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Effects of temperature and atmospheric moisture on the early growth of apple powdery mildew (*Podosphaera leucotricha*) colonies

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Abstract

Effects of four temperatures and nine water vapour pressure deficits on the early growth of apple powdery mildew colonies on young leaves inoculated with conidia were studied on potted apple rootstocks in controlled environment cabinets. The number of hyphae (germ tubes + primary and secondary hyphae) per colony, total hyphal length per colony and the length of time from inoculation to the first observation of secondary hyphae were recorded on the upper surfaces of stained preparations of leaves sampled at three intervals up to 60 h after inoculation. Analyses of variance of these variables describing colony growth revealed significant differences between treatments (temperature × vpd), with most (c. 61–79%) of the treatment effects due to temperature, as shown by regression analysis. The response to temperature (13–28 °C) was non-linear, with the optimum c. 22 °C. In contrast, there was no detectable trend in the response of colony growth to vapour pressure deficit (1.6–10.4 mmHg). The results suggest that the rate of development of young colonies depends more on temperature than on moisture stress.

Abbreviations: vpd – vapour pressure deficit; rh – relative humidity; CE – controlled environment; CV – coefficient of variation; c. – approximately.

Introduction

Like most powdery mildews, the ectophytic colonies of apple powdery mildew caused by *Podosphaera leucotricha* (Ell. & Everh.) Salm. are sustained by haustoria in epidermal host cells. Conidia do not require surface wetness to germinate and infect young susceptible leaves (Butt, 1978), and so annual epidemics on apple are effectively continuous during the vegetative season.

Burchill (1958) recorded the percentage of germinated conidia of apple powdery mildew on detached leaves incubated at six temperatures (5–30 °C), each at four humidities (14–98% rh), 48 h after inoculation. The optimal temperature for germination was 20 °C irrespective of rh and the percentage of germinated conidia increased with increasing humidity, with a maximum of 70% germinated at 98% rh and 20 °C. Coyier (1968) and Molnar (1971) obtained similar responses of germination to temperature, 24 h after inoculation, for conidia of apple powdery mildew on leaves incubated at 97% and 100% rh. Leaves of apple rootstocks M. II and M. III have been infected at humidities as low as 40% rh (Roosje, 1961). In most studies of the germination of *P. leucotricha* conidia only the percentage of germination has been measured; the few studies reporting germ-tube growth were conducted under limited ranges of environmental conditions.

Data were needed to develop a model describing the early growth of *P. leucotricha* colonies to a wide range of temperature and atmospheric moisture. Such a model could help growers to rationalise their management of this disease. This paper reports a study conducted to generate this type of data.

Materials and methods

Treatments

Nine levels of water vapour pressure deficit (vpd) from 1.6 to 10.4 mmHg, at intervals of 1.1 mm, were chosen to represent the range of value normal in UK orchards in the growing season. Each vpd was studied at up to four temperatures (13, 16, 22, and 28 °C) representing the range of ambient temperatures normal in late spring and summer in UK orchards. Only 20 treatments (i.e. temperature × vpd combinations) were tested because for the other combinations either the conditions could not be achieved in the cabinets or the conditions occur rarely in UK orchards (Table 1). The appropriate rh to achieve the required vpd at a set temperature was calculated using the equation

$$rh = 100\left(\frac{SV_t - vpd}{SV_t}\right)$$

where SV_t is the saturated water vapour pressure at temperature *t*.

