Influence of Temperature, Leaf Wetness, and High Relative Humidity Duration on Sporulation of *Cercospora carotae* on Carrot Leaves

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ABSTRACT

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The influence of temperature (16–32 C) and duration of moist period (6–96 h) on sporulation of *Cercospora carotae* was quantified on carrot plants under three types of moisture conditions (leaf wetness, 96% relative humidity [RH], and 96% RH with an initial 12 h of leaf wetness). Sporulation was quantified as the number of spores per lesion and then transformed to proportion of maximum number of spores (PMS). The highest PMS (1.78×10^3 spores/lesion) was obtained at 28 C after 96 h of leaf wetness. The effect of leaf wetness and 96% RH duration on sporulation was similar for most of the temperatures, except that no sporulation was observed at any time at 16 and 32 C for 96% RH. Under each moisture condition, PMS increased with increasing temperature up to the optimum (28 C) and then declined. The presence of an initial 12 h of leaf wetness enhanced sporulation and accelerated the beginning of sporulation as compared to continuous 96% RH. The PMS was modeled as a nonlinear logistic function of time for the leaf wetness ($R^2 = 0.98$) and 96% RH moisture conditions ($R^2 = 0.97$). A polynomial model was used to describe sporulation as a function of temperature and duration of 96% RH with initial 12 h of leaf wetness ($R^2 = 0.95$).

Additional keywords: quantitative epidemiology.

Production of carrots is an important industry in Canada, with an annual production of 6,529 ha representing a value of 37 million $US in 1991. Cercospora blight of carrot, caused by *Cercospora carotae* (Pass.) Solheim is a common disease of carrots. Under warm and humid conditions, blighted leaves become covered by small, grayish tan lesions. When leaves are blighted, the carrots are more difficult to harvest with a mechanical harvester, and harvested carrot roots are generally smaller (5). The incidence of *C. carotae* in the organic soil region of Quebec was reported to be 99 and 92% in 1988 and 1989, respectively (3). In Quebec, Cercospora blight is the only carrot disease requiring field applications of fungicides. Recently, efforts have been made to reduce the number of fungicide applications required to manage the disease (4,6,13,14).

Studies on the influence of weather components on infection of carrot leaves by *C. carotae* were reported (8,9). These studies can be used to construct a forecasting system to manage Cercospora blight more efficiently. However, additional information on the effect of weather on sporulation is needed to complete the development of a weather-based forecasting system. The objective of this study was to establish the temperature and time requirements for sporulation under high relative humidity and leaf wetness conditions. This experiment constitutes one of the first studies on sporulation of *C. carotae* on carrot leaves and it presents three models that describe the influence of temperature and time on sporulation under three moisture conditions: leaf wetness, 96% RH, and 96% RH preceded by 12 h of leaf wetness.

MATERIALS AND METHODS

Inoculum production. All inoculum used for this study was obtained from a single spore isolate of *C. carotae* isolated from

naturally infected carrot leaves collected in 1987 at the Agriculture Canada Experimental Farm in Sainte-Clotilde, Quebec. The fungus was cultured on carrot leaf infusion agar (CLA) as previously described (7). Conidial suspensions were prepared from 12-day-old cultures incubated at 26 C and 18 h per day of fluorescent light (100 $\mu E \cdot m^{-2} \cdot s^{-1}$). Conidia were suspended in a solution of 0.01% Tween 80 (v/v) in distilled water and the concentration was adjusted to 1×10^4 conidia per milliliter using a hemacytometer.

Plant production. Carrot plants (cv. Dagger) were grown in a greenhouse maintained at 22 ± 5 C with 12 h of light per day. The plants were produced in 13-cm-diameter pots with a 5:1:1 (v/v) mixture of organic soil (27–30% organic matter), perlite, and peat moss. Fertilizers (200 ppm of 15-15-17 N-P-K) were applied twice a week. The plants were sprayed with insecticides (Bendiocarb 80W 0.75 kg/1,000 L, and diatomaceous earth) every week to prevent thrip infestation. At the six-leaf stage (5 wk after sowing) the second and third leaves were tagged.

Inoculation procedure. Both surfaces of the tagged leaves were inoculated with a conidial suspension of *C. carotae* applied with an artist airbrush (model 350, BadgerAir Brush Co., Franklin Park, Il-350) operated at 100 kPa. After inoculation the plants were placed in another greenhouse at 25 ± 5 C for 72 h to promote infection (8). Free water on leaf surfaces was provided by a misting of 5 sec every 8 min. During the incubation period the plants were kept in a greenhouse at 22 ± 5 C and RH ≤ 65 ± 5%.

