Effects of Solar Radiation and Temperature on Fusarium Wilt in Carnation

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ABSTRACT

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Effects of solar radiation intensity and of temperature on wilt induced by *Fusarium oxysporum* f. sp. *dianthi* in carnation were examined in seven experiments conducted under conditions in which these parameters were varied. In each experiment, plants were inoculated with *F. o. dianthi* at four different spore concentrations and grown under screen covers, which produced four different levels of shade with respect to incoming radiation intensity. Disease intensity varied substantially among the seven experiments due to solar radiation intensity or temperature, among the four levels of shade within each experiment, and among inoculum concentrations within each shade level. The most severe epidemics developed at low radiation intensities (200–300 μE m^{-2} s^{-1}) and at temperatures close to 25–26 C. At solar radiation intensities above 1,000 μE m^{-2} s^{-1} and temperatures below 18 C plants remained symptomless. Nevertheless, *F. o. dianthi* was isolated from most of the symptomless plants. In all cases where symptoms were apparent, disease intensity was affected by the inoculum concentration, being more severe as the concentration increased.

Fusarium oxysporum Schlechtend.:Fr. f. sp. *dianthi* (Prill. and Delacr.) W.C. Snyder & H.N. Hans. (*F. o. dianthi*) is a serious pathogen of greenhouse grown carnation (*Dianthus caryophyllus* L.) in Israel. Wilt symptoms induced by *Fusarium* spp. are substantially affected by soil temperatures. The temperatures causing specific effects vary among different pathosystems. Gardiner et al (12) reported that rooted cuttings of *Chrysanthemum* × *morifolium* Ramat. inoculated with *F. o.* f. sp. *chrysanthemi* and incubated at 35 C during the day but at different night temperatures did not develop symptoms until night temperatures were at least 24 C. In crucifers, wilt induced by *F. o.* f. sp. *conglutianas* increased with increasing temperatures (7). Fusarium wilt in chickpea was more severe at 25 and 30 C than at 10, 15, or 20 C (5). In carnation, wilt symptoms and stem colonization were similarly affected by temperature: no symptoms and very little colonization were observed at 14 C; nearly all stems were colonized at 18–20 C but remained symptomless; and at temperatures >23 C, wilt symptoms were severe (11,14).

Photoperiod or solar radiation intensity influence the expression of wilt induced by *Verticillium* spp. in various crops. For example, symptom development was more rapid and much more severe under short-day than under long-day growing conditions in tomato (15) and potato (9,21). Similarly, wilt induced by *V. dahliae* in watermelon (2) was more pronounced at low than at high solar radiation intensities.

In preliminary experiments, we observed that wilt symptoms in inoculated carnation were detectable during the summer (June–October) only in plants grown under screen covers that partially shaded solar radiation. In the winter (November–March), when both solar radiation intensity and temperatures were low, inoculated plants remained symptomless; nevertheless, the fungus was isolated from most symptomless plants. Accordingly, we hypothesized that low solar radiation intensity and high temperature interactively affect colonization and symptom expression of *F. o. dianthi* in carnation. The objective of this study was to ascertain quantitatively the integrated effects of the abiotic factors solar radiation and temperature on wilt induced by *F. o. dianthi* in carnation.

MATERIALS AND METHODS

Experimental design. Effects of solar radiation intensity and temperature on wilt induced by *F. o. dianthi* in carnation were examined in seven experiments conducted under diverse conditions. Carnation plants of the susceptible cv. Hermon were planted in the first week of each of the following months in 1992: July (experiment 1), August (experiment 2), September (experiment 3), October (experiment 4), November (experiment 5), December (experiment 6), and March 1993 (experiment 7). Plants were grown in 3-L pots filled with steamed tuff (crushed volcanic stones). In each experiment, plants were inoculated with *F. o. dianthi* at four different spore concentrations and grown under screen covers producing four different levels of shade. There were five pots (replicates) per treatment and each pot contained four plants.