The study was conducted in two commercial Conviron controlled environment (CE) cabinets (model S10h, c. 2.5 m^3), each with c. 1 m^2 shelf area and fitted with mixed fluorescent and tungsten lights. Each cabinet was set for a 16 h light/8 h dark daily regime (light intensity c. 230 μmol $m^{-2}s^{-1}$ at shoot tip height). Sensors built into the air-conditioning section of each cabinet continuously recorded air temperature and rh; in into the air-conditioning section, temperature was regulated by a heater and cooler, and humidity by a humidifier and drying unit. In the growing section of each cabinet, air flowed vertically and upward through the perforated shelf. Temperature and rh of the conditioned air were continuously displayed on a chart. In the growing section, temperature and rh were also monitored using a pair of thermocouples, connected to an external digital thermometer (Fluke 52 K/J). The wet thermocouple was fitted with a tubular wick kept moist from a reservoir of distilled water and ventilated by a small fan. The dry thermocouple was at shoot-tip height and the wet thermocouple was 10 cm above the shelf. Ideally, the wet thermocouple should have been at shoot-tip height, but the shoot tips were only about 40 cm above the wet thermocouple, and the difference in conditions between the heights of the shoot-tip and the wet thermocouple was likely to have been small. These thermocouples confirmed that the conditions in the growing section of each cabinet were as set.

Plants

Bare-rooted 1-year-old MM106 rootstocks, stored at 1 °C, were potted as needed and grown in a glasshouse compartment at c. 23 °C and c. 70% rh, with a 16 h light/8 h dark daily regime. The plants were checked frequently for contaminant mildew and diseased leaves were removed. Before the plants were placed in the CE cabinets, their shoots were briefly immersed in 0.05% v/v DDAB (didecyldimethylammonium bromide) to eradicate any contaminant colonies (Kirby et al., 1963) and sprayed with water. For each treatment, six plants (each with 3–4 shoots) were placed in a CE cabinet 4 days before inoculation.

Inoculum source

Fresh colonies of apple powdery mildew were maintained on potted 1-year-old MM106 rootstocks in a separate glasshouse compartment at c. 23 °C and c. 70% rh under a 16 h light/8 h dark daily regime. Plants used previously in experiments in the CE cabinets and with young mildew colonies were added to this stock collection. Stock plants were shaken twice weekly to disperse conidia to young susceptible leaves and also on the day before inoculation to remove old spores.

Inoculation

Conidia from fresh colonies on the stock plants were collected in a 1.5 ml eppendorf using a cyclone collector. The plants in the CE cabinet were inoculated at c. 0900 GMT by gently brushing the collected conidia onto the upper surface of leaves, near their tips, with a fine brush. On each of the six plants, leaves at positions '0' and '+1' on each of two shoots were inoculated: leaf '0' is the youngest unrolled leaf and leaf '+1' is the oldest rolled leaf next to and younger than leaf '0'. Small labels were attached to the 24 petioles of the inoculated leaves in each cabinet. On the same day, the inoculum was tested for germination on a glass slide supported over water inside a sealed Petri dish incubated at 20 °C.

Leaf sampling and preparation

Five plants in each cabinet were sampled three times. On each occasion, three inoculated leaves (one from each of three plants selected at random) were removed at random and placed immediately in a mixture of acetic acid and alcohol (3 : 1). After a few hours, when

the chlorophyll had been extracted, the leaves were placed in distilled water for 2 min to soften. The tips of the leaves were then cut off, stained in 0.5% methyl blue for 5 min, rinsed in distilled water and mounted with the upper surface upwards on glass slides in a mixture of gelvatol, lactic acid and phenol.

Leaves were sampled 24 h and 36 h after inoculation. The timing of the third sample was estimated from the observed fungal growth of the 24-h sample in order to coincide with the earliest observation of secondary hyphae and therefore varied with treatment. The third sample was not taken for treatments at 22 °C because secondary hyphae were already present in the second sample. After the final leaf-sampling, the sixth plant in each cabinet, chosen at random, was taken to a glasshouse to incubate.

Table 1. Values of relative humidity set to achieve the required water vapour pressure deficit (vpd) at each temperature in the CE cabinets

Vapour pressure deficit (mmHg)	Temperature (°C)			
	13	16	22	28
1.6	86	88	92	(94)
2.7	76	80	86	90
3.8	66	72	81	87
4.9	(56)[a]	(64)	75	83
6.0	(47)	(56)	70	79
7.1		(48)	64	75
8.2			(59)	71
9.3			(53)	67
10.4			(48)	63

[a] Values of relative humidity in brackets are for the treatments (vpd × temperature) not tested.