The percent spore germination of the inoculum was estimated for each inoculation. Nine water agar plates were sprayed, three at the beginning, three in the middle, and three at the end of the inoculation procedure. After 6 h, the percent spore germination was estimated for each plate by counting the number of conidia with germ tubes at least one-half the length of the spore.

Treatments. Thirteen days after inoculation (when the plants exhibited small chlorotic lesions), the number of lesions on each inoculated leaf was counted on all plants. The plants were then transferred to an RH-controlled chamber (model PGW36 M10, Conviron, Winnipeg, with RH controlled by bypass dehumidification) maintained at a specific temperature and 96 ± 2% RH. Temperature and relative humidity in the chamber were monitored using a data logger (CR-10, Campbell Scientific Canada Corp., Alberta). The plants were exposed to a 12-h photoperiod supplied by fluorescent and incandescent fixtures producing a light intensity of 250 $\mu E \cdot m^{-2} \cdot s^{-1}$. The experiment included three types of moisture conditions: leaf wetness (LW), 96% RH (96RH), and 96% RH with an initial 12 h of leaf wetness (96RHW). The moisture durations were 6, 12, 24, 48, 72, and 96 h. The plants exposed to the leaf wetness conditions were misted with distilled water and enclosed in plastic bags for the different durations. The plants exposed to an initial leaf wetness period were also misted with distilled water and enclosed in plastic bags that were removed after 12 h. At the end of the exposure time, three plants per moisture type were removed for observations (number of spores per lesion). This procedure was repeated five times for temperatures in the RH-controlled chamber of 16, 20, 24, 28, and 32 C tested in a random order. The entire experiment consisted in 30 temperature and moist period duration combinations for each moisture conditions (five temperatures × six durations). The whole experiment was conducted twice. The three moisture conditions were selected based on preliminary tests where the effect of temperature (16–32 C) at various %RH levels (65–100%) on sporulation was studied. For all temperatures tested no sporulation occurred at %RH ≤ 92%, while abundant spores were produced under leaf wetness and 96% RH conditions.

Estimation of sporulation. The sporulation was quantified as the number of spores produced per lesion per plant. Two inoculated leaves per plant were harvested, rolled in a wax paper, and then inserted into a test tube containing 10 ml of a solution of 1% formaldehyde and 0.01% Tween 80. The test tubes were agitated for 2 min and then the number of spores in the suspension was evaluated with an hemacytometer (four counts). The total number of spores per lesion per plant (average of the four counts) was calculated as follows: (number of spores/ml × 10 ml of suspension)/total number of lesions per plant.

Data analysis. The data were transformed to proportion of maximum sporulation (*PMS*) by dividing the number of spores/lesion/plant obtained for each plant by the maximum obtained from any of the moisture conditions.

Tests for equality of variance (*F* test) were carried out to determine whether the data from each experimental trial could be pooled. Because the temperatures were tested over time and using different inoculum suspensions (temperature and inoculum effects were confounded), an *F* test was used to determine whether the percent spore germination of inoculum significantly varied among inoculations (18). Two types of models were used to describe the effects of temperature (T) and moist period duration (D) on PMS; a nonlinear logistic model (PROC NLIN) for the LW and for the 96RH moisture types, and a polynomial model (PROC GLM, and PROC REG) for the 96RHW using the Statistical Analysis System (SAS) program (16). The nonlinear logistic models were evaluated based on coefficient of determination (R^2), size of asymptotic standard error associated with the estimated parameters and by visual inspection and analysis of residuals plots (11,12). The polynomial model was evaluated based on the coefficient of determination (R^2 and R^2 adjusted for the degree of freedom), by the significance of the estimated regression parameters, and by analysis of residuals distribution (11,18).

Model development for the LW and 96RH conditions. The proportion of maximum number of spore increased sigmoidally with increasing leaf wetness or 96% RH duration. The nonlinear logistic model used for the LW and 96RH treatments was of the form:

$$PMS = \frac{PMS_m}{1 + [(PMS_m - PMS_0)/\ PMS_0]\ \mathrm{EXP}(-rD)} \quad (1)$$

where *PMS* is the proportion of maximum sporulation at time *D*, PMS_m is the maximum *PMS* at any time for a given temperature (asymptote), PMS_0 is the initial level of sporulation (Y-intercept), *r* is the rate of sporulation, and *D* is the moist period duration (h). The logistic model was fitted separately to the data of each experimental trial and the pooled data using the nonlinear procedures with Marquardt iteration methods (16). Because it is a nonlinear regression and because some parameters must be initially set, the logistic model had to be fitted in four steps that are briefly described below for both LW and 96RH (8,15). These steps are used to determine the value of some parameters in order to run the NLIN procedure on data for all temperatures together.

