Response Models for Conidiospore Germination and Germ Tube Elongation of *Mycosphaerella fragariae* as Influenced by Temperature and Moisture

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ABSTRACT

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The influence of temperature on conidiospore germination of *Mycosphaerella fragariae* was evaluated on water agar. Germination was modeled as a nonlinear logistic function of time. The logistic rate of germination, calculated from this model, showed a maximum rate at 22.4 C. The maximum fraction of germination was constant at 0.94 from 5 to 30 C but dropped sharply between 30 and 35 C. Moisture requirements for conidiospore germination were determined by incubation on glass slides held at different moisture conditions. No germination was seen below 98% relative humidity, and the germination rate at 98–100% relative humidity did not differ from germination with free moisture. Germ tube elongation was evaluated on water agar over a temperature range of 5–37 C. The maximum rate of elongation was seen at 22.7 C with minimum and maximum growth near 5 and 37 C, respectively.

Additional key words: common leaf spot, *Fragaria* × *ananassa*, *Ramularia tulasnei*, strawberry.

Common leaf spot of strawberry, incited by *Mycosphaerella fragariae* (Tul.) Lindau (= *Ramularia tulasnei* Sacc.) has caused major production problems in California strawberry nurseries and production fields in recent years. Fungicide programs have been the main control measure in California, but this measure has not been entirely effective in recent years. It was felt that an improved understanding of the epidemiology of the disease would enhance the success of management efforts.

The long-range goal was to develop the information necessary to construct a simulation model. The first phase in building a simulation model requires the formulation of submodels to describe the influence of key environmental variables on the individual stages of pathogen development, such as spore germination. Precise information on spore germination is important in developing predictive systems for fungal diseases. A good estimate of the rate and total fraction of spore germination is critical in determining the onset and intensity of an infection period. This information in turn can be used for maximizing the eradicant capabilities of newer fungicides (3).

Several models explaining spore germination of various fungi have been described in the literature (4,7,10,11,14). Waggoner and Parlange (14) presented a germination model for *Alternaria solani* that used probit's to model the effects of time and temperature. Pearson et al (11), working with *Gymnosporangium juniperi-virginianae*, presented a multiple regression model with time represented as a logarithmic function and temperature effects represented by a polynomial. Payandeh and Wallace (10) presented a nonlinear, polymorphic version of Richard's growth function, which incorporated time and temperature effects to explain germination of spores of *Entomopthora aphidis* and *G. juniperi-virginianae*. Imhoff et al (7) used a series of equations based on Richard's model to describe the germination of urediospores of *Uromyces phaseoli*. Eisensmith et al (4) presented a stochastic germination model to explain spore germination of five different fungi. Their model used an approach similar to the probit model of Waggoner and Parlange (14).

Some epidemiological information concerning the germination and growth requirements for *M. fragariae* has been reported (5,8), but this information, while a useful starting point, was not suitable for calculating development rates. This paper presents a conidiospore germination model similar to the above models but based on a nonlinear logistic function. In addition, models are also presented for relating germ tube elongation rates to temperature and for determining the influence of moisture on the germination process.

MATERIALS AND METHODS

All inoculum for these studies was obtained from single conidiospore isolates of *M. fragariae* isolated from infected strawberry leaves collected in California. Cultures were maintained on Czapek-Dox agar and stored at 4 C. Conidiospore suspensions were prepared from 10-day-old cultures incubated at 18 C with 14 hr per day of fluorescent light (100 μE m^{-2} s^{-1}). Conidiospores were suspended in sterile distilled water, collected on a 0.45-μm filter, and then resuspended in sterile distilled water. Concentrations were adjusted to 1.5×10^4 conidiospores per milliliter for all experiments.

The effects of temperature on germination were evaluated by plating 25-μl aliquots of the conidiospore suspension onto water agar plates. Germination was evaluated over a temperature range of 5–37 C in unlighted incubators. Germination was assessed at periodic time intervals by counting the number of conidiospores with germ tubes at least one-half the length of the spore. Three replicate counts of 150 conidiospores were done at each temperature for each sample period. The entire experiment was conducted twice.