Inoculation. Four isolates of *F. o. dianthi* classified as race 2 (3,16), were plated on potato-dextrose agar supplemented with 250 mg of dihydrostreptomycin (PDAS). Equal quantities of spores from each isolate were suspended in water to a final concentration of 10^3, 10^4, 10^5, or 10^6 spores per milliliter. For each concentration of inoculum, 20 rooted cuttings were immersed in 300 ml of the suspension for 20 s before planting. After planting, equal quantities (~20 ml) of the remaining spore suspension were poured onto the tuff surface. To ensure successful inoculation, plants were kept unwatered on the first day and on the following 5 days were watered to avoid run-through. Rooted cuttings immersed in water and treated as described above served as uninoculated controls.

Solar radiation and temperature. Solar radiation intensity and temperature varied naturally among the seven experiments. In Israel (30° E, 31° N), solar radiation intensity (under clear skies) is maximal in June (about 2300 μE m^{-2} s^{-1}) and minimal in December (about 900 μE m^{-2} s^{-1}). To obtain further variation within experiments, plants were grown under screen covers, which shaded a portion of the incoming sunlight. Four different levels of shade were imposed: 0 (plants grown outdoors), 55, 72, and 85%. Solar radiation intensity in the four environments was mea-

sured by means of a Lambda Quantum-meter Model LI-185 (LI-CORE Inc., U.S.A.). The values of solar radiation intensity reported were measured in bi-weekly intervals near noon (maximum daily value). Temperature was measured with a thermometer inserted to a depth of 5 cm in one pot for each of the light environments. Daily maximum and minimum temperatures were used to calculate a daily mean, which was used for data analysis.

Analysis of the solar radiation and temperature data revealed that, within a shade treatment, the daily variation among experiments was substantially greater than the variation within an experiment. For example, solar radiation intensity and temperature (mean ± SE) in experiment 1 were 2,078 ± 80 μE m^{-2} s^{-1} and 31.5 ± 1.2 C, whereas in experiment 5 they were 907 ± 130 μE m^{-2} s^{-1} and 16.5 ± 2.4 C. Consequently, mean values of solar radiation intensity and temperature were averaged over days to compare results among experiments.

Disease assessment. Disease was assessed visually at weekly intervals, starting 24–30 days after inoculation and continuing for an additional 30–36 days until experiments were terminated. As shown in a previous study, records of disease incidence provide an adequate measure of disease severity in the *F. o. dianthi*–carnation pathosystem (4). We therefore recorded the proportion of plants showing wilt symptoms (disease incidence) throughout the epidemic. In addition, disease severity was assessed on the last assessment date in each experiment with the aid of a 0–4 scale developed by Garibaldi (13). Plants without visible disease symptoms on termination of the experiment were cut, and a 5–10 mm segment of the aboveground stem was plated on PDAS and examined for the presence of *F. oxysporum*-like mycelia.

Disease progress over time was used to calculate two variables reflecting disease intensity: disease development rate and the relative area under the disease progress curve (RAUDPC) (20). The rate of disease development was calculated from the linearized form of the monomolecular equation, after regressing log (100/(100-x)) and days, when x is disease incidence (22). The RAUDPC (in percentage units) was calculated as follows:

$$\text{RAUDPC} = [\sum_{i=1}^{n} ((X_{i+1} + X_i) / 2 (t_{i+1} - t_i)] / (t_n - t_i) \quad (1)$$

where X_i = disease incidence (%) and t_i = days after inoculation and n assessment dates (i = 1.....n). The most severe epidemics was assigned a maximum RAUDPC of 100%. Values are calculated on the basis of disease assessments during the entire epidemic and therefore represent the integrated response of the carnation plants to the disease under certain conditions.

Data analysis. Regression models were developed to describe the influence of inoculum concentration (I), solar radiation intensity (R) and temperature (T) on disease variables (D). The general model was:

$$D = f(I, R, T) \quad (2)$$

Statistics were computed for the following disease variables: final disease incidence, final disease severity, rate of disease development, and RAUDPC. Linear and quadratic terms of R and T were evaluated. The models were evaluated on the basis of the significance of the estimated parameters, normality of the residuals, and the coefficients of determination. Of all models (>30) and parameters tested, the following response functions were found to fit best to the data:

$$D = \beta_0 + \beta_1 I + \beta_2 R^2 \quad (3)$$

$$D = \beta_0 + \beta_1 I + \beta_2 T + \beta_3 T^2 \quad (4)$$

$$D = \beta_0 + \beta_1 I + \beta_2 R^2 + \beta_3 T + \beta_4 T^2 \quad (5)$$

where D is the RAUDPC in percent, I is the logarithm (base 10) of inoculum concentration, T is temperature in degrees centigrade, R is solar radiation intensity in μE m^{-2} s^{-1}, and βs are regression coefficients. Epidemics with RAUDPC values of 0 or 100% were excluded from the analysis to avoid possible bias imposed by these extreme values on the estimated regression parameters.

