Influence of Temperature and Moisture on Growth, Spore Production, and Conidial Germination of *Monilinia laxa*

L. Tamm and W. Flückiger

Institute for Applied Plant Biology, CH-4124 Schönenbuch, Switzerland.
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ABSTRACT

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The effect of temperature on mycelial growth and spore production of *Monilinia laxa*, the brown rot fungus of sweet cherry, was studied in vitro as well as the effect of temperature, moisture, and relative humidity on conidial germination. Mycelial growth was observed at 2.5–30 C. A model was fitted to the data, and the optimum was calculated as 24.8 C. A comparison in a second experiment between observed and predicted growth indicated that diurnal cycles of temperature (3/12 or 10/22 C) did not alter the growth rates compared to growth at constant temperatures. *M. laxa* produced the highest daily number of conidia at 10 C, with 29.4×10^6 conidia per colony within 15 days. The maximum germination fraction of conidia reached 98% when suspended in deionized water and exposed to 15–25 C. Germination was evident after 2 to 4 h. *M. laxa* was able to germinate in the absence of free moisture at relative humidities from 97 to 100%. A mechanistic model was evaluated to predict the germination process as a function of time and temperature. The model yielded close fits to the observed data.

In western Europe, the brown rot fungus *Monilinia laxa* (Aderh. & Ruhl.) Honey is known as an important pathogen on apricots and sour cherry (*Prunus cerasus* L.) (3). In Switzerland, *M. laxa* has recently become a major problem on sweet cherry (*Prunus avium* L.) as well. Serious yield losses have been reported (12, 21,24). Preliminary studies show that *M. laxa* is now a common disease in most Swiss orchards. On sweet cherry, *M. laxa* causes blossom blight, blight of spurs, and fruit rot of immature and mature fruit. Primary infections occur from conidia produced on overwintering fruit mummies and other infected tissues (6).

Little is known about the epidemiology of this particular plant pathosystem because most studies either describe *M. laxa* on different hosts (17,18,25) or deal with *M. fructicola*, which causes similar symptoms (5,22). Planning rational disease-control management requires knowledge about the fungus's epidemiology. As a first step, basic information about the pathogen's performance in vitro is useful.

The aim of this study was first to determine in vitro the influence of temperature on mycelial growth and spore production and second to study the influence of temperature and moisture on germination of conidia of *M. laxa*. In addition, models were evaluated to predict the response of *M. laxa* to these climatic parameters.

MATERIALS AND METHODS

Inoculum production and maintenance. The investigated isolate (BL8) of *M. laxa* was collected during 1989 from naturally infected blossoms of sweet cherry (*P. avium)* in an orchard near Liestal, Switzerland. BL8 was considered representative for Switzerland based on experiments presented elsewhere. The isolate was maintained on malt extract agar 2% (w/v) (Oxoid CM59) at 2 C in darkness. To obtain conidia, a medium consisting of agar 2% (w/v) (Oxoid L11), yeast powder extract 0.2% (w/v) (Oxoid L21), and macerated frozen apricot 8% (w/v) was used. Agar and apricot extract were autoclaved separately. Each petri dish (9.5 cm diameter; 17.5 ml of medium) was placed without cover into a sterile transparent box (polyethylene, $100 \times 110 \times 40$ mm) using the cover of the petri dish as a stand. The bottom of the box was filled with a saturated sterile solution of NaCl that kept the relative humidity (RH) at approximately 75% (10). A mycelial plug of the stock culture was transferred to each dish, and the box was sealed with Parafilm and incubated for 10 days at 15 C with a photoperiod of 14 h/day at 45 μE m^{-2} s^{-1}. The conidia were removed from the colonies by adding 5 ml of sterile deionized water and carefully scraping off the spores with a glass rod. The resulting suspension contained conidia and a few particles of mycelium that, due to dimensions similar to the conidia, could not be removed with filters.