Germ tube elongation was chosen as a method of measuring mycelial growth of *M. fragariae* because the small colony size (1–3 mm after 10 days) did not allow for accurate assessment of colony growth rates. Germ tube elongation experiments were conducted over the same temperature range and with the same general procedures as described for conidial germination studies. Agar disks with germinating conidiospores were removed at periodic intervals up to 36 hr, placed on filter paper saturated with sodium azide (0.03%), and stored at 4 C to arrest growth. Photomicrographs of germ tubes were prepared. The negatives were then projected onto paper and hand traced. Measurements to the nearest millimeter were taken from the tracings and converted back to actual lengths in microns. Three replicates of 20 germ tubes apiece were measured for each time and temperature evaluated.

Germination, under the influence of moisture in the form of relative humidity or a free water film, was evaluated on cleaned

glass slides. Conidial suspensions were sprayed onto slides and allowed to briefly air dry. Deposits were adjusted so that conidia were spread evenly with a minimum of clumping.

Slides were then placed in humidity chambers. Each humidity chamber consisted of a 500-ml polyethylene bottle with a tight sealing lid. A slotted plastic block was fitted inside the lid such that several glass slides could be held in a vertical position inside the bottle. Constant humidities in the chambers were maintained by using glycerol solutions in distilled water (1). The humidity chambers were sealed and submerged in a temperature bath at 18 ±0.5 C. A free water film was achieved by using a thin-walled condensation cell. The cell was constructed by joining three microscope slides at the long edges with epoxy adhesive to form a three-sided tube. The tube ends were closed with rigid polystyrene and the top end was fitted with inlet and outlet ports. Water at 18 ±0.5 C was circulated inside the cell. The entire cell was placed in a 500-ml humidity chamber containing 150 ml of distilled water, and the entire assembly was sealed and submerged in a 18 ±2.0 C bath. With this apparatus, a thin water film could be maintained for extended periods on glass cover slips attached to the sides of the condensation cell.

The germination was evaluated at periodic intervals by evaluating three groups of 150 spores. The experiment was conducted twice. All statistics were performed using SAS (Version 82.3)(12).

RESULTS

Germination versus temperature. Conidial germination was evident as early as 4 hr at temperatures between 20 and 25 C (Fig. 1). Initial germination was increasingly delayed above and below these temperatures. Only low and abnormal germination was seen above 35 C. The maximum germination fraction was reached after 12 and 18 hr at temperatures between 18 and 25 C and was increasingly delayed above and below these temperatures.

A model to explain conidiospore germination was developed through the following considerations. The germination of a single conidiospore can be viewed as a binary event. When such binary events are accumulated for a population over time, a sigmoid response is often seen (2,15). Although several models could be used to describe the resulting response, Cox (2) states that the logistic model is often of greater utility than normal probability models. A nonlinear logistic of the form

$$G = g_{max}/[1 + (g_{max} - g_0)*\exp(-r_g*t)/g_0] \quad (1)$$

where G is the proportion of germinated spores at time t, g_0 is the initial level of germination (y-intercept), g_{max} is the maximum fraction of spores eventually germinating, and r_g is the rate of germination, was chosen to relate the germination response to time. This model provides an estimate of the rate of germination as well as an estimate to the total fraction of spores germinating at a specific given temperature.

The logistic model was fitted to the data using nonlinear regression methods. A separate equation was derived for each