RESULTS

Disease progress. Disease intensity varied among the seven experiments, among the four levels of shade within each

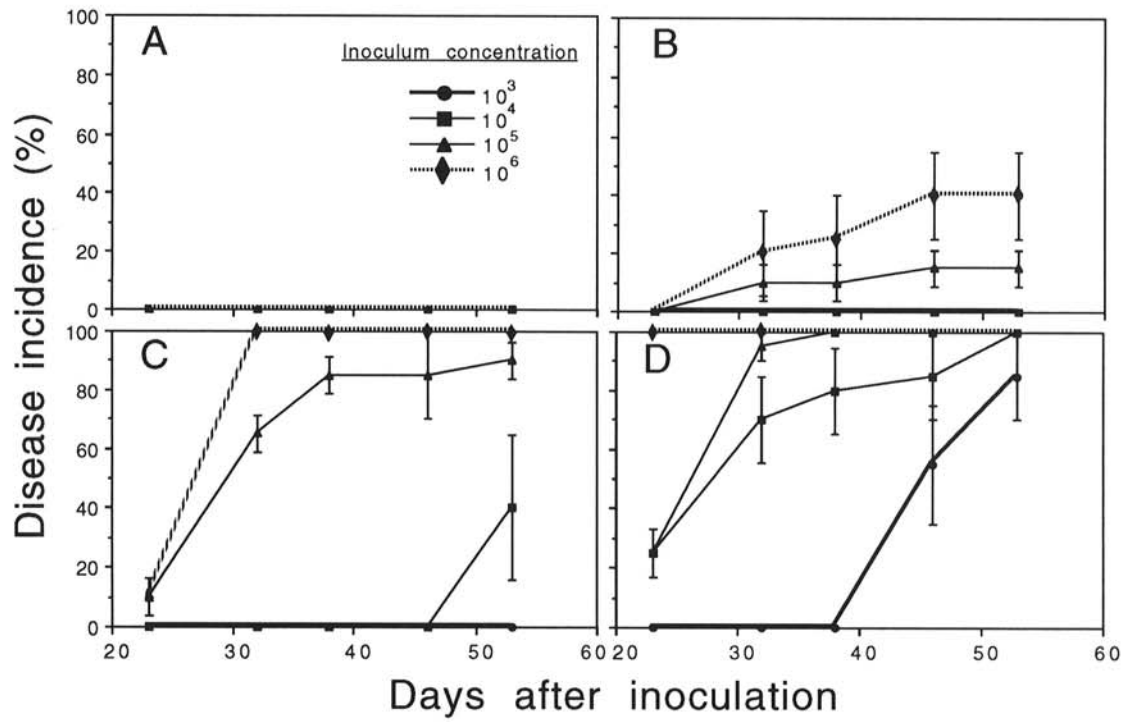

Fig. 1. Disease progress curves of carnation plants inoculated with four inoculum concentrations (spores/ml) of *Fusarium oxysporum* f. sp. *dianthi*. Plants were grown under four levels of shade: **A,** outdoors (i.e., 0% shade), and under screen covers producing **B,** 55% of shade, **C,** 72% of shade, and **D,** 85% of shade. Results are for experiment 2 (planted in the first week of August). Bars indicate the SE.

experiment, and among the four inoculum concentrations within shade treatment. The total number of epidemics was 112 (seven experiments, four levels of shade, and four inoculum concentrations). In general, disease intensity was directly affected by solar radiation; no symptoms of wilt developed under direct solar radiation (0% shade), whereas the most severe wilt was observed under the 85% shade covers (e.g., Fig. 1). Disease severity was generally proportional to inoculum concentration.