First, a separate equation for predicting the maximum sporulation (PMS_m) as a function of temperature was derived using polynomials or generalized form of the Analytis' beta function (2) (Eq. 2).

$$PMS_m = pt^m(1 - T)^n \quad (2)$$

where, *p,n,m* are parameters and $t = (T - T_{min})/(T_{max} = T_{min})$. The maximum temperature (T_{max}) and minimum temperature (T_{min}) were not known precisely, and values of 12 and 36 C were assigned for T_{min} and T_{max}, respectively. Other values did not result in good fit of the model.

In the second step, the nonlinear logistic function (Eq. 1) was fitted to the data for each temperature separately with the maximum sporulation (PMS_m) parameter replaced by the equation developed in the first step. The value of PMS_0 was arbitrarily assigned to 0.0001 since the intercept values for all temperatures were not significantly different from 0.0 when estimated by the regression procedures. The value of the rate parameter was estimated for each temperature from this regression procedures.

The third step consisted of deriving an equation for predicting the rate parameter obtained from the second step, as a function of temperature. Polynomials models and beta function were tested. Regressions were performed for the pooled data only (*r* values obtained for each experiment were pooled). The fourth and final step consisted of incorporating the equations predicting the PMS_m

and r parameters into the logistic model and fitting the resulting model to the data for all temperatures together.

Model development for the 96RHW condition. The effect of 96%RHW duration on sporulation did not follow a pattern that could be adequately explained by the logistic function. For this reason, two types of multiple regression models were evaluated. The first was an extension of the Schodter (17) sine-model ($\arcsin(\sqrt{PMS}) = f(T,D)$) and the second model was a general form of the polynomial function ($PMS = f(T,D)$).

These two models were fitted to the data for each experiment and the pooled data and all possible combinations of temperature (T) and moist period duration (D) terms (T, D, ..., T^4D^5) were tested for the significance of the estimated parameters (12). The appropriate tests and techniques, as suggested by Freud and Littell (12), were used to verified the existence of multicolinearity and autocorrelation.

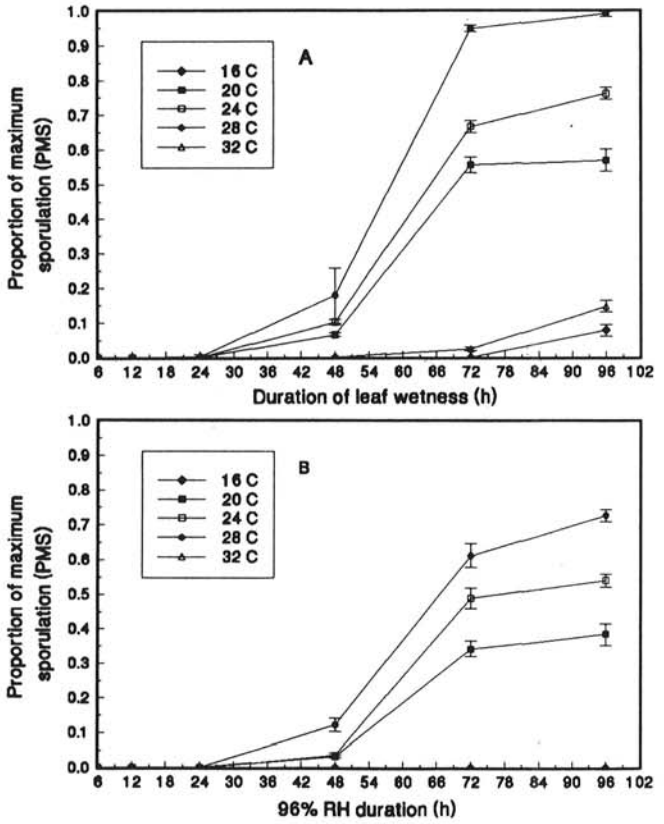

Fig. 1. Observed effect of duration of moist period and temperature on the number of spores per lesion of *Cercospora carotae*. Infected carrot plants were subjected to constant temperatures of 16, 20, 24, 28, and 32 C. In **A,** the plants were misted and enclosed in plastic bags. In **B,** the plants were placed in a RH-controlled chamber adjusted at 96% RH. Data are presented as proportion of maximum number of spore/lesion (1,928 and 1,632, for the first and second trial, respectively) observed at 28 C and 96 h of leaf wetness. Each point is the mean of six plants (three plants/treatment/experiment). Bars represent standars error of the mean.