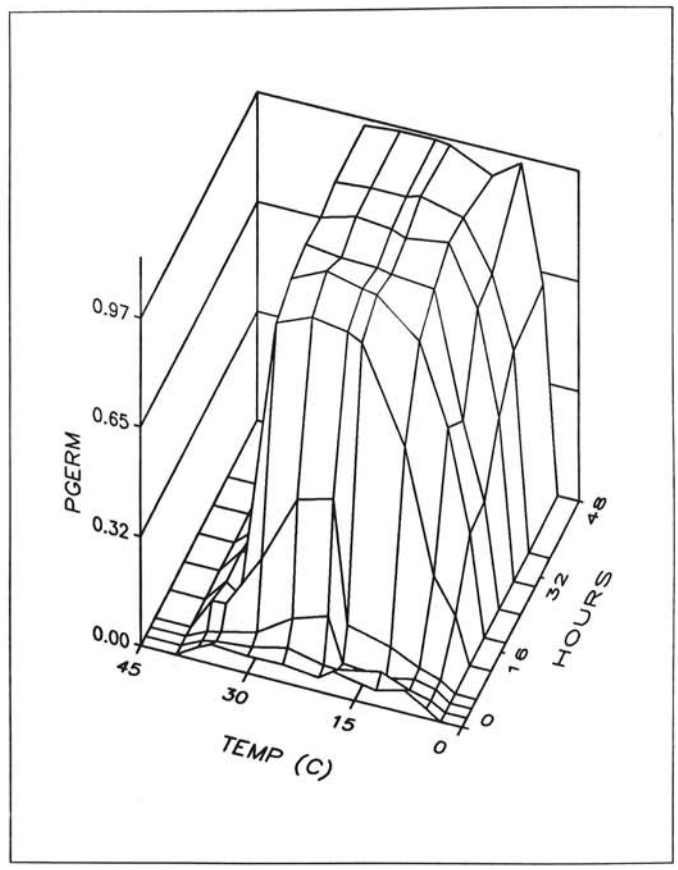

Fig. 1. The effect of temperature on the time course of conidiospore germination of *Mycosphaerella fragariae*. Response surface points represent the mean value for both experiments with three replications per experiment.

TABLE 1. Parameter estimates and associated statistics for equation 1 relating conidial germination of *Mycosphaerella fragariae* to time for each temperature tested

Experiment	Temp (C)	Parameter estimates[a]			R^2_{adj}
		g_0	r_g	g_{max}	
1	5	0.0516 (0.0176)	0.0872 (0.0118)	0.8779 (0.0323)	0.95
	8	0.0491 (0.0083)	0.1301 (0.0080)	0.9380 (0.0120)	0.99
	12	0.0111 (0.0027)	0.4116 (0.0225)	0.9232 (0.0079)	0.99
	18	0.0028 (0.0010)	0.7021 (0.0530)	0.9468 (0.0099)	0.99
	20	0.0110 (0.0041)	0.7533 (0.0695)	0.9197 (0.0105)	0.99
	25	0.0126 (0.0039)	0.7032 (0.0584)	0.9413 (0.0092)	0.99
	30	0.0087 (0.0036)	0.6096 (0.0644)	0.9114 (0.0128)	0.99
	35	0.0243 (0.0152)	0.1489 (0.0854)	0.1070 (0.0137)	0.34
2	5	0.1212 (0.0319)	0.0485 (0.0090)	1.0027 (0.0881)	0.90
	8	0.0881 (0.0423)	0.1076 (0.0246)	0.9786 (0.0527)	0.88
	12	0.0119 (0.0087)	0.4037 (0.0680)	0.9036 (0.0245)	0.96
	18	0.0010 (0.0019)	0.7972 (0.2200)	0.9044 (0.0278)	0.96
	20	0.0121 (0.0085)	0.7225 (0.1312)	0.9356 (0.0205)	0.97
	25	0.0109 (0.0097)	0.7140 (0.1634)	0.9447 (0.0244)	0.96
	30	0.0135 (0.0072)	0.5543 (0.0816)	0.9469 (0.0210)	0.98
	35	0.0914 (0.0422)	−0.1252 (3.144)	0.0915 (0.1057)	−0.08

[a] G_0 is the initial level of germination (y-intercept), rate parameter, r_g, is calculated in terms of hours. Maximum germination fraction, g_{max}, is given as a proportion. Numbers in parentheses are asymptotic standard deviations of parameters. R^2_{adj} is the adjusted coefficient of determination.

temperature level and each experiment was analyzed separately. Estimated parameters for both experiments are given in Table 1. Generally, the logistic model described the germination response quite well and no patterns were seen in the residuals. The model was not applicable at temperatures above 35 C since germination was low and abnormal.