Influence of temperature and moisture. To investigate the influence of temperature on growth and spore production, the system described above was used. Additionally, a ruler was placed between petri dish and stand. This allowed precise measurement of the radial growth of the colonies without opening the boxes. To inoculate, 5 μl of spore suspension (5×10^5 of conidia per milliliter) was placed in the center of each dish, which had been preconditioned at the desired temperature for 24 h. The experiment was conducted in two incubators (a photoperiod of 14 h/day at 45 μE m^{-2} s^{-1}) with 10 plates per treatment. The temperatures were assigned to the incubators at random. Experiments were conducted at 5, 10, 15, 20, 25, or 30 C and repeated once. To achieve a better description of the growth process, additional experiments at 2.5, 7.5, 12.5, 17.5, 22.5, 26, 27, 28, or 29 C were carried out. The daily growth rates were calculated when the radius of the cultures reached 23–27 mm, i.e., before growth was delayed by limited space or nutrient resources.

The conidia were collected as described above after 140–150 degree-days, i.e., 30 days after inoculation at 5 C, 10 days at 15 C, 7 days at 20 C, and 6 days at 25 C, and counted by means of a hemacytometer. The calculation of degree-days with a basal threshold of 0 C was chosen as a first approximation to comparable physiological ages of the cultures.

A second experiment was carried out to verify whether a model that describes the in vitro growth of *M. laxa* as a function of the temperature can be applied to diurnal cycles. Two possible cycles were simulated in "cold" and "warm" treatments. The treatments were 14 h of light at 14 C per 10 h of dark at 3 C (cold) and 14 h of light at 22 C per 10 h of dark at 12 C (warm), with 10 plates per treatment. The experiments were repeated once.

The influence of temperature and relative humidity on germination of conidia of *M. laxa* was studied by simulating both "wet" deposition during rainfall and "dry" deposition by wind spread. The wet and dry treatments were conducted simultaneously in six incubators at 100, 98, 94, and 88% RH (wet) and 100, 99, 98, and 97% RH (dry) at 5, 10, 15, 20, 25, and 30 C.

The required moisture conditions were obtained by the "agar dish isopiestic equilibration technique" described by Harris et al (11) and modified by Arauz and Sutton (2). To expose the conidia, the technique of Arauz and Sutton (2) was slightly modified: petri dishes (9.5 cm diameter) were filled with 17.5 ml of agar 2% (w/v) (Oxoid L11) amended with different molalities of NaCl according to data given by Lang (15). Four microscope glass slides (19 × 19 mm) were cleaned with 96% EtOH and attached to the inner side of the cover of each dish. The glass slides were fixed on short glass tubes (5 × 8 mm) by means of a therapeutic plasticine (Mastiplast 70, Fango Co., GmbH, Rapperswil, Switzerland) to avoid direct contact with the petri dish. Petri dishes were preconditioned for 24 h at the desired temperature. Conidia were either brought on the glass slides suspended in a 5-μl droplet of deionized water (5×10^5 of conidia per milliliter) (wet) or carefully transferred from the cultures with a camel-hair brush (dry). After 6, 12, 24, and 48 h, one glass slide per dish was removed, and the conidia were stained with lactophenol. After each manipulation, the dishes were resealed with Parafilm. The germination rate was determined by counting 100 conidia per sample. A conidium was considered germinated if the germ tube reached the width of the conidium (approximately 9 μm).

In a second experiment, the dynamics of germination after 2, 4, and 6 h were determined. Both treatments (wet and dry) were conducted at 100% RH and 5, 10, 15, 20, 25, or 30 C. All experiments were repeated once with four samples per treatment.

Data analyses. To describe the influence of temperature on mycelial growth of *M. laxa*, the model of Logan et al (16), modified by Baumgärtner and Gutiérrez (4), was used. This model was chosen based on the following criteria: randomness and normality of residuals, significance of regression coefficients, and R^2. Emphasis was placed on good fit at low temperatures and precise prediction of growth at changing temperatures. For data analysis, the absolute growth rates were standardized to values between 0 and 1 (1):

$$y^i = y / y_{max} \tag{1}$$

in which y^i is the relative growth, y is the measured radial growth per day, and y_{max} is the highest rate observed. The modified model of Logan et al (16) can be written as:

$$R(T) = \left(p_1 \{\exp[p_2 (T - T_b)] - \exp[p_2 (T_m - T_b) - p_3 (T_m - T)]\}\right) - p_4 \tag{2}$$

in which R is the relative growth, T is the actual temperature, T_b is the lowest temperature tested, and T_m is the upper developmental threshold. T_m was set to 31 C based on analysis of the residuals. Parameters p_1–p_4 were estimated by nonlinear least square regression techniques. Parameter p_4 was added to the model to achieve a better fit at low temperatures. The influence of temperature on spore production was analyzed by linear regression. The data were square-root transformed prior to calculation.

