on a leaf. Given that artificial inoculation generally results in a high inoculum dose, this assumption was unlikely to be violated.

Although visible colonies did not develop at 30 °C during the experiment (19 days), the incubation period at 30 °C was assumed to be 20 days when fitting non-linear models, for the following reasons. First, the fitting scheme (equation 3) does not permit a rate being zero (i.e. an infinite length of incubation period) because integration is operated within the length of an incubation period. Secondly, the inoculation experiment at 30 °C indicated that the incubation period was at least 20 days, i.e. the maximum development rate at 30 °C was $0.002\,h^{-1}$. Thirdly, as low percentages of germination of rose powdery mildew conidia have been observed at 30 °C (Longree, 1939; Pathak and Chorin, 1969), it would have been inappropriate to have set the development rate at 30 °C to zero. Finally, if the 30 °C point had been excluded, the fitted non-linear models would have overestimated considerably the development rate for temperatures above 26 °C. Moreover, the models, which fitted the full data set with the incubation period at 30 °C taking one of the four values: 20, 30, 40, 60 days, differed little with the differences being restricted almost entirely to temperatures >28 °C.

The two non-linear models derived from the constant temperature experiments well described the relationship between temperature and the rate of development of mildew colonies during the incubation period. As expected, the model with four parameters (thermodynamic) accounted for more variation than the model with three parameters (exponential). The response of mildew development to temperature is nearly linear for temperatures below 22 °C. This was confirmed by results from the fluctuating temperature experiments where the length of the incubation period was more or less related linearly to mean temperature except for several inoculations with an average temperature >20 °C. It is more difficult to derive non-linear models from the fluctuating temperature data than from the constant temperature data. This is due to the fact that only about 5.6% of the recorded temperatures were in the range 23.5–30.5 °C whereas 89.6% were in the range 1.5–23.5 °C (Figure 3).

When the models derived from the constant temperature experiments were used to predict the development under fluctuating temperatures, they gave equally accurate predictions. This is surprising since, compared with the thermodynamic, the exponential model considerably underestimated the development rate over the temperature range 22–24 °C (Figure 2). This may have resulted from the fact that, in the fluctuating regime, the proportion of time with temperatures in this range (22–24 °C) was low in all inoculations. Thus, the large differences between the models over this temperature range may not have resulted in large differences in the predicted rate of development. In conducting constant temperature experiments, all biologically viable temperatures are usually given an equal weight. In natural environments, however, temperature fluctuates with unequal frequencies.

The results obtained with the inoculated plants exchanged between 20 °C and 30 °C indicate that the sequence of temperature was important for fungal development. The valid use of rate summation methods to predict development under fluctuating temperatures assumes that the order in which different temperatures occur does not affect development (Hau et al., 1985). The violation of this assumption may not lead to large

errors in predicted development because, under field conditions, the fungus is unlikely to be subjected to such high temperatures for a prolonged period in its early developmental stages. A more detailed quantitative description of the effects of environmental factors on conidial mortality is needed.

In the present study, incubation period is defined as the time from inoculation to the time when the median number of colonies appeared, rather than from infection to the first appearance of visible symptoms. Thus, the two models reflect the overall effect of temperature on rose powdery mildew during the initial infection and the 'incubation' periods. It would be ideal to subject all treatments to a common initial infection period, however, this is not possible. Unlike most other fungi, infection by powdery mildew is more or less continuous and does not depend on a single critical infection condition such as duration of wet period, thus it is difficult to determine the exact time required for infection. It could be argued that the two models do represent the relationship of rate of mildew development within the incubation period to temperature for the following reasons. First, it is expected that the time required for infection is considerably shorter than the incubation period. Secondly, the effect of temperature on germination is non-linear (Longree, 1939; Pathak and Chorin, 1969); the effect of temperature on initial hyphal growth is also non-linear for apple powdery mildew (Xu and Butt, 1998). Therefore, the relationship of the initial infection rate to temperature is expected to be non-linear, similar to the two models. Furthermore, because the relationship between the infection rate and temperature is difficult to obtain, it would be more practical to use the current 'overall' models to predict rate of epidemic development in field conditions.

Powdery mildew epidemics are usually continuously monitored. However, because of the nature of 'continuous' infection by powdery mildew conidia, it is difficult to interpret such observed continuous epidemics in relation to weather conditions. Using the present models, it is possible to estimate the compositions of new colonies observed on each date: i.e. colonies resulting from infection on which days would appear between two successive observations. Thus it is possible to interpret field epidemics in relation to initial infections and subsequent colony development. A warning system to assist growers in timing fungicide applications against rose powdery mildew and adjusting fungicide doses more rationally may be developed by incorporating the effects of weather on spore mortality and colony growth leading to visible colonies. Such a warning system may be improved further by incorporating the effects of environmental factors on the quantity and quality of spores produced by colonies.

The present study deals only with the development of powdery mildew on young susceptible leaves. It is well known that other rose tissues, such as pedicels, are also highly susceptible to powdery mildew. Indeed, the pedicels have been found to be susceptible to mildew even on cultivars with leaves resistant to mildew (Wheeler, 1978). In experiments with detached leaves and pedicels, Perera (1972) showed that pedicels lost their susceptibility with age more slowly than leaves and that conidia germinated and grew more quickly on pedicels than on leaves in only a few instances. It is likely, therefore, that the models developed from the data on foliage mildew are also applicable to mildew on other tissues.

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