To more clearly address the influence of temperature on the germination rate, the logistic rate parameters were further analyzed as a function of temperature. Because an F test showed no difference due to experiment ($PR > F$ as 0.79), parameter estimates were combined for this analysis. Several models were considered including polynomials, segmented polynomials, and Schrodter's sine function (13). A segmented polynomial of the form

$$r_g = b_0 + b_1 T + b_2 T^2 \qquad (\text{for } T \leqslant 12) \qquad (2)$$

$$r_g = b_0 + b_1 T + b_2 T^2 + b_3(T-12) + b_4(T-12)^2 \qquad (\text{for } T > 12) \qquad (3)$$

in which r_g is the rate of germination, the b's are the estimated parameters, and T is temperature. Equations 2 and 3 were fitted to the data using ordinary least squares regression. The joint point for this and other segmented models was determined through iterative regressions. The coefficient of determination (adjusted for degrees of freedom) was high ($R^2_{adj} = 0.98$), and no patterns were evident in the residuals. Predicted values based on equations 2 and 3 are plotted with the data in Figure 2.

An analysis of maximum germination fractions was conducted using the g_{max} estimates from equation 1. A segmented polynomial of the form

$$g_{max} = b_0 + b_1 T \qquad (\text{for } T \leqslant 30) \qquad (4)$$

$$g_{max} = b_0 + b_1 T + b_2(T-30)^2 \qquad (\text{for } T > 30) \qquad (5)$$

was fit to the data by using regression analysis. The coefficient of determination was high ($R^2_{adj} = 0.99$), and no patterns were evident in the residuals. Predicted values based on equations 4 and 5 are plotted with the data in Figure 3. Maximum germination was essentially constant between 5 and 30 C and dropped sharply between 30 and 35 C.

Predicted values for conidial germination as a function of time and temperature were calculated using equation 1 with the rate defined by equations 2 and 3 and maximum germination defined by equations 4 or 5 (Fig. 4). When the predicted germination was regressed against actual germination, a high coefficient of determination was obtained ($R^2_{adj} = 0.97$). Furthermore, no patterns were seen in a three-dimensional plot of residuals against time and temperature.

Germ tube elongation rates. Germ tube growth rates were estimated by regressing germ tube lengths against time for each temperature tested. A simple linear model was found to be suitable

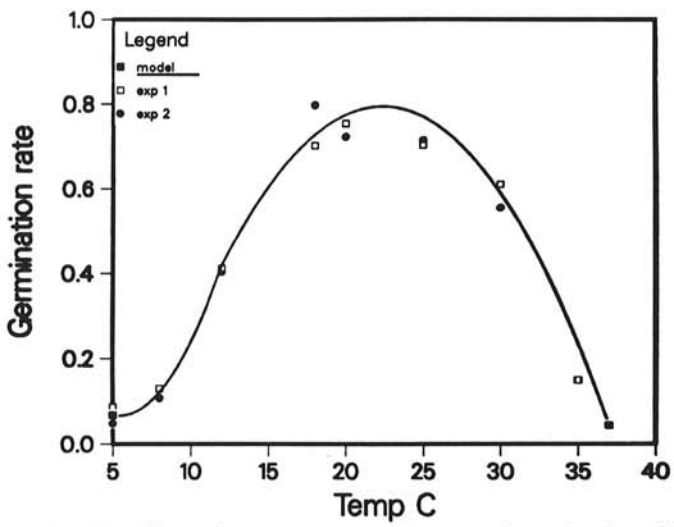

Fig. 2. The effect of temperature on the rate of germination of *Mycosphaerella fragariae*. Model is the regression solution for equations 2 and 3. Parameter estimates and standard deviations are as follows, $b_0 = 0.304(0.197)$, $b_1 = -0.088(0.050)$, $b_2 = 0.008(0.003)$, $b_3 = -0.034(0.023)$, $\beta_4 = -0.012(0.003) R^2_{adj} = 0.98$.