In some cases, plants remained symptomless during the entire experimental period (i.e., RAUDPC = 0%). This happened for all nonshaded plants in all experiments, for some plants that received low inoculum doses and 55% shade and for all treatments in experiments 5, 6, and 7. The pathogen *F. o. dianthi* was reisolated from most of the symptomless plants, indicating that the plants were colonized by the fungus. Results in Table 1 represent the frequency of recovery of *F. o. dianthi* from symptomless plants in experiments 5, 6, and 7. Among the three experiments, variation in fungal colonization of the symptomless plants was relatively low.

TABLE 1. Frequency of recovery of *Fusarium oxysporum* mycelia from symptomless stems of carnation plants (cv. Hermon) inoculated with *Fusarium oxysporum* f. sp. *dianthi*[a]

Level of shading (%)[b]	Inoculum concentration (spores/ml)			
	10^3	10^4	10^5	10^6
0	20.0[c]	28.3	65.0	78.3
	(6.2)	(10.1)	(5.0)	(3.5)
55	15.0	50.0	53.3	78.3
	(9.7)	(10.8)	(10.9)	(7.2)
72	10.0	41.7	70.0	81.6
	(6.5)	(3.3)	(7.6)	(8.8)
85	42.5	41.7	75.0	90.0
	(9.5)	(18.7)	(5.0)	(5.0)

[a]Twenty rooted cuttings were immersed in 300 ml of each spore suspension for 20 s prior to planting. The remaining spore suspension was poured onto the tuff surface. Stem segments (5–10 mm) from symptomless plants (60 days after planting) were surface sterilized with hypochlorite 1%, rinsed twice with sterile water subsequently plated on potato-dextrose agar supplemented with 250 mg dihydrostreptomycin. Each number represents frequency of recovery for 60 plants.
[b]Shading treatments were imposed by growing plants outdoors, or under screen covers that shaded incoming solar radiation.
[c]Means (and SE) of the results obtained in trials 5, 6, and 7.

TABLE 2. Estimated regression coefficients and associated statistics for regression of the relative area under the disease progress curve (RAUDPC) on inoculum concentration and solar radiation intensity in four experiments in which carnation (cv. Hermon) was inoculated with *Fusarium oxysporum* f. sp. *dianthi* and grown under various levels of shade

Experiment[a]	Regression coefficients[b]			df	*F*	R^2
	β_0	β_1	β_2		*P* value	
1	−65.1	29.8	−0.087	5	0.001	0.934
	(18.6)[c]	(4.1)	(0.012)			
2	−16.8	22.9	−0.082	7	0.001	0.855
	(20.8)	(4.5)	(0.015)			
3	−59.6	36.6	−0.129	7	0.003	0.907
	(20.1)	(5.6)	(0.021)			
4	−44.3	17.8	−0.032	9	0.001	0.791
	(16.0)	(3.4)	(0.008)			

[a]Carnation plants were planted in the first week of July (experiment 1), August (experiment 2), September (experiment 3), and October (experiment 4). Inoculum concentrations were 10^3, 10^4, 10^5, and 10^6 spores/ml; plants were grown under four levels of shade: outdoors (i.e., 0% shade) and under screen covers producing 55, 72, and 85% of shade.
[b]Regression coefficients were estimated for the equation $RAUDPC = \beta_0 + \beta_1 I + \beta_2 R^2$; where RAUDPC = relative area under the disease progress curve; I = logarithm (base 10) of inoculum concentration (spores/ml) and R = solar radiation intensity (μE m^{-2} s^{-1}). Curves are presented in Fig. 2.
[c]Standard error.

Effect of radiation intensity. The influence of solar radiation intensity at various inoculum concentrations on wilt induced by *F. o. dianthi* was determined by fitting of equation 2 to the data (Table 2). The RAUDPC values increased with decreasing solar radiation intensity (Fig. 2). The intensity of solar radiation at which symptoms of wilt failed to develop (RAUDPC values of 0%) increased with increasing inoculum concentration. Very severe epidemics (RAUDPC values of 100%) developed in experiments 1, 2, and 3, in treatments which had the lowest solar radiation intensities (200-300 μE m^{-2} s^{-1}).