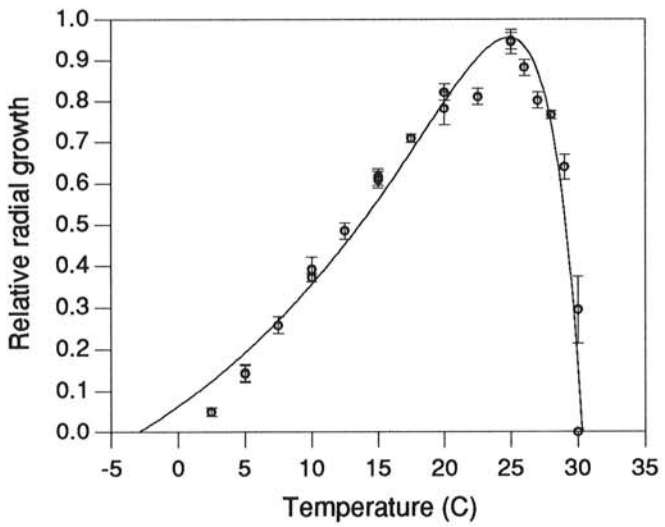

Fig. 1. Influence of temperature on radial growth of colonies of *Monilinia laxa* in vitro. Each data point represents the mean value of 10 replicates. Bars indicate the standard deviation. The function is the regression solution of the modified model of Logan et al (equation 2).

The time-dependent germination rates were described with the model of Richards (20), which can be written as:

$$G(t) = g_{max} [1 - (1 - g_0^{(1-m)}) \exp(-r_g \cdot t)]^{1/(1-m)} \tag{3}$$

if $m < 1$,

in which G is the estimated fraction of germinated conidia at time t, g_{max} is the maximum germination rate, g_0 is the initial germination fraction, r_g is the rate parameter, and m is the shape parameter. The value of g_0 was known to be 0. The parameters g_{max}, r_g, and m were estimated by nonlinear regression for each set and temperature of the "wet 100% RH" treatment. The value of m ranged between 0.28 (5 C) and 0.98 (25 C). However, a value of $m = 0.9$ yielded the best overall fit. To simplify the model, m was set to this value. This function is intermediate in shape between the monomolecular and the Gompertz models (8). To decide whether the pooling of all data was appropriate, the replications were introduced into the model as a dummy variable (23). Because most coefficients of the dummy variables proved to be nonsignificant (Student's t test; $P > 0.05$) and the parameters g_{max} and r_g of the pooled data showed values intermediate to those of the sets computed separately, the data were combined for further analysis.

In a second step, the model was extended to allow the description of spore germination dependent on both time and temperature: Parameters g_{max} and r_g were replaced with the BETE function of Analytis (1), which can be written as:

$$g_{max} = \gamma_1 \phi^{\gamma 2} (1 - \phi)^{\gamma 3} \tag{4}$$

and

$$r_g = \rho_1 \phi^{\rho 2} (1 - \phi)^{\rho 3} \tag{5}$$

and

$$\phi = (T - T_{min}) / (T_{max} - T_{min}) \tag{6}$$

in which T is the actual temperature and T_{min} and T_{max} are the lower and upper developmental thresholds. T_{min} and T_{max} were set to 0 and 35 C, respectively. T_{min} was set to 0 C because considerably lower temperatures prevent germination due to frost. Because spore germination ceased at higher temperatures than did mycelial growth, the upper threshold, T_{max}, was set to 35 C. The parameters γ_1, γ_2, γ_3, ρ_1, ρ_2, and ρ_3 of the combined model (optimized for the wet treatment at 100% RH) were estimated by nonlinear regression separately for all moisture regimes to study the appropriateness of the model with various data sets.