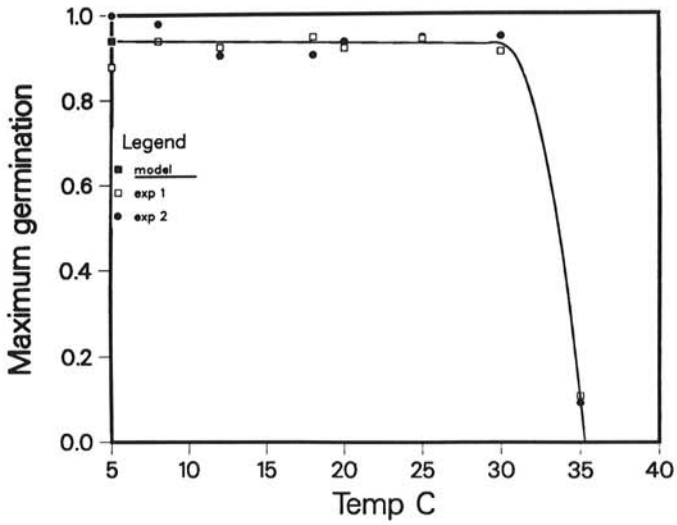

Fig. 3. The effect of temperature on the maximum germination fraction of *Mycosphaerella fragariae*. Model is the regression solution for equations 4 and 5. Parameter estimates and standard deviations are as follows, $b_0 = 0.941(0.019)$, $b_1 = -0.0004(0.0010)$, $b_2 = -0.033(0.001)$, $R^2_{adj} = 099$.

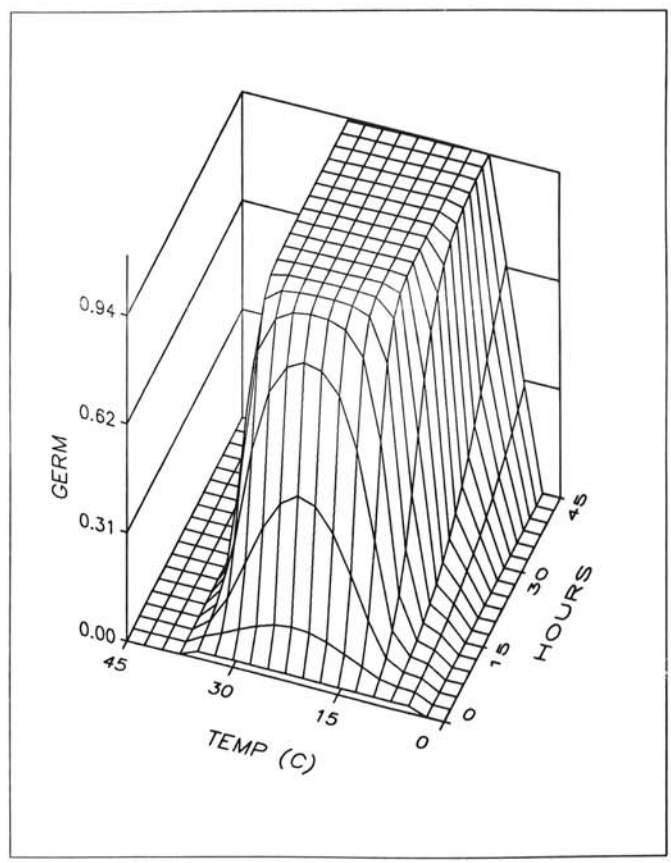

Fig. 4. Predicted values for conidiospore germination as a function of time and temperature. Response surface generated using regression model based on equation 1 with rate values given by equations 2 and 3 and maximum germination fraction given by equations 4 and 5.

over the 36-hr period of evaluation, and the resulting elongation rate parameters are given in Table 2. Rate parameters from both experiments were then regressed against temperature to develop a model relating germ tube elongation to temperature. A segmented quadratic of the form

$$r_e = b_0 + b_1 T + b_2 T^2 \qquad (\text{for } T \leqslant 30) \qquad (6)$$

$$r_e = b_0 + b_1 T + b_2 T^2 + b_3(T-12) + b_4(T-12)^2 \qquad (\text{for } T > 12) \qquad (7)$$

where r_e is the elongation rate, b's are the estimated parameters, and T is the temperature. The segmented quadratic equation was found to be the most suitable model when compared with different order polynomials and other segmented polynomials. The predicted elongation rates are plotted against temperature in Figure 5.

Moisture requirements. The response of germination to moisture is shown in Figure 6. No significant germination occurred below 100% relative humidity in experiment 1 or below 98% relative humidity in experiment 2. Data were analyzed according to a logistic model of the form

$$\ln(g/(1-g)) = f(t) \qquad (8)$$

in which g is the proportion of germinated conidia and t is the time in hours. This form of the logistic model was employed because the number and spacing of the time intervals did not allow for effective use of nonlinear regression methods. A separate equation was fitted for each moisture level tested, and each experiment was analyzed separately. The resulting parameter estimates are presented in Table 3. Predicted values of the logit of germination are plotted against time in Figure 7.