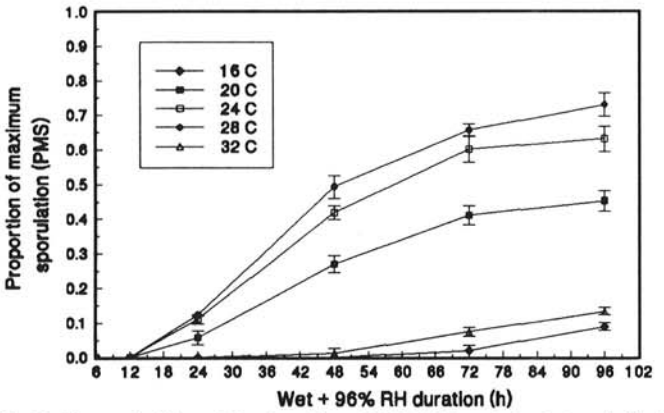

Fig. 2. Observed effect of the duration of 96% RH periods with an initial 12 h of leaf wetness and temperature on the number of spores per lesion of *Cercspora carotae*. Data are presented as proportion of maximum number of spores/lesion (1,928 and 1,632, for the first and second trial, respectively) observed at 28 C and 96 h of leaf wetness. Each point is the mean of six plants (three plants/treatment/experiment). Bars represent standars error of the mean.

RESULTS

In general, sporulation occurred after 48 h. Maximum number of spores per lesion was obtained after 96 h under leaf wetness and 28 C (1.928 and 1.632×10^3 spores per lesion for the first and second experiment, respectively). For all temperatures, sporulation increased with increasing leaf wetness or moist period duration. Number of spores per lesion was higher under leaf wetness than 96% RH with or without initial wetness period. For all moisture types, sporulation increased with increasing temperature from 16 to 28 C then diminished through 32 C. Proportion of maximum sporulation increased sigmoidally with increasing duration of leaf wetness and 96% RH period at 20, 24, and 28 C. The sporulation increased slowly from 6 to 48 h, and increased very rapidly between 48 and 72, then slowly again between 72 and 96 h (Fig. 1). Under leaf wetness, the number of spores per lesion obtained at 16 and 32 C was very low for the 6–72 h durations and increased slowly from 72 to 96 h, while no sporulation was obtained at 96% RH at these two temperatures. The effect of 96RHW duration on proportion of maximum sporulation was different, where the PMS increased gradually over time (Fig. 2). The sporulation started after only 12 h and increased until 72 h.

Estimation of logistic model parameters for LW and 96RH moisture conditions. No difference between the inoculum sus-

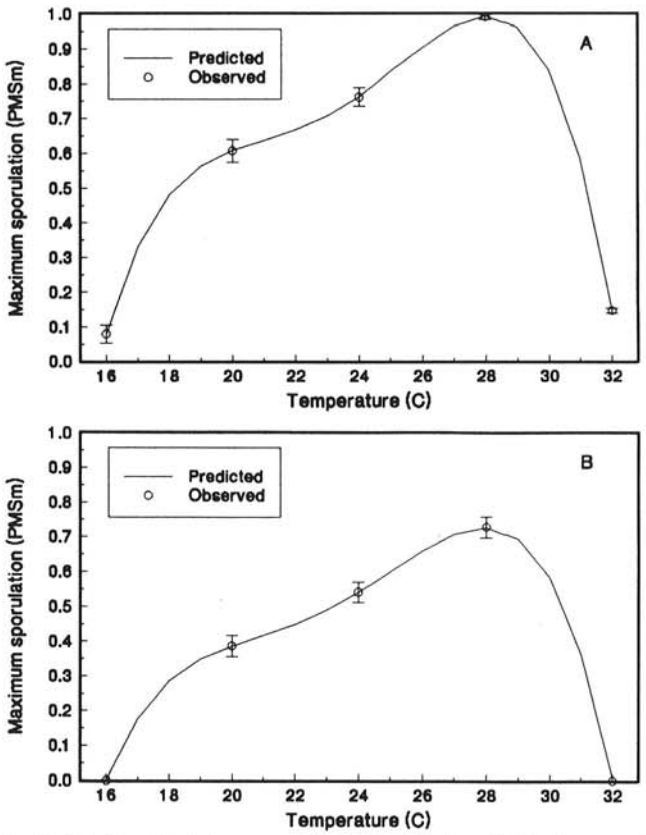

Fig. 3. Relationship between maximum sporulation (PMS_m) parameter of the logistic function and temperature. In **A,** the plants were exposed to leaf wetness conditions. In **B,** the plants were exposed to 96% RH conditions. Each point is the mean of six values (three plants/treatment/experiment). Bars represent standard error of the mean.