Effect of temperature. The influence of temperature on wilt induced by *F. o. dianthi* at various inoculum concentrations was determined by fitting of equation 3 to the data (Table 3). In general, the relationship between temperature and disease intensity was parabolic, i.e., there were lower and upper temperature extremes at which symptoms did not develop and an optimum temperature with maximal RAUDPC values (Fig. 3). For all inoculum concentrations, the optimal temperature for development of wilt symptoms, derived from the results shown in Fig. 3, was 25–26 C. Estimates of the upper and lower temperature extremes were influenced by the inoculum concentration treatments and their difference was greater at higher than at lower inoculum concentrations. For example, ranges between temperature extremes at which symptoms did not develop was 4–9.5 C for 10^3 spores per milliliter and 11.5–15 C for 10^6 spores per milliliter. In experiments 5, 6, and 7, in which average temperatures were below 18 C, no wilt symptoms developed regardless of the radiation intensity.

Effects of solar radiation intensity and temperature. The combined effects of solar radiation intensity and temperature on wilt induced by *F. o. dianthi* were determined by fitting of equation 5 to the data. The regression equation was $RAUDPC = -1{,}410.1 + 24.7I - 0.05R^2 + 104.8T - 1.99T^2$ ($P < 0.0001$; $R^2 = 0.714$). Of the variance in RAUDPC explained by the regression ($R^2 = 71.4\%$), 22% was attributed to inoculum concentration, 40% to solar radiation intensity and 38% to temperature. To determine values of solar radiation intensity and temperature at which wilt symptoms would begin to develop, the equation was solved separately for each inoculum concentration treatment assuming RAUDPC > 0% (Fig. 4). These curves summarize, for every combination of solar radiation intensity and temperature, the conditions delimiting whether or not symptoms of Fusarium wilt developed. For example, under a solar radiation intensity of 900 μE m^{-2} s^{-1} and a temperature of 24 C, carnation wilt symptoms did not develop when the inoculum concentration was 10^3 spores per milliliter, but did develop in plants inoculated with 10^5 spores per milliliter or more (Fig. 4).

TABLE 3. Estimated regression coefficients and associated statistics for regression of the relative area under the disease progress curve (RAUDPC) on inoculum concentration and temperature in which carnation (cv. Hermon) was inoculated with *Fusarium oxysporum* f. sp. *dianthi* and grown under three levels of shade

Level of shading (%)[a]	Regression coefficient[b]				df	*F*	R^2
	β_0	β_1	β_2	β_3		*P* value	
55	−1227.7	19.5	94.5	−1.9	6	0.012	0.821
	(385.2)[c]	(4.3)	(30.0)	(0.58)			
72	−1667.6	31.4	123.4	−2.4	10	0.001	0.909
	(320.2)	(3.4)	(24.7)	(0.48)			
85	−1500.5	22.4	114.3	−2.2	12	0.001	0.838
	(386.1)	(3.7)	(30.5)	(0.60)			

[a]Carnation plants were grown under screen covers that shaded incoming solar radiation intensity. Inoculum concentrations were 10^3, 10^4, 10^5, and 10^6 spores/ml.
[b]Regression coefficients were estimated for the equation: $RAUDPC = \beta_0 + \beta_1 I + \beta_2 T + \beta_3 T^2$; where RAUDPC = relative area under the disease progress curve; I = logarithm (base 10) of inoculum concentration (spores/ml) and T = temperature (C). Curves are presented in Fig. 3.
[c]Standard error.

DISCUSSION

In all experiments conducted in this study, solar radiation intensity was partially controlled (by the use of screen covers) and spore concentration was fully controlled. Temperature was controlled by conducting experiments at different times of the year and by use of the screen covers. On the basis of the variation among experiments when compared with variation within an experiment, daily values of temperature and values of solar radiation were averaged within experiments. The use of average values did not substantially affect the precision of the analysis, since all regressions were highly significant ($0.01 < P < 0.001$) and the coefficients of determination were reasonably high ($0.791 < R^2 < 0.934$) (Tables 2 and 3).

In general, disease was most severe at low solar radiation intensities (200–300 μE m^{-2} s^{-1}) and at temperatures near to 25–26 C. At high solar radiation intensities (above 1,000 μE m^{-2} s^{-1}), and at low or high temperatures (under 18 C and above 34 C) plants remained symptomless, regardless of the spore concentration. When symptoms were apparent, disease severity was proportional to the inoculum concentration.