Data collection

The sampled leaf tips were examined with a light microscope (Leitz Laborlux S). First, each was scanned using a × 10 objective and a × 10 eyepiece to assess the approximate proportion of conidia germinated, i.e. conidia with the length of one or more germ tubes exceeding the spore length. In the rest of this paper, the word 'hyphae' is used to refer to germ tubes, primary hyphae (germ tubes ≥ spore length) and secondary hyphae resulting from the branching of primary hyphae.

Five colonies, i.e. germinating or germinated conidia, were selected at random on each of the three leaf tips in each sample and drawn on paper (magnification × 394) using a drawing-arm attachment with a × 25 objective. The drawings were digitised with a Graf/Bar Mark II digitiser. Each hyphae of a colony was digitised separately. For each colony, the total hyphal length (mm) and the number of hyphae were calculated; the number of secondary hyphae per colony was counted from the drawings.

Mildew intensity was recorded 10 days after inoculation on the plant moved from the CE cabinet after the final sampling. Intensity was assessed in five grades of percentage of leaf area diseased.

Data analysis

A nested (hierarchical) analysis of variance was applied to the colony growth data. Variation between leaves within treatments was used to test the effects of treatments (temperature × vpd), and leaf-to-leaf variation was compared with the variation between colonies within a leaf. A full factorial analysis of variance was not possible because the two factors (temperature, vpd) were not orthogonal (Table 1). To quantify the effects of temperature, vpd and their interaction on colony growth, regression analyses were applied to treatment (temperature × vpd) means. In the regression analyses, temperature was scaled down by a factor of 10 to avoid small regression coefficients.

Two variables were analysed statistically: the increase of total hyphal length per colony per day and the increase of number of hyphae per colony per day. Both variables were analysed for incubation periods 0–24 h and 0–36 h following inoculation at time 0. Data from the third sample were not statistically analysed because of differences in sampling times. The increase in total hyphal length per colony per day during the incubation period 24–36 h was also analysed by regression analysis.

Results

From Table 1 it can be seen that the effect of vpd is best assessed at 22 °C and 28 °C, with six or more levels of vpd studied at each of these temperatures; likewise, the effect of temperature is best assessed at 2.7 and 3.8 mmHg, with all four temperatures studied at each of these moisture stress levels.

Spore germination

The percentages of germinated conidia were 0.8–6.6% on slides and 10–45% on leaves over the 20 treatments.

Table 2. Number of hyphae per colony on three occasions after inoculating conidia of *P. leucotricha* on to young apple leaves (values are average of 15 colonies)

Vapour pressure deficit (mmHg)	Temperature (°C)											
	13			16			22			28		
	24 h	36 h	60 h	24 h	36 h	48 h	24 h	36 h		24 h	36 h	48 h
1.6	1.4	2.0	4.5	2.0	2.4	4.4	2.3	4.7	–[a]			
2.7	1.7	–[b]	6.1	2.0	2.5	4.2	2.4	3.3	–	2.0	2.3	4.8
3.8	1.5	2.0	4.2	2.0	2.2	4.4	2.4	4.5	–	2.1	2.7	5.5
4.9							2.1	4.1	–	1.9	2.1	4.8
6.0							2.0	4.0	–	1.9	2.3	5.2
7.1							2.0	2.9	–	2.0	2.4	3.5
8.2										2.0	2.1	5.5
9.3										1.9	2.5	4.8
10.4										1.9	2.2	6.1

[a] At 22 °C the third sample was not taken because secondary hyphae were already present at 36 h.
[b] Sampling failed.