In a third step, a linear correction term was added to the combined model to study the influence of relative humidity on germination rate:

$$G(T,t,RH) = (\alpha_0 + \alpha_1 \cdot RH)\, G_{RH = 100\%}(T,t) \tag{7}$$

TABLE 1. Estimated parameters and associated statistics for the modified model of Logan et al (equation 2) relating mycelial growth of *Monilinia laxa* in vitro and temperature

Parameter	Estimate	ASE[a]	Residual df	R^2[b]
p_1	0.535	0.069	206	0.941
p_2	0.048	0.005		
p_3	0.385	0.041		
p_4	0.412	0.066		

[a] ASE: Asymptotic standard error of the parameter estimate.
[b] R^2: 1-residual SSQ/regression SSQ.

in which G is the estimated fraction of germinated conidia dependent on temperature, time, and relative humidity. $G_{RH=100\%}(T,t)$ is the predicted germination rate of the combined model at 100% RH (parameters γ_1, γ_2, γ_3, ρ_1, ρ_2, and ρ_3 estimated at 100% RH). The regression parameters α_0 and α_1 were estimated for both the wet and dry treatments. All regression analyses were performed with SYSTAT version 5.1 (Systat Inc., Evanston, IL).

RESULTS

Mycelial growth and production of conidia. Relative growth of *M. laxa* increased from 2.5 C to a maximum of approximately 25 C and then declined rapidly toward 31 C (Fig. 1). The parameter estimates for the modified model of Logan et al (16) are given in Table 1. Based on this model, the mycelial growth was simulated for two conditions of changing temperatures (i.e., diurnal cycles). The calculated radii of the colonies are compared to the observed values in Figure 2.

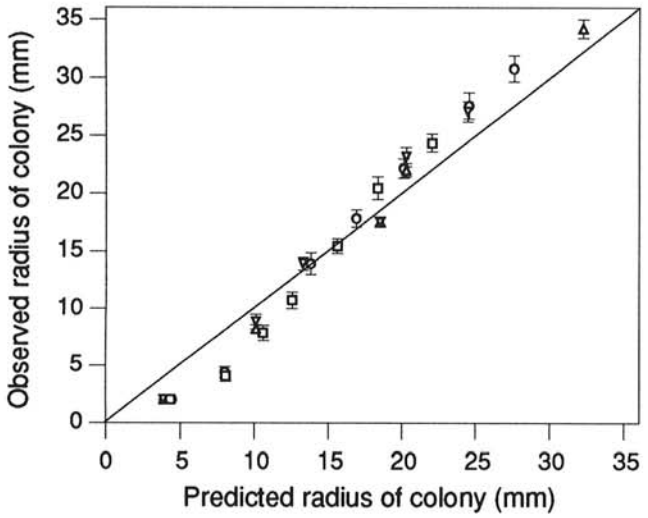

Fig. 2. Prediction of radial growth of *Monilinia laxa* as determined by diurnal cycles of temperature (modified model of Logan et al; equation 2). Temperature conditions were 14 h of light at 12 C/10 h of dark at 3 C (○,□) or 14 h of light at 22 C/10 h of dark at 10 C (△,▽). Each data point represents the mean value of 10 replicates. Bars indicate the standard deviations.

TABLE 2. Estimated regression parameters[a] and associated statistics for the regression relating the sporulation of *Monilinia laxa* in vitro after 140–150 degree-days[b] to the incubation temperature

Parameter	Estimate	SE	Residual df	R^2
Constant	1,578.2 ($P<0.001$)	26.7	182	0.903
β	−53.834 ($P<0.001$)	1.31		

[a] Original data were square-root transformed prior to analysis.
[b] 150 degree days for all temperatures except for 20 C (140 degree days).

Exposed to 76% RH, *M. laxa* produced conidia abundantly. Conidiophores were formed in concentric rings according to the daily cycles of light within the range of 2.5 to 30 C. The number of conidia produced per colony surface area increased significantly ($P < 0.001$; Table 2) with lower temperatures (Fig. 3). At 5 C, 2.4×10^6 conidia per square centimeter were collected after 150 degree-days (Table 3). The colonies produced maximum daily numbers of conidia at 10–15 C. At temperatures above 20 C, only sparse production of conidia occurred. In all treatments, *M. laxa* produced conidia of normal viability.