Analysis of the results revealed that the influence of solar radiation intensity and temperature on the pathogenic process may be understood in terms of two general concepts: the law of the minimum (8) and compensation (19). Liebig (8) codifies the concepts of the law of the minimum as follows: "If several factors affecting outcome are presented in abundance and one factor is deficient, adding more of the deficient factor will change the outcome greatly whereas increasing the abundant ones will change the outcome little." The concepts of the law of the minimum have been developed and implemented in several studies in plant physiology (6,18) and plant pathology (23). In our study, effects of solar radiation and temperature on wilt incidence were consistent with the law of the minimum whenever the abiotic variables were extreme. For example, when temperatures were lower than 18 C or higher than 34 C, plants remained symptomless even if solar radiation intensity was optimal for wilt incidence. Similarly, at high solar radiation intensities (> 1000 μE m^{-2} s^{-1}) plants remained symptomless even at temperatures optimal for *F. o. dianthi* activity. Within the ranges of these variables, the concepts of compensation rather than the law of the minimum are more applicable. Rotem (19) developed the theory and concepts of compensation, which postulate that a highly favorable state of one factor essential for development of a given phase in the life cycle of a pathogen can compensate for the limitations imposed by the simultaneously less favorable state of other factors. Compensation has been described in several pathosystems (1). Compensation was evident in our system when the abiotic variables were at intermediate levels. The amount of inoculum concentration was associated in the compensation phenomenon as well (Figs. 2 and 3). As expected, very severe epidemics (i.e., RAUDPC of 100%) developed when both abiotic variables were at their optimal levels.

In the equation depicted in Fig. 4, for the ranges of treatments we imposed, solar radiation intensity and temperature were equally important in determining the severity of wilt imposed by *F. o. dianthi* in carnation. The effects of solar radiation intensity on wilt imposed by the pathogen are rather complicated to interpret, and might be explained in terms of an interaction between the host and the pathogen rather than by a direct effect of solar radiation intensity on host and pathogen separately. However, the precise mechanisms of these effects in the *F. o. dianthi*-carnation pathosystem are still unknown. Solar radiation, a primary component of photosynthesis, affects the rate of net photosynthesis (10). In our experiments, plants grown under lower light intensity (85 vs 55% level of shade) were smaller in aboveground biomass and stem circumference but taller in height (data not presented). In a recent work (17), Pennypacker et al reported that pathogenicity of *V. albo-atrum* on the susceptible alfalfa clone was constant under three different photosynthetic photon flux density (PPFD) (100, 70, and 40% of ambient) levels and time whereas the resistant alfalfa clone lost host resistance under 40% PPFD. They suggest that the corresponding reduction in net photosynthesis was critically involved in the loss of resistance. Our results on the effects of temperature or solar radiation on wilt induced by *F. o. dianthi* are in good agreement with those