Table 3. Parameter estimates for quadratic equations describing the effects of temperature on the early growth of *P. leucotricha* colonies (per day)

Terms	Time periods				
	0–24 h		0–36 h		24–36 h
	Total hyphal length	Numbers of hyphae	Total hyphal length	Numbers of hyphae	Total hyphal length
c[a]	− 0.667 ± 0.115	− 1.383 ± 0.468	− 1.383 ± 0.369	− 6.990 ± 1.470	− 4.711 ± 0.995
b	0.750 ± 0.116	3.234 ± 0.470	2.284 ± 0.363	8.910 ± 1.440	5.319 ± 0.978
a	− 0.161 ± 0.027	− 0.728 ± 0.111	− 0.518 ± 0.085	− 2.088 ± 0.336	− 1.244 ± 0.228
% variance accounted for	79.4	74.1	68.9	67.0	60.7

[a] rate = $aT^2 + bT + c$ where T is temperature/10 (°C).

This difference between the germination on the leaves and slides has been reported (Burchill, 1958; Molnar, 1971). There was no discernible pattern of response to either temperature or vpd.

Number of hyphae per colony

Table 2 shows the number of hyphae per colony on three sampling occasions. Treatment differences were small 24 h after inoculation, but were larger for longer incubation periods, especially between temperatures. There was an optimal response to temperature at both 24 h and 36 h sampling times, at vapour pressure deficits of 2.7 and 3.8 mmHg, with most hyphae per colony at 22 °C. For example, at 3.8 mmHg and 36 h after inoculation, there was an average c. 4.5 hyphae per colony at 22 °C but only c. 2.0, 2.2 and 2.7 hyphae per colony at 13 °C, 16 °C and 28 °C, respectively. At each temperature, the number of hyphae per colony varied considerably with vpd, but without any discernible trend. The variation between the fifteen colonies in each treatment was expressed as the Coefficient of Variation (CV). The CV ranged from 0–37% (average 11.7%) at 24 h and from 0–59% (average 20.5%) at 36 h and did not show any discernible trend with either vpd or temperature.

Analyses of variance showed highly significant treatment effects. Treatments accounted for 34% of the total variation 24 h after inoculation and increased to 62% 36 h after inoculation. Variation between the three leaves within a treatment was small but significant ($P < 0.05$) 36 h after inoculation, accounting for 9% of the total variation. Regression analyses showed that effects on the number of hyphae per colony were due mostly to temperature (Table 3): all the significant terms identified by regression analyses involved temperature only. The optimum temperature estimated by the equations was c. 21–22 °C.

Table 4. Total hyphal length (mm) per colony on three occasions after inoculating conidia of *P. leucotricha* on to young apple leaves (values are average of 15 colonies)

Vapour pressure deficit (mmHg)	Temperature (°C)											
	13			16			22			28		
	24 h	36 h	60 h	24 h	36 h	48 h	24 h	36 h		24 h	36 h	48 h
1.6	0.04	0.16	0.92	0.12	0.42	0.82	0.18	0.66	–[a]			
2.7	0.05	–[b]	0.82	0.11	0.37	0.79	0.24	0.72	–	0.21	0.42	1.14
3.8	0.04	0.11	0.85	0.11	0.45	0.73	0.26	0.98	–	0.17	0.48	0.85
4.9							0.24	0.78	–	0.18	0.23	0.84
6.0							0.16	0.70	–	0.19	0.61	0.96
7.1							0.18	0.68	–	0.12	0.31	0.65
8.2										0.16	0.39	1.15
9.3										0.19	0.72	0.98
10.4										0.17	0.56	1.06

[a] At 22 °C the third sample was not taken because secondary hyphae were already present at 36 h.
[b] Sampling failed.