TABLE 1. Estimated regression parameters and associated statistics for the regression of maximum sporulation (PMS_m)[a] of *Cercospora carotae* as a function of temperature for the leaf wetness and 96% RH conditions

Model	Error df	F P value	R_a^2 [b]	Estimate/P value				
				b_0	b_1	b_2	b_3	b_4
Leaf wetness								
Exp. 1	10	0.0001	0.99	−70.18 0.0001	12.48 0.0001	−0.823 0.0001	0.024 0.0001	−0.0002 0.0001
Exp. 2	10	0.0001	0.99	−70.82 0.0001	12.56 0.0001	−0.826 0.0001	0.024 0.0001	−0.0002 0.0001
Pooled	25	0.0001	0.99	−70.51 0.0001	12.53 0.0001	−0.825 0.0001	0.024 0.0001	−0.0002 0.0001
96% relative humidity								
Exp. 1	10	0.0001	0.99	−58.89 0.0001	10.48 0.0001	−0.692 0.0001	0.020 0.0001	−0.0002 0.0001
Exp. 2	10	0.0001	0.99	−43.81 0.0001	7.894 0.0001	−0.529 0.0001	0.016 0.0001	−0.001 0.0001
Pooled	25	0.0001	0.99	−51.35 0.0001	9.190 0.0001	−0.611 0.0001	0.018 0.0001	−0.0002 0.0001

[a] Asymptote parameter (PMS_m) of the logistic function; $PMS = PMS_m/(1 + [(PMS_m - PMS_0]\ \mathrm{EXP}(-rD))$ see text, equation 1.
[b] Coefficient of determination adjusted for the number of independent variables.

pensions used in time (different temperature tested) ($P > 0.05$) was apparent in the F test, so parameters of the logistic function obtained for each temperature levels (PMS_m and r) were combined for the analysis. Maximum sporulation (PMS_m) was observed at 28 C for both LW and 96RH moisture types, but the temperature effect on PMS_m produced a curve skewed to the right that could be adequately described only by a fourth-degree polynomial model (Fig. 3). Other models were considered, including lower levels of polynomial and beta-function. These models resulted in unacceptable overestimation at 24 C and underestimation at 28 C of PMS_m. Considering the importance of the asymptote parameter (PMS_m) in the logistic model, the fourth-degree polynomial model was retained. This model yielded high coefficients of determination with all parameter estimates significant ($P < 0.0001$) (Table 1). The distribution of residuals was normal and no patterns could be detected. This model predicted a maximum PMS of 0.99 and 0.73 for the LW and 96RH moisture type, respectively (observed were 1.00 and 0.73).

The rate parameter (r) for both moisture types was high at 20, 24, and 28 C, and low at 16 and 32 C (Fig. 4). The effect of temperature on the rate parameter produced a bell-shaped curve with small variation between 20, 24, and 28 C (Fig. 4). Several models were tested including two- to four-degree polynomials, segmented polynomials, and beta-function. The second-order polynomial provided a good fit, explaining 0.87 and 0.92% of the variation in the rate parameter (r) with temperature for the LW and 96RH moisture type, respectively. All parameter estimates were significant ($P < 0.0001$) (Table 2), and no patterns were evident in the residuals. However, the rate of sporulation predicted by the model was slightly overestimated at 24 and underestimated at 28 C (Fig. 4). The rate parameter was predicted to reach a maximum of 0.25 and 0.26 at 24 C for the LW and 96RH moisture types, respectively.

Fitting the nonlinear logistic model to the pooled data resulted in high coefficients of determination, 0.98 and 0.97% for the LW and 96RH moisture conditions, respectively. Furthermore, no patterns were seen in three-dimensional plots of residuals against temperature and duration of moist period for both moisture conditions. For the LW moisture condition, the logistic equation describing the proportion of maximum sporulation at duration D (h) (Eq. 1) used the following parameters: $PMS_m = -70.5082 + 12.5259T - 0.8247T^2 + 0.0240T^3 - 0.0002595T^4$ (Table 1), $PMS_0 = 0.0001$, $r = -0.7231 + 0.0797T - 0.001632T^2$, where T is the temperature (C) (Fig. 5A).

For the 96RH moisture conditions, the parameters for the same logistic equation are $PMS_m = -51.3554 + 9.1902T - 0.6112T^2 + 0.0179T^3 - 0.0001966T^4$ (Table 1), $PMS_0 = 0.0001$, $r = -2.0092 + 0.1888T - 0.003929T^2$, and where T is the temperature (C) (Fig. 5B).