TABLE 2. Estimated rate parameters and associated statistics for the regression of germ tube length of *Mycosphaerella fragariae* against time for the different temperatures tested

Experiment	Temp (C)	b_1[a]	$s(b_1)$	R^2_{adj}	$\sqrt{\text{MSE}}$
1	5	0.0609	0.0106	0.80	0.3102
	8	0.0957	0.0113	0.90	0.3310
	12	0.1755	0.0173	0.90	0.6891
	18	0.4213	0.0448	0.89	1.7894
	20	0.4279	0.0445	0.89	1.7747
	25	0.3981	0.0375	0.91	1.4951
	30	0.1694	0.0259	0.79	1.0321
	35	0.0465	0.0187	0.46	0.3448
	37	0.0254	0.0102	0.39	0.2292
2	5	0.0472	0.0098	0.74	0.2871
	8	0.1103	0.0108	0.90	0.4314
	12	0.2366	0.0151	0.96	0.6011
	18	0.3978	0.0241	0.97	0.5404
	20	0.5367	0.0376	0.96	0.8439
	25	0.4097	0.0439	0.91	0.9867
	30	0.2959	0.0257	0.94	0.5766
	35	0.0692	0.0186	0.54	0.7411
	37	−0.1062	0.0382	0.57	0.2807

[a] Growth rate parameter, b_1, given in terms of microns per hour, $s(b_1)$ is the standard deviation of the parameter estimate, R^2_{adj} is the adjusted coefficient of the determination, and $\sqrt{\text{MSE}}$ is the square root of the mean squared error for the regression model.

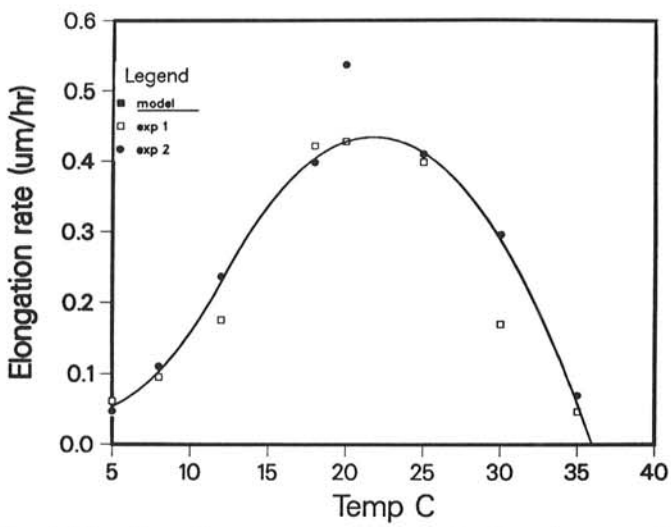

Fig. 5. The effect of temperature on germ tube elongation rate of *Mycosphaerella fragariae*. Model is the regression solution for equations 6 and 7. Parameter estimates and standard deviations are as follows, $b_0 = 0.059(0.270)$, $b_1 = -0.012(0.069)$, $b_2 = 0.002(0.004)$, $b_3 = 0.002(0.031)$, $b_4 = -0.004(0.004)$, $R^2_{adj} = 0.91$.

DISCUSSION

The logistic model worked well in describing the time course of conidiospore germination. The model fit the experimental data well at all temperatures except 35 C and above, where germination was low and no logistic response could be discerned against the background variation. The second stage of regression relating the rate parameters to temperature was best accomplished with a segmented quadratic model (Eqs. 2 and 3). This model was chosen over other polynomials and Schrodter's sine function on the basis of a higher coefficient of determination and the absence of patterns in the residuals that were present with other models. Some of the segmented model parameters did have large standard errors and collinearity diagnostics indicated a degree of collinearity among some independent variables. This was deemed acceptable because, although the interpretation of the parameters is not reliable in this situation, the predictive value of such a model is still good (9). Because this model is to serve an empirical function, strict interpretation of the regression coefficients is not necessary.