Total hyphal length per colony

Table 4 shows the total hyphal length per colony on three sampling occasions. Treatment differences were small 24 h after inoculation, but were larger for the longer incubation periods, especially between temperatures. At vapour pressure deficits of 2.7 and 3.8 mmHg, there was an optimal response to temperature at both 24 h and 36 h sampling times, with the longest hyphae per colony at 22 °C. For example, at 3.8 mmHg 36 h after inoculation, the average total hyphal length per colony was c. 0.98 mm at 22 °C but only c. 0.11, 0.45 and 0.48 mm at 13 °C, 16 °C and 28 °C, respectively. At each temperature, the total hyphal length per colony varied considerably with vpd, but without any discernible trend. The variation between the fifteen colonies in each treatment varied greatly, with CV of 21–74% (average 34.7%) at 24 h and 16–44% (average 27.5%) at 36 h, with no discernible trend with vpd or temperature.

Analyses of variance showed that the effects of treatments were highly significant. The treatments accounted for 58% of the total variation 24 h after inoculation and increased to 74% 36 h after inoculation. For both sampling occasions, the variation between the three leaves within a treatment was significant but less than 8% of the total variation. The regression analyses showed that in all three incubation periods the effects of treatments were due mostly to temperature (Table 3): all the significant terms identified by regression analyses involved temperature only. The optimum temperature estimated by the models was c. 23 °C, c. 22 °C and c. 21 °C for 0–24 h, 0–36 h and 24–36 h incubation periods, respectively.

Length of time to the first observed secondary hyphae

Table 5 shows the length of time from inoculation to the first observation of secondary hyphae and also the number of secondary hyphae per colony at that stage. Secondary hyphae were present 36 h after inoculation at 22 °C , 60 h at 13 °C, and 48 h at 16 °C and 28 °C. The number of secondary hyphae per colony at these times were 1.8, 1.3, 0.9 and 2.1 at 13 °C, 16 °C, 22 °C and 28 °C, respectively. Over the range of vpd tested, the number of secondary hyphae per colony at 13 °C and 28 °C were c. 2, indicating that the branching of hyphae had begun considerably earlier than 60 and 48 h after inoculation, respectively.

Disease intensity

All the inoculated leaves were severely mildewed when assessed in the glasshouse 10 days after inoculation. The differences between treatments were very small.

Discussion

In this study, two groups of plants were inoculated and exposed to treatments (temperature × vpd) each week, and so any effect of treatments was confounded with any temporal changes in inoculum quality and plant susceptibility. Therefore, to assess the effects of the treatments it must be assumed that successive

Table 5. Length of time from inoculation to the first observation of secondary hyphae of *P. leucotricha* and number of secondary hyphae per colony at that time

Vapour pressure deficit (mmHg)	Temperature (°C)							
	13		16		22		28	
	Time (h)	No. of 2^{ndy} hyphae	Time (h)	No. of 2^{ndy} hyphae	Time (h)	No. of 2^{ndy} hyphae	Time (h)	No. of 2^{ndy} hyphae
1.6	60	1.2	48	1.4	36	0.7		
2.7	60	2.9	48	1.2	36	0.4	48	1.8
3.8	60	1.2	48	1.3	36	1.4	48	2.5
4.9					36	1.1	48	2.0
6.0					36	1.0	48	2.3
7.1					36	0.3	48	1.1
8.2							48	2.4
9.3							48	1.6
10.4							48	3.2

groups of plants were similarly susceptible to infection and received inocula that were similarly aggressive. These assumptions were satisfied because the inoculated leaves on the plants set aside for disease assessment became severely mildewed and there was no trend in disease intensity over time.

Early colony growth was affected significantly by the treatments, as shown by analyses of variance. Effects of treatments on total hyphal length per colony were greater than on the number of hyphae per colony. The effects of vpd on colony growth were small and there was no discernible trend in the response to this factor. Temperature accounted for most of the treatment effects on early colony growth. Three quadratic equations relating temperature to the increase of total hyphal length per colony per day, one equation for each of the three incubation periods (0–24 h, 0–36 h and 24–36 h after inoculation), each estimated an optimum in the range 21–23 °C. This range of optimal temperatures for colony growth is similar to optima for conidial germination (Burchill, 1958; Coyier, 1968; Molnar, 1971) and incubation period (Xu, 1996). The magnitude of the response to temperature was greatest for the period 24–36 h and least for the period 0–24 h (Figure 1a), as expected from the dynamics of mycelial growth of young colonies (Prosser, 1995). According to Prosser (1995), number of hyphae and the total hyphal length per colony increase exponentially. Therefore, to better model the effects of temperature on these variables taking into account the exponential growth characteristics, the growth of young colonies would have to been assessed more frequently and at shorter time intervals than in the present study.