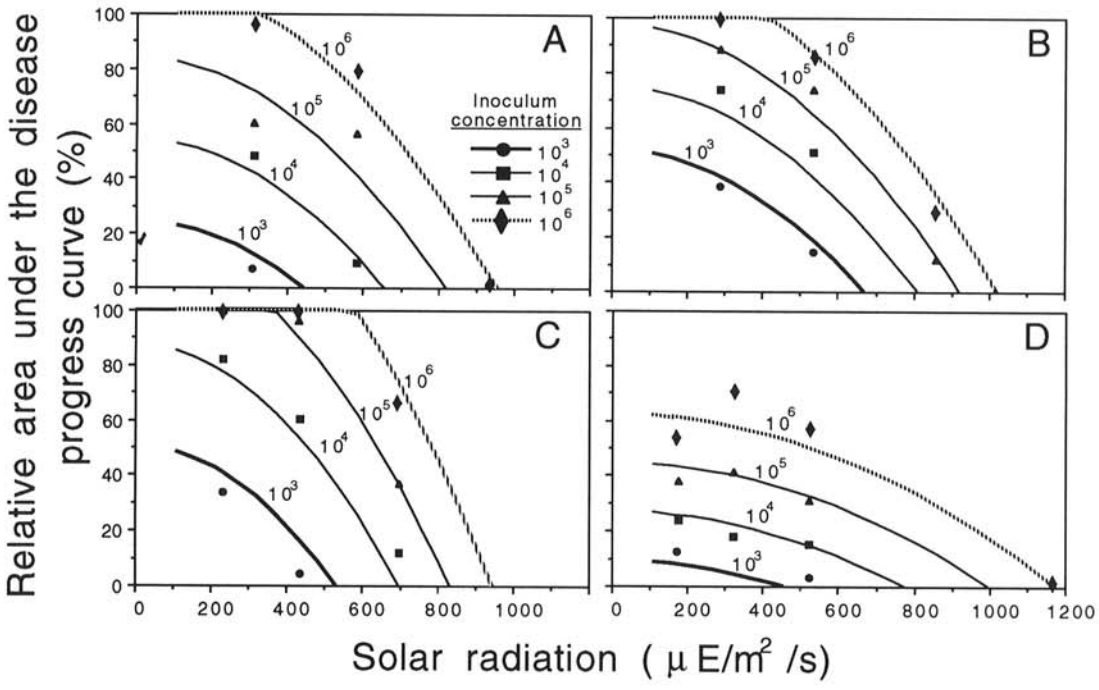

Fig. 2. Effects of solar radiation on the relative area under the disease progress curve (RAUDPC) at four inoculum concentrations of *Fusarium oxysporum* f. sp. *dianthi*. Carnation plants planted in the first week of **A,** July (experiment 1), **B,** August (experiment 2), **C,** September (experiment 3), and **D,** October (experiment 4). Symbols represent observed mean RAUDPC values and lines are predicted RAUDPC values calculated for model RAUDPC = $\beta_0 + \beta_1 I + \beta_2 R^2$; where I = logarithm (base 10) of inoculum concentration (spores/ml) and R = radiation intensity (μE m^{-2} s^{-1}). Regression coefficients are in Table 2. SE values for the data points ranged from 0.8 to 12.3%.