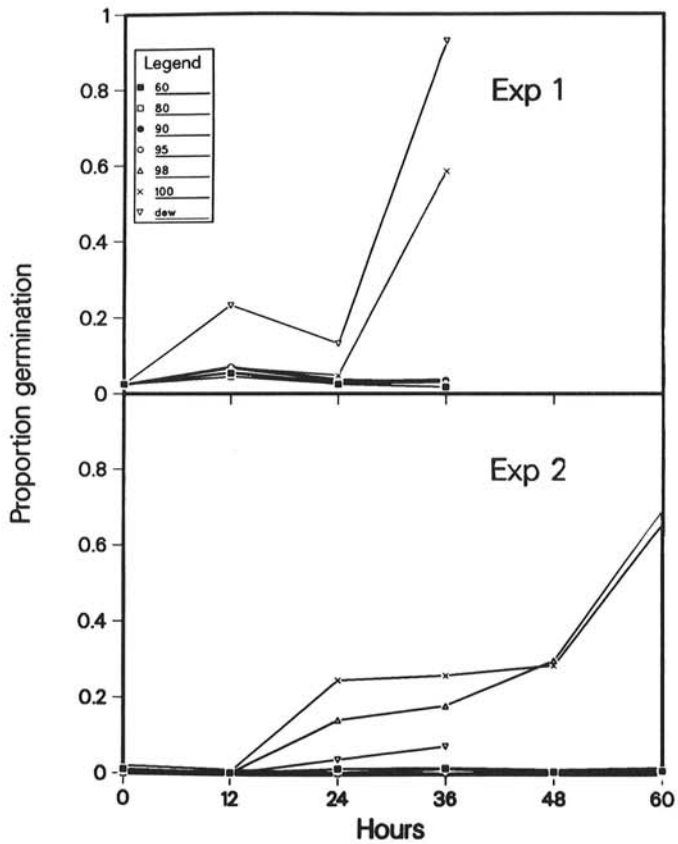

Fig. 6. The influence of different moisture regimes on conidiospore germination of *Mycosphaerella fragariae* at 18 C. Curves represent the experimental germination data. Each point represents the mean of three replications.

TABLE 3. Parameter estimates and associated statistics for logistic model (equation 8) relating conidiospore germination of *Mycosphaerella fragariae* to time in hours under different moisture conditions at 18 C

Exp	Moisture[a]	Parameter estimates[b] b_0	b_1	R^2_{adj}	$\sqrt{MSE}$
1	60	−3.301 (0.250)	−0.017 (0.011)	0.11	0.517
	80	−3.488 (0.180)	0.000 (0.008)	−0.10	0.373
	90	−3.426 (0.231)	0.003 (0.010)	−0.09	0.478
	95	−3.274 (0.226)	0.002 (0.010)	−0.10	0.469
	98	−3.326 (0.214)	0.004 (0.010)	−0.08	0.444
	100	−4.083 (0.443)	0.100 (0.020)	0.69	0.918
	dew	−3.801 (0.668)	0.150 (0.030)	0.69	1.382
2	60	−6.907 (0.000)	0.000 (0.000)	1.00	...
	80	−6.758 (0.189)	−0.001 (0.005)	−0.06	0.453
	90	−6.311 (0.382)	−0.005 (0.011)	−0.05	0.915
	95	−6.907 (0.000)	0.000 (0.000)	1.00	...
	98	−6.950 (0.473)	0.136 (0.130)	0.86	1.133
	100	−6.375 (0.566)	0.127 (0.016)	0.79	1.354
	dew	−7.304 (0.415)	0.134 (0.019)	0.80	0.890

[a] Moisture given as percent relative humidity or as dew-like layer.
[b] The intercept is b_0 and the slope is b_1. Slopes near zero indicate that no germination occurred. Standard deviations of parameters are in parentheses, R^2_{adj} is the adjusted coefficient of determination, and $\sqrt{MSE}$ is the square root of the mean square error for the regression model.