To compare the relative response to temperature in the three incubation periods, treatment means were re-scaled as the percentage of the maximum total hyphal length in each period, and regression analyses applied to the logit of the re-scaled treatment means. The curves for 0–36 h and 24–36 h were nearly identical whereas the curve for 0–24 h showed a higher tolerance to temperatures > 23 °C (Figure 1b). In comparison to mycelial growth, the protrusion of germ tubes occupied a greater proportion of time in the period 0–24 h than in the other two periods; this may indicate that the early phase of the germination process is more tolerant to high temperatures than is subsequent hyphal growth.

The quadratic equations give negative (thus zero) rates of hyphal growth below 12 °C, which is wrong (Burchill, 1958; Molnar, 1971; Xu, 1996). Results for the four temperatures in this study, however, agree well with other data describing the relative effects of temperature on hyphal growth of this fungus at 100% rh in the 24 h following inoculation (Molnar, 1971). A more accurate model could have been developed if more than four temperatures had been used. On the basis of published work on both glass slides and detached leaves before the start of this study, atmospheric moisture stress was thought to be at least as important as temperature in influencing conidial germination and subsequent colony development.

The production of the first haustorium is a good phenological indicator of an established parasitic relationship. Although florescence staining methods enabled microscopic detection of haustoria of old mildew colonies on mature apple leaves, the same techniques failed on young leaves. Therefore the earliest

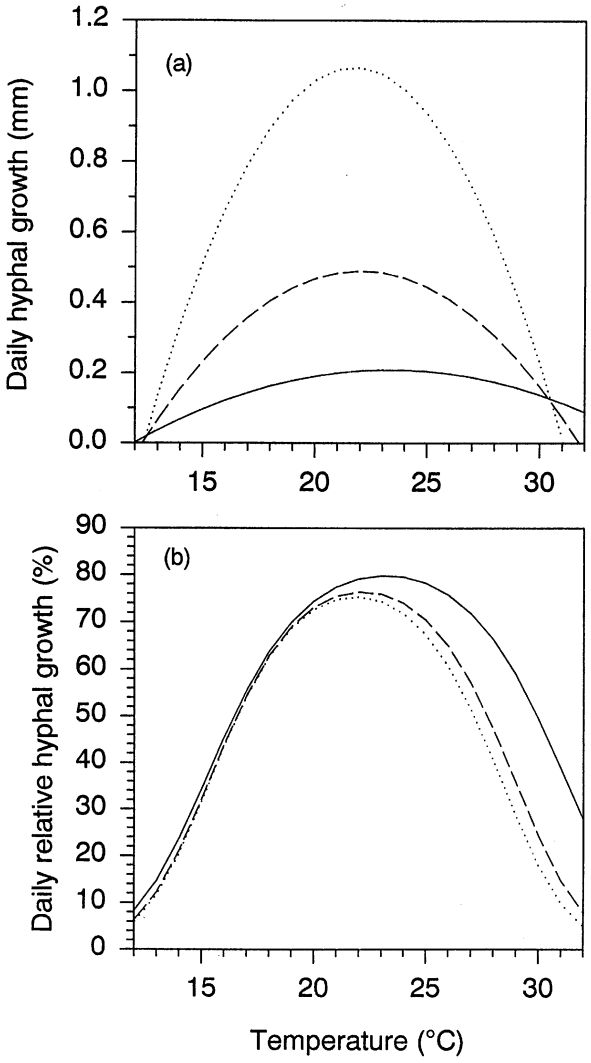

Figure 1. Three quadratic models describing the relationship between temperature and daily hyphal growth for three incubation periods: solid line – 0–24 h, dashed line – 0–36 h, dotted line – 24–36 h. (a) Hyphal growth (mm/day); see Table 3 for the equations. (b) Relative hyphal growth; the equations were derived as follows: treatment means were re-scaled as the percentage of the maximum total hyphal length in each period and regression analyses applied to the logit of the re-scaled treatment means.