Spore germination. Germination of *M. laxa* was observed as early as 2 h after inoculation and reached up to 98% at favorable temperatures (15–25 C) if conidia were deposited in free water and kept at 100% RH (Fig. 4). At 30 C, the conidia germinated readily, but the germ tubes were abnormal, and subsequent growth was inhibited. The effect of the relative humidity on germination of *M. laxa* is shown in Figure 5A (wet deposition) and 5B (dry deposition). In general, treatments with conidia in free water (wet) germinated faster and led to higher maximum germination fractions than did treatments with dry deposited conidia (dry) within similar time intervals. In wet treatments, lower relative humidity decreased the maximum germination fraction rather than the velocity of the germination process. In dry treatments, the conidia were able to germinate at 98–100% RH, whereas germination at 97% RH was negligible.

The combined model of Richards and Analytis (equations 3–6) yielded fairly high coefficients of determination ($R^2 = 0.68$–0.95) for all moisture regimes, except the dry treatment at 97% RH (Table 4). Applied to this treatment, the model failed because the maximum germination fraction reached only 3%. The regression solution (i.e., the response surface) of the wet 100% RH treatment is shown in Figure 6.

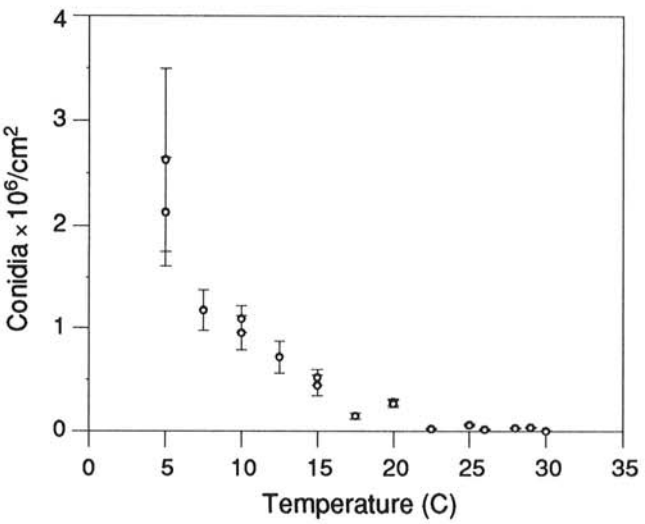

Fig. 3. Production of conidia per surface area of a colony of *Monilinia laxa* in vitro as influenced by temperature. Conidia were collected after 150 degree-days (20 C at 140 degree-days). Each data point represents the mean value of 10 replicates. Bars indicate the standard deviations.

TABLE 3. Effect of temperature on sporulation of *Monilinia laxa* in vitro[a] after 140–150 degree-days[b] (14-h photoperiod at 45 μE m^{-2} s^{-1})

Temp. (C)	Incubation (days)	Radius of colony (mm)	Spores/colony (1×10^6)	Spores/day (1×10^6 d^{-1})	Spores/surface area of colony (1×10^6/cm^2)
5	30	24.0 (3.0)	40.0 (14.2)	1.4 (0.4)	2.4 (0.8)
10	15	31.7 (1.3)	29.4 (4.6)	2.2 (0.4)	1.0 (0.2)
15	10	33.8 (0.8)	15.5 (3.1)	1.7 (0.3)	0.5 (0.1)
20	7	33.5 (1.1)	11.7 (1.5)	1.3 (0.1)	0.3 (0.05)
25	6	30.9 (1.2)	1.8 (0.4)	0.3 (0.06)	0.06 (0.01)
30	5	8.7 (9.5)	0.01 (0.02)	0.0 (0.00)	0.0 (0.0)

[a] Data are means of two experimental sets with 10 replicates. Values in parentheses represent standard deviations.
[b] 150 degree-days for all temperatures except for 20 C (140 degree-days).