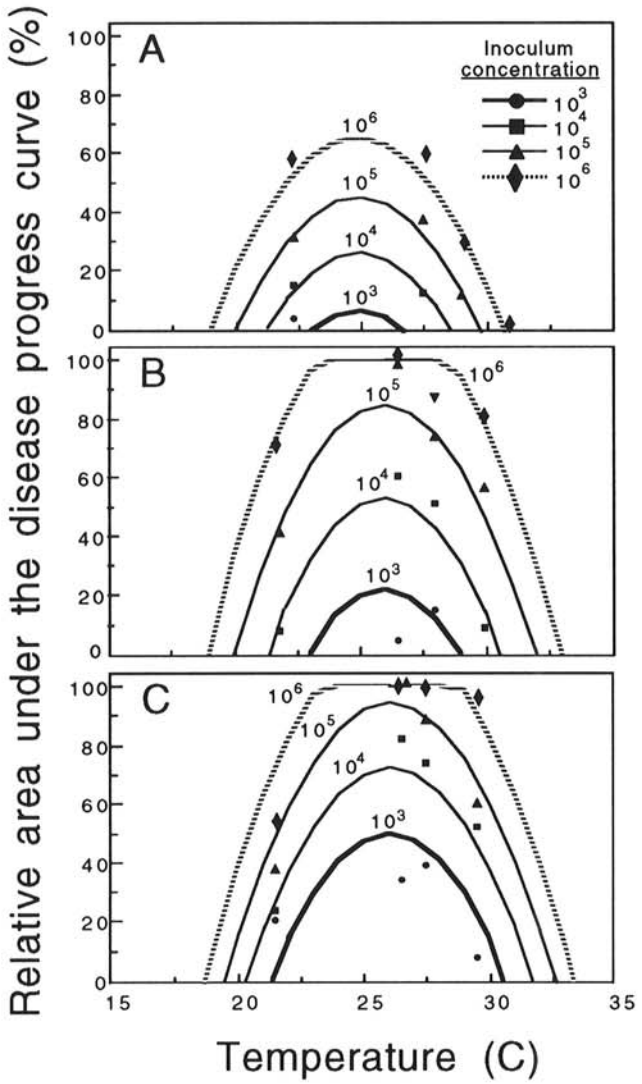

Fig. 3. Effects of temperature on the relative area under the disease progress curve (RAUDPC) at four inoculum concentrations of *Fusarium oxysporum* f. sp. *dianthi*. Carnation plants were grown under screen covers producing three levels of shade: **A,** 55% shade, **B.** 72% shade, and **C,** 85% shade. Symbols represent observed mean RAUDPC values and lines are predicted RAUDPC values calculated for model $\text{RAUDPC} = \beta_0 + \beta_1 I + \beta_2 T + \beta_3 T^2$; where I = logarithm (base 10) of inoculum concentration (spores/ml) and T = temperature (C). Regression coefficients are in Table 3. SE values for the data points ranged from 0.8 to 12.3%.

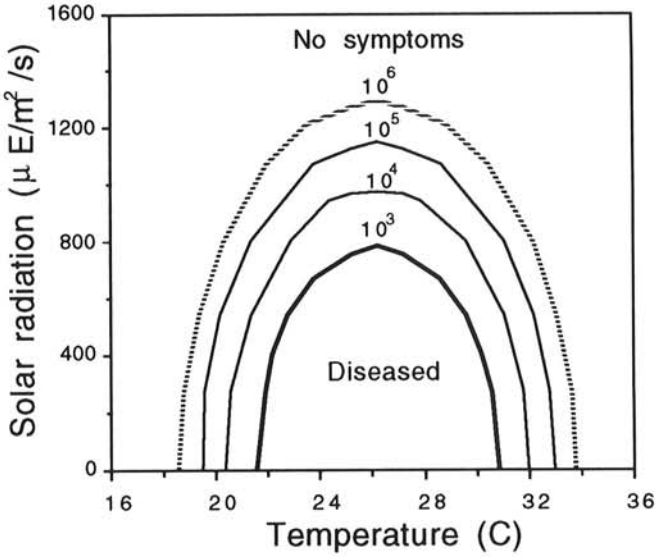

Fig. 4. Estimated functions of solar radiation intensity and temperature where, at values greater (outside) the depicted curves, symptoms of Fusarium wilt did not develop in plants of carnation (cv. Hermon) inoculated with spores suspension of *Fusarium oxysporum* f. sp. *dianthi* varying from 10^3 to 10^6 spores/ml. Curves were calculated according to model $\text{RAUDPC} = -1410 + 25\,I - 0.05\,R^2 + 105\,T - 2\,T^2$; where RAUDPC = relative area under the disease progress curve (%); I = logarithm (base 10) of inoculum concentration, R = solar radiation intensity (μE m^{-2} s^{-1}) and T = temperature (C). Statistics for the regression analysis are: $P < 0.0001$; $R^2 = 0.714$; (see text for details).

reported previously (2,11,14).

The effects of photoperiod could not be estimated in this study because day length was positively correlated with temperature. In addition, differences between the longest day length (14 h of daylight in experiment 1) and the shortest day length (10 h of daylight in experiment 6), were relatively small. Nevertheless, when inoculation tests were conducted in December under the natural photoperiod of 10 h and radiation intensity of 210 μE m^{-2} s^{-1}, very severe epidemics developed at 26 C but plants remained symptomless at 15.2 C (Ben-Yephet and Shtienberg, *unpublished data*). These results could indicate that in the winter (i.e., short photoperiod and low temperatures), temperature is more important than photoperiod in determining Fusarium wilt expression.

The results of the present study open the way to a better understanding of the epidemiology of *F. o. dianthi* in carnation following artificial inoculation. When conducting pathogenicity tests or determining the wilt reaction of new carnation cultivars, it is important to choose a suitable combination of solar radiation intensity and temperature in the experimental design. If this is done, pathogenicity experiments can be conducted throughout the year in controlled environments.

The results of this research suggest two supplementary studies concerning selection resistance cultivar. Whether or not this method can be reliably used on its own to predict resistance of new cultivars in the field has yet to be determined. It is reasonable to assume that light and temperature also will affect the expression of disease intensity in fields with natural inoculum. Thus, it would be worthwhile to do cultivar selection in a growth with light and temperature conditions that favor disease development.

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