branching of primary hyphae to form secondary hyphae was used as the indicator of successful infection. The time to the first observation of branched hyphae was independent of the vapour pressure deficit, suggesting that moisture stress in the range tested has little effect on the length of time before primary hyphae branch.

In general, the concentration of water vapour inside a leaf is near saturation. In daytime, the concentration of water vapour of the outside air at the level of the leaf surface is normally much less than saturated but is higher than that of the ambient air beyond the unstirred (boundary) layer (Nobel, 1974). The gradient of water vapour concentration across the boundary layer depends on factors such as leaf size, wind velocity, temperature gradient, inter-cellular, cuticular and stomatal resistance to water vapour flow, and the density of stomata. In the present study, colony development was assessed on the upper leaf surface where there are few, if any, stomata. Thus, the water vapour concentration immediately outside the upper leaf surface during light periods in the cabinets was expected to be much lower than inside the leaf and to be only slightly higher than the ambient air because of the high cuticular resistance to water vapour flow. Furthermore, because the temperature of the outer leaf surface during light periods can be expected to be higher than the ambient temperature, the rh at the level of the outer leaf surface was thus probably similar to the ambient rh. During the dark periods, because of the balanced energy exchange to and from the leaves in the closed small system of the cabinet, leaf surface temperature can be expected to be similar in the ambient and so water condensation was unlikely for most treatments. In this study it is likely, therefore, that the relative humidity of the air surrounding the conidia and young colonies on the upper leaf surfaces was probably similar to the nominal treatment value. In practice, disease forecast models are driven by weather variables describing ambient conditions rather than the micro-climate at leaf surfaces.

The effects of temperature and humidity on conidial germination have been reported for many species of powdery mildew. In most of these studies, only the percentage of germinated conidia is reported. It is likely that results from such studies reflect the effects of temperature and relative humidity on conidial mortality rather than on early colony growth. The results of the present study indicate that, for the range of atmospheric moisture stress experienced in UK orchards during the growing season, it is mainly temperature rather than moisture stress that determines the rate of early colony growth.

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References

Burchill RT (1958) Studies on apple mildew. Ph.D. thesis, University of Bristol, UK

Butt DJ (1978) Epidemiology of powdery mildews. In: Spencer DM (ed) The powdery mildews (pp. 51–81) Academic Press, London

Coyier DL (1968) Effects of temperature on germination of *Podosphaera leucotricha* conidia. Phytopathology 58: 1047–1048

Kirby AHM, Frick EL, Burchill RT and Moore MH (1963) Effect of didecyldimethylammonium bromide against powdery mildews and other fungal diseases. Nature 197: 514

Molnar L (1971) The effect of environmental factors on the germination of conidia of *Podosphaera leucotricha* (Ell. et. Ev.) Salm. Ochrana Rostlin (Praha) 7: 203–210

Nobel PS (1974) Introduction to biophysical plant physiology. W.H. Freeman and Company, San Francisco

Prosser JI (1995) Kinetics of filamentous growth and branching. In: Gow NAR and Gadd GM (eds) The growing fungus (pp. 301–318) Chapman & Hall, London

Roosje GS (1961) The importance of short time intervals between sprays against apple powdery mildew. Proceedings of British Insecticide and Fungicide Conferences Volume 1: 185–196

Xu X-M (1996) The effects of constant and fluctuating temperatures on the length of incubation period of apple powdery mildew (*Podosphaera leucotricha*). Plant Pathology 45: 924–932

Yarwood CE (1957) Powdery mildew. The Botanical Review 23: 235–301