Difficulties in estimating parameters arose for moisture regimes below 100% RH. Lack of data within the first 6 h of the germination process led to large confidence intervals and, partly, to nonsignificant parameter estimates of ρ_1, ρ_2, and ρ_3 (Student's t test; $P > 0.05$). These parameters determine the rate, i.e., the velocity, of the germination process. For the two replicates of the wet treatment at 88% RH, the regression had to be computed separately because of serious differences between the two replicates. We suppose that a small delay during manipulation (i.e., the earlier deficiency of free water available for germination) caused this effect.

The influence of relative humidity on the germination process was studied by adding a linear correction term to the combined model of Richards and Analytis (equation 7). The influence of decreasing relative humidity, therefore, was interpreted as a cause for linear reduction of germination compared to the predicted rate at 100% RH. The analysis showed that lower relative humidity led in both the wet and dry treatments to highly significant ($P < 0.001$) reductions of the germination rates (Table 5). The combined models with implemented correction terms yielded satisfactory predictions (wet: $R^2 = 0.878$; dry: $R^2 = 0.776$) for

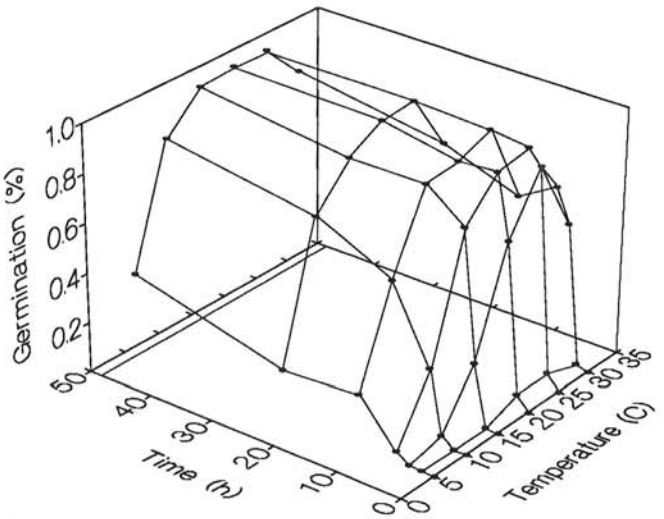

Fig. 4. Germination fractions of conidia of *Monilinia laxa* suspended in a 5-μl droplet at 100% relative humidity determined by time and temperature. Each data point represents the mean of two experimental sets with four replicates.