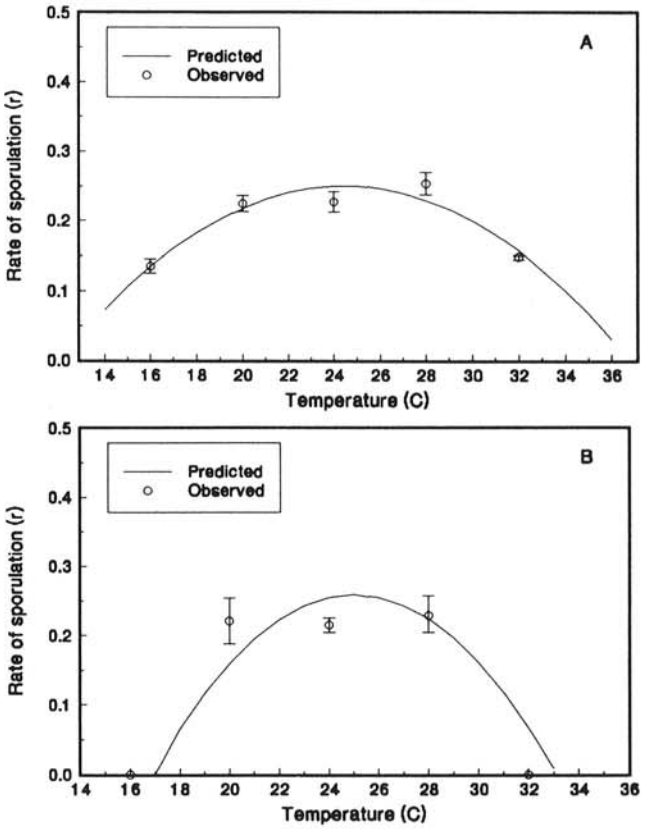

Fig. 4. Relationship between rate of sporulation (r) parameter of the logistic function and temperature. In **A**, the plants were exposed to leaf wetness conditions. In **B**, the plants were exposed to 96% RH conditions. Each point is the mean of the two experiments (one r value/experiment). Bars represent standars error of the mean.

Estimation of polynomial model parameters for 96RHW moisture conditions. The best polynomial model describing the relationship of T, and D with PMS was of the form: $PMS = -0.04391$

TABLE 2. Estimated regression parameters and associated statistics for the regression of rate of sporulation (r)[a] of *Cercospora carotae* as a function of temperature for the leaf wetness and 96% RH conditions

Model	Error df	F P value	R_a^2 [b]	Estimate/P value b_0	b_1	b^2
Leaf wetness (pooled)	5	0.0001	0.87	−0.7231 0.0001	0.0797 0.0001	−0.0016 0.0001
96% relative humidity (pooled)	5	0.0001	0.92	−2.009 0.0001	0.1888 0.0001	−0.0039 0.0001

[a] Rate parameter (r) of the logistic fuction; $PMS = PMS_m/(1 + [(PMS_m - PMS_0)/PMS_0]\ \mathrm{EXP}(-rD))$ see text, equation 1.
[b] Coefficient of determination adjusted for the number of independent variables.