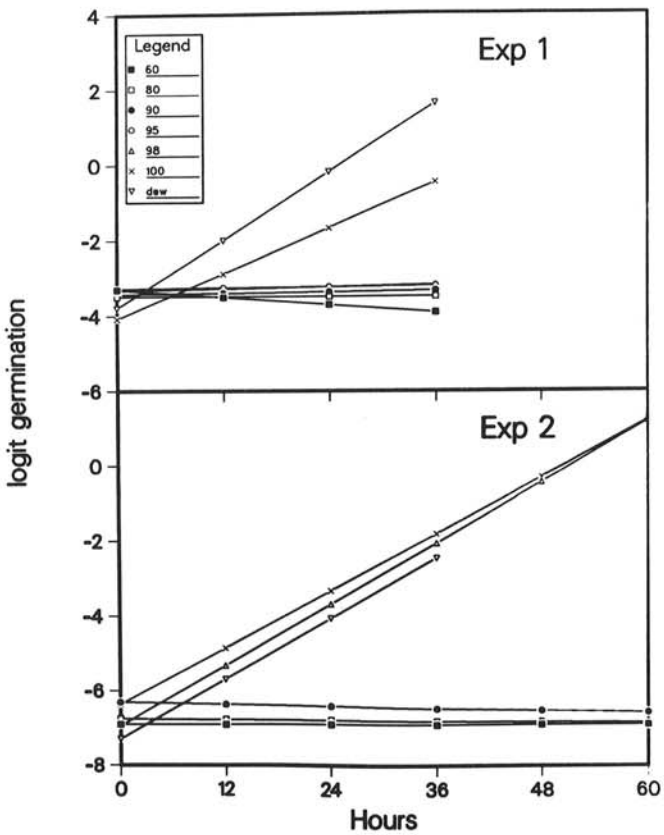

Fig. 7. The influence of different moisture regimes on conidiospore germination of *Mycosphaerella fragariae* at 18 C. Curves represent the logit regression against time for each treatment.

The maximum rate of germination, determined through the first derivative of equation 3, was seen at a temperature of 22.4 C. This optimum differs somewhat from the results presented by Fall (5), who reported and optimum between 15 and 20 C.

The maximum germination fraction (Fig. 3, Eqs. 4 and 5) remained constant over a temperature range of 5–30 C and dropped sharply above 30 C. A similar response was reported for *G. juniperi-virginianae* (10) in which the maximum germination fraction drops at high temperatures and also at low temperatures. The low temperature response might also result with *M. fragariae* if colder temperatures were tested.

The overall performance of the two-stage germination model (Fig. 4) was good when model predictions were compared with the original data. The nonlinear logistic model used in this paper is similar to other germination models in literature. It is similar in structure to the probit model used by Waggoner and Parlange (14). However, test for normality, including the Shapiro-Wilk statistic and normal probability plots, indicated that germination times for conidiospores of *M. fragariae* were not normally distributed (*unpublished*). Hence, a probit model would not be appropriate. The two-stage model also incorporates an upper asymptote which varies as a function of temperature and is similar to the germination model presented by Payandeh and Wallace (10) or the model of Imhoff et al (7).

The nonlinear logistic germination model, coupled with segmented polynomial models may have general utility in describing the time course of spore germination as influenced by temperature. Grove et al (6) successfully used a logistic model to describe strawberry fruit infection by *Phytophthora cactorum* as a function of time and temperature. Hence, the model presented in this paper may have applicability to other phases of pathogen development that show a sigmoidal relationship with time.

The maximum elongation rate, determined through the first derivative of equation 7, was seen at 22.7 C. This optimum is very close to the optimum seen for conidial germination. Fall (5), in a visual quantification of mycelial and conidial density at 5 days, saw an optimum growth temperature of 25 C. Nemec (8), in an assessment of colony area after 23 days on PDA, found an optimum growth near 18 C. The reasons for the different reported optimum growth temperatures cannot be fully determined, but the procedures used in obtaining the estimates did differ considerably, and differences among isolates cannot be ruled out.

From the results of this study, it appears that conidiospore germination of *M. fragariae* requires free moisture or relative humidities near saturation. This agrees with Fall (5), who reported that germination did not occur below 98% relative humidity. The results in Figure 7 show a trend toward more rapid germination with free moisture compared with high humidity, but no significant differences in intercepts or slopes were seen when tested with an indicator variable regression model. That germination did occur on glass surfaces, indicates that no stimulus other than adequate moisture is necessary for germination. The rates of germination on glass were considerably lower than on water agar and this may be due to less favorable osmotic or nutritional factors.

The information presented in this paper forms the initial part of an infection model. Events of the infection cycle from penetration to lesion formation have yet to be modeled. When this phase of the research is concluded, it will be possible to predict infection periods for *M. fragariae* on strawberry.

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