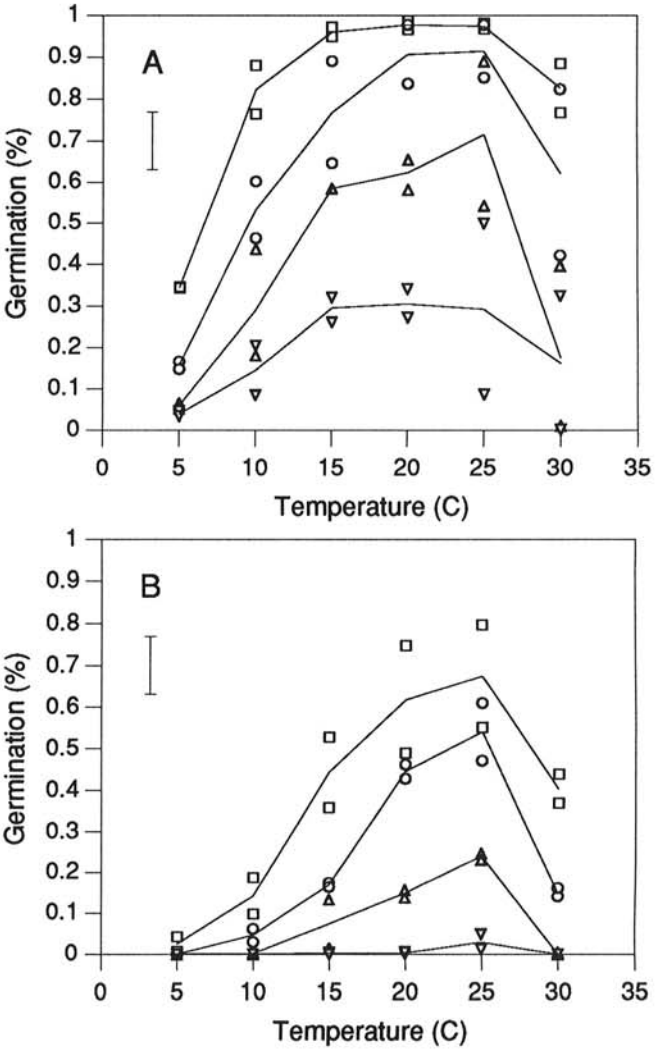

Fig. 5. Effect of temperature and relative humidity (RH) on germination fractions of *Monilinia laxa* after 48 h. Each data point represents the mean of four replicates; lines are the mean of both experimental sets. Bars indicate the pooled standard deviations. **A,** Conidia deposited in a 5-μl droplet (5×10^5 conidia per milliliter) and exposed to 100% (□), 98% (○), 94% (△), or 88% RH (▽). **B,** Dry deposited conidia exposed to 100% (□), 99% (○), 98% (△), or 97% RH (▽).

TABLE 4. Estimated parameters and associated statistics for the combined model of Richards and Analytis (equations 3–6) relating germination rates of *Monilinia laxa* to time and temperature under different conditions[a]

Treatment	Parameter estimates						Residual df	R^2
	γ_1	γ_2	γ_3	ρ_1	ρ_2	ρ_3		
Wet, 100% RH[b]	3.258	1.061	0.684	2.160	1.258	0.363	416	0.950
	(0.244)	(0.061)	(0.041)	(0.351)	(0.131)	(0.088)		
Wet, 98% RH	5.946	1.721	1.058	1.547	0.609	0.335	229	0.896
	(0.770)	(0.103)	(0.073)	(0.867)	(0.372)	(0.316)		
Wet, 94% RH	18.250	2.888	1.900	40.614	2.716	2.112	211	0.792
	(5.066)	(0.245)	(0.157)	(66.759)	(1.166)	(0.795)		
Wet, 88% RH	2.533	1.935	0.896	0.293	0.935	−10.006	110	0.873
(replicate 1)	(0.545)	(0.195)	(0.110)	(36.657)	(50.134)	(218.547)		
Wet, 88% RH	11.610	2.969	2.800	1.838	−40.063	11.986	109	0.859
(replicate 2)	(1.905)	(0.122)	(0.127)	(0)	(0)	(0)		
Dry, 100% RH	4.123	2.171	1.085	23.536	3.414	2.159	424	0.777
	(1.370)	(0.297)	(0.181)	(14.245)	(0.543)	(0.331)		
Dry, 99% RH	566.420	7.231	3.717	17.440	3.091	1.992	229	0.881
	(334.841)	(0.557)	(0.324)	(22.957)	(1.210)	(0.724)		
Dry, 98% RH	0.021	−0.343	−1.771	2.178 E+8	17.327	11.861	230	0.680
	(0.048)	(2.108)	(1.293)	8.487 E+8	(3.357)	(2.242)		
Dry, 97% RH	0.884	12.658	−22.599	2.097	4.111	4.741	234	0.271
	(n/a)[c]	(n/a)	(n/a)	(n/a)	(n/a)	(n/a)		

[a] Numbers in parentheses correspond to the asymptotic standard error of the parameter estimates; R^2: 1-residual SSQ/regression SSQ.
[b] RH: Relative humidity.
[c] (n/a): not available.

all combinations of temperature, time, and relative humidity within the range observed.

DISCUSSION

M. laxa is well adapted to the moderate weather conditions in Switzerland during spring and summer. In vitro mycelial growth was observed at 2.5 C up to 31 C, and maximum growth rates were observed at 25 C (maximum calculated as 24.8 C). A similar range of temperature was reported by earlier authors (7,13,14).