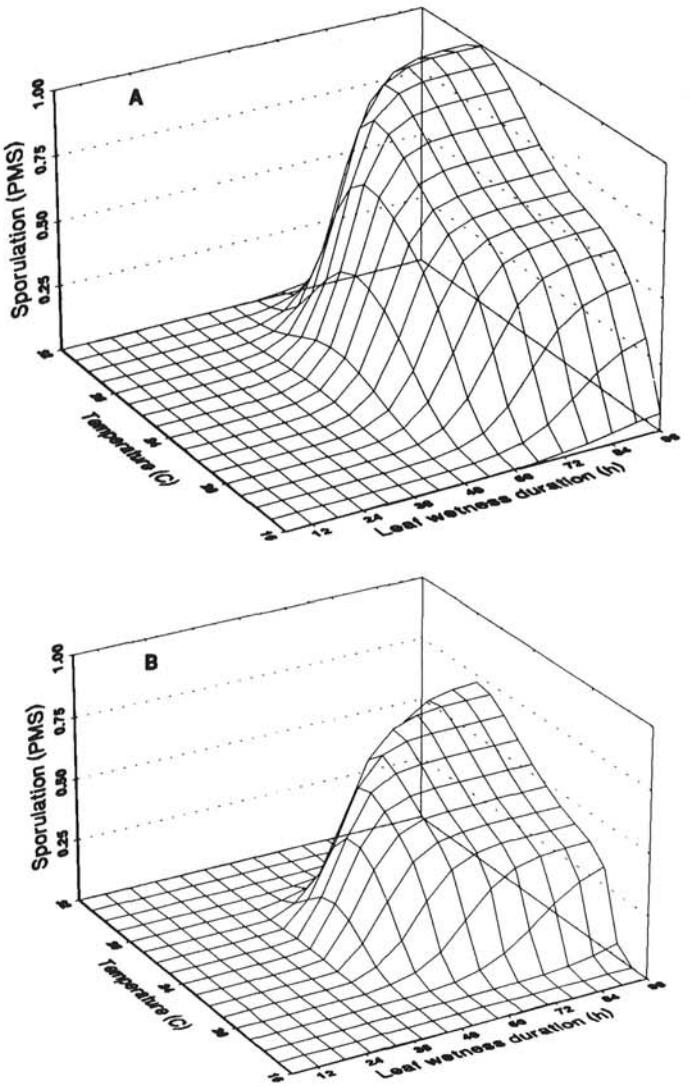

Fig. 5. Predicted values for proportion of maximum sporulation as a function of duration of moist period and temperature. In **A,** the response surface was generated for the plants exposed to leaf wetness conditions. In **B,** the response surface was generated for the plants exposed to 96% RH conditions (see text).

$+ 0.05380D - 0.3983 \times 10^{-4} D^2 - 0.001865T - 0.0002765T^2 + 0.08292 \times 10^{-4} T^3 - 0.008849TD + 0.000502DT^2 - 0.085 \times 10^{-4} TD^3$, where PMS is the proportion of maximum sporulation, T is temperature and D is the moist-period duration. The terms appearing in the equation were significant in the ANOVA (12). This model explained 96% of the variation in PMS (Table 3). Furthermore, no patterns were seen in a three-dimensional plot of residual against temperature and duration of moist period and multicolinearity problems were not detected based on variance inflation statistics. This model provided excellent prediction at temperatures of 20, 24, and 28 C, but it tended to overestimate sporulation at temperature of 16 and 32 C for all durations except at 96 h where the sporulation was slightly underestimated (Fig. 6).

TABLE 3. Estimated regression parameters and associated statistics for the polynomial regression of proportion of maximum sporulation of *Cercospora carotae* as a function of temperature and duration of 96% RH period preceded by 12 h of leaf wetness

Statistics	Exp. 1	Exp. 2	Pooled
Error df	66	66	141
F P value	0.0001	0.0001	0.0001
R^2	0.96	0.96	0.96
R_a^2 [a]	0.95	0.96	0.95
Estimate/P value			
b_0	−0.0191/0.0001	−0.0191/0.0001	−0.0439/0.0001
$b_1$1	0.0517/0.0001	0.0558/0.0001	0.0538/0.0001
b_2	−0.3633/0.0001 ($\times 10^{-4}$)	−0.4333/0.0001 ($\times 10^{-4}$)	−0.3983/0.0001 ($\times 10^{-4}$)
b_3	−0.0086/0.0001	−0.0049/0.0002	−0.0018/0.0001
b_4	−0.2592/0.0001 ($\times 10^{-}$)	−0.0005/0.0001	−0.0003/0.0001
b_5	−0.0533/0.0001	0.1124/0.0001 ($\times 10^{-4}$)	0.0829/0.0001 ($\times 10^{-4}$)
b_6	−0.0008/0.0068	−0.0091/0.0111	−0.0088/0.0002
b_7	0.0005/0.0001	0.0005/0.0001	0.0005/0.0001
b_8	−0.0836/0.0001 ($\times 10^{-4}$)	−0.0838/0.0001 ($\times 10^{-4}$)	−0.0850/0.0001 ($\times 10^{-4}$)

[a] Coefficient of determination adjusted for the number of independent variables.

DISCUSSION

The optimum conditions for sporulation of *C. carotae* on carrot leaves was 28 C with a minimum of 24 h of leaf wetness or high relative humidity. Spores were numerous only when the wet period exceeded 48 h at 20–28 C. Although sporulation of *C. carotae* has not been previously quantified on carrot leaves, observations have been reported on sporulation at different temperatures on agar media. The optimum temperature of 28 C observed for sporulation on carrot leaves was also found to be optimum for mycelial growth and sporulation in vitro (7). In general, our results agree with those of Thomas (19) who also observed maximum sporulation at 28 C on carrot petioles. However, the latter study also reported abundant sporulation at 13 C after only 24 h. Unfortunately, no detailed information on the conditions under which the experiment was conducted is available to compare. Nevertheless, our results stand in accordance with those from experiments on other species of *Cercospora* (1,10).