The mycelial growth of *M. laxa* at constant temperatures was described with the modified model of Logan et al (4,16). Based on the model, *M. laxa* is able to grow even below 0 C. This might be true, provided that neither fungus nor host freezes. Kröber (14) reported that *M. laxa* ceased growth at 0 to −1 C. The model also was used to predict growth at changing temperatures. The radius of the colonies was slightly overestimated at low values and underestimated at high values. This difference was caused by delayed growth in the early stage of the colonies. However, the predicted radial growth did not differ remarkably between the "cold" and "hot" temperature conditions. Hence, there is no evidence that, under moderate conditions, diurnal cycles either stimulate or decrease the growth of *M. laxa* compared to development at constant temperatures. The model, therefore, might be useful in predicting temperature-dependent processes in vivo, such as the incubation period. There may be a restriction to this model: Kröber (14) reported a 'memory effect' when cultures of *M. laxa* were exposed to temperatures below −8 C. The growth of these colonies was somewhat delayed when subsequently grown at 'optimum temperatures' compared to colonies without precondition. He suggested that the low temperatures had damaged parts of the fungal tissue that needed to recover. This effect is only of minor practical importance because temperatures below −2 C damage any part of the plant susceptible to the fungus.

Several authors reported the difficulties of producing large numbers of conidia of *M. laxa* on artificial media such as potato-dextrose or malt-extract agar (3,7). An improved method has been presented recently by Pascual et al (19). With the method used in our investigation, high amounts of conidia can be produced because the method takes into account that sporulation of *M. laxa* depends both on the moisture content of the host substrate and on the ambient relative humidity (9). Low temperatures seemed to enhance conidial production. However, a comparison of the temperature treatments has to be interpreted carefully, because the calculation of degree-days as an approximation to the true physiological age of a culture may be biased.

Conidia of *M. laxa* germinated best if deposited in free water, although germination was possible in the absence of free moisture. The dry exposure led to reduced germination fractions, and the process was strongly delayed. Nevertheless, these results suggest that the absence of free water is a limiting but not an excluding factor in the infection mechanism of *M. laxa*. This may be significant if dry conidia are deposited at susceptible and humid sites on the plant, such as the bottom of the calyx, stigma, or the stamen of blossoms. Zwygart (25), for example, infected blossoms of sour cherries by inoculating the stamen with dry conidia at relative humidities as low as 91%.

A combination of the Richards model (20) and Analytis' BETE model (1) was evaluated to predict the germination of *M. laxa* as a function of time and temperature. The combined model produced satisfactory results for the purpose of our work. At temperature extremes, it yielded more plausible results than did polynomials. Furthermore, the model was applicable to several data sets and allowed reasonable predictions even if based on relatively few data points.

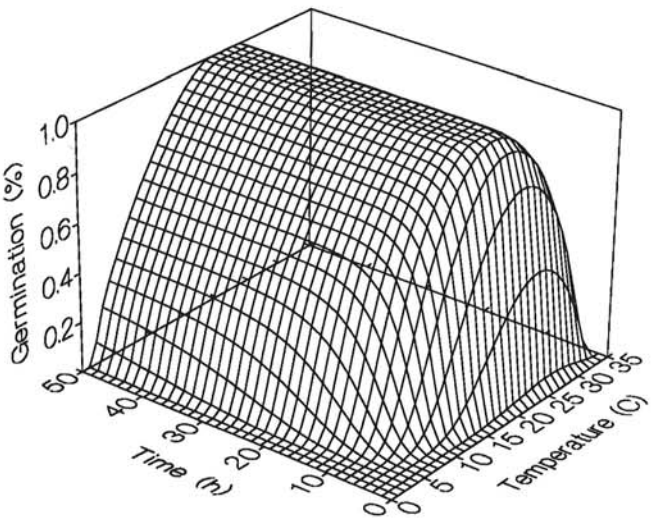

Fig. 6. Predicted germination fractions of conidia of *Monilinia laxa* suspended in a 5-µl droplet exposed to 100% relative humidity determined by time and temperature. The response surface is the regression solution of equations 3–6 ($R^2 = 0.95$; parameter estimates are given in Table 4).

TABLE 5. Estimated regression parameters and associated statistics for the regression relating the functional response of the germination rate of *Monilinia laxa* to temperature and time to relative humidity[a]

Treatment	Parameter estimate α_0	Parameter estimate α_1	Residual df	R^2
Wet	−5.087 ($P < 0.001$)	0.061 ($P < 0.001$)	1,103	0.878
Dry	−33.884 ($P < 0.001$)	0.349 ($P < 0.001$)	1,139	0.776

[a] Parameters of the combined model of Richards and Analytis (equations 3–6) estimated at 100% relative humidity (Table 3).

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