The effect of leaf wetness or 96%RH duration on conidial production by *C. carotae* in controlled conditions produced a sigmoid

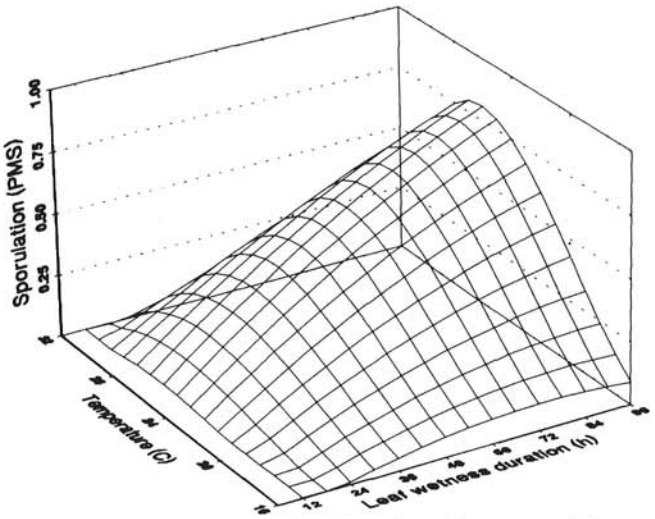

Fig. 6. Predicted values for proportion of maximum sporulation as a function of moist period and temperature. The response surface was generated for the plants exposed to 96% RH after 12 h of leaf wetness (see text).

response for temperature between 20 and 28 C. Although several models could be used to describe such response (15,20), the logistic model worked well in this case in describing the effect of temperature and moisture duration on sporulation of *C. carotae*. Maximum sporulation was observed at 28 C, so the effect of temperature on maximum sporulation produced a curve skewed to the right difficult to describ with a second-order polynomial. The beta-function was proposed to address this problem (2). However, with our data this model was not suitable and did not work well, probably because the minimum and maximum temperatures for sporulation were not known. The use of a fourth-degree polynomial was satisfactory in this work. Conidial production increased gradually over time for all temperatures tested when the plants were exposed to 96% relative humidity preceded by 12 h of leaf wetness. The polynomial model was appropriate, although nine terms were needed to explain the combined effect of temperature and time. Coefficients of determination adjusted for the degrees of freedom (R^2_a) were high 0.95, 0.96, 0.95 for experiments one, two, and pooled data, respectively, indicating the importance of various terms in the model. The values of R^2_a were similar to the values of R^2, indicating that all terms were necessary.

This study demonstrated that sporulation was favored by high relative humidity (>96%) or leaf wetness and warm temperature (20–28 C). Leaf wetness is more favorable than high relative humidity in supporting abundant conidial production. A period of leaf wetness is not necessary to trigger sporulation, but the presence of a short leaf wetness period prior to a prolonged period of high relative humidity accelerates the production of conidia.

The infection of *C. carotae* has been shown to occur at temperature ranging from 20 to 28 C (8). Maximum infection occurred after 24 h at 28 C. Consequently, the range of temperatures for infection is similar to that for sporulation. Thus we can speculate that when conditions are favorable for infection (>24 h of leaf wetness at 20–28 C) sporulation does not limit the epidemic development. In a forecasting system, periods of leaf wetness or relative humidity above 96% for more than 24 h at temperature greater than 16 C and less than 32 C could be considered favorable for sporulation of *C. carotae*.

There are limitations inherent to this type of study including instrumentations, sampling methods, integration of temperature-RH or temperature-leaf-wetness interactions, and effects of preconditioning of the lesions. These results may not reflect the exact amount of conidia available in the field for infection because the harvesting technique was probably too vigorous. Under field conditions only mature spores become detached. Nevertheless, from the results of this study the environmental requirements for sporulation of *C. carotae* have been established as well as the needs for more detailed investigations. These results cannot be used to predict the exact amount of conidia available for infection but rather to estimate the conductiveness of the environment for sporulation. The effects of temperature and time on sporulation were examined during a single sporulation period in this work. In the field, however, sporulation may occur over consecutive wet or humid periods.

Further research is needed to examine the effect of factors such as lesion age, fluctuating temperature, and interrupted wet period on conidial production of *C. carotae* and to determine if the behavior of the fungus in the controlled environment depicts the fungal behavior in the field.

LITERATURE CITED

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