Conditions for Development of Powdery Mildew of Tomato Caused by *Oidium neolycopersici*

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ABSTRACT

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Oidium neolycopersici causes severe powdery mildew on all aerial parts of tomato, excluding the fruit. The objective of the present work was to examine factors that influence the development of *O. neolycopersici* on tomato and to identify potential methods for managing tomato powdery mildew. Under controlled conditions, the highest rates of conidial germination were observed at 25°C, 99% relative humidity (RH) and minimal light, and the lowest on leaves adjacent to fruits. Optimal conditions for appressoria formation were 25°C, RH ranging from 33 to 99%, and 1,750 lux light intensity. More conidia were formed at 20°C, 70 to 85% RH, and 5,150 lux light intensity than at 16 and 26°C, 99% RH, and 480 to 1,750 lux, respectively. Conidia survived and remained capable of germination for over four months when initially incubated at lower temperatures and higher RH, as compared with their fast decline under more extreme summer shade conditions. In growth chamber experiments, disease

did not develop at 28°C. Within the range of 70 to 99% RH, disease was less severe under the higher RH than the drier conditions. Disease was also less severe at lower light intensities. Data collected in three commercial-like greenhouse experiments involving various climate regimes were used to draw correlations regarding the effects of temperature and RH on the development of epidemics. Severity of powdery mildew was positively correlated with the duration of the range 15 to 25°C, 1 to 4 weeks before disease evaluation (BDE), RH levels of 60 to 90% at 2 to 4 weeks BDE, and RH of 50 to 60% during the week BDE. Conversely, disease was negatively correlated with the duration of temperatures in the low and high ranges (5 to 15°C and 35 to 40°C) at 1 to 4 weeks BDE, with the duration of RH levels of 40% and below at 1 to 4 weeks BDE, and with 50 to 60% RH during the third week BDE. High (90 to 100%) RH was also negatively correlated with disease severity. These results suggest that the combination of high temperatures and low RH may help reduce *O. neolycopersici* powdery mildew severity in greenhouse tomatoes.

Additional keywords: *Lycopersicon esculentum*.

Two powdery mildew diseases affect cultivated tomato. *Leveillula taurica* has been known for many years as a tomato pathogen (31). However, in 1986, reports from Europe and North America described a second, similar pathogen on tomato crops, especially those grown under glass (27). This second pathogen, which first appeared on tomato in the United Kingdom during the 1986 to 1987 growing season, was classified as *Erysiphe orontii* (anamorph *Oidium violae*) (9,37). Later, this disease was also described in North America (2,26). On the basis of production of conidia singly, in the absence of chains, the presence of nipple-shaped to moderately lobed appressoria and its straight conidiophores, it has been suggested that this fungus should actually be referred to as *Oidium lycopersicum* (37). This fungus causes disease on a number of tomato cultivars at growth stages ranging from seedling to mature plant in the greenhouse and the field. Eastern black nightshade (*Solanum ptycanthum*), eggplant, tobacco, and potato have also been infected by this fungus in the greenhouse (25). A worldwide study of the *Oidium* species that cause economic damage to tomato identified two taxa, despite the fact that no sexual stage was found. One taxon found in various locations worldwide (except Australia) was identified as *O. neolycopersici* and a second, which was first described in Australia, was named *O. lycopersici* (22,23).

O. neolycopersici was described by Jones et al. (19) as having superficial mycelia with hyaline hyphae; unbranched, erect

conidiophores; ellipsoid-ovoid or doliform, singly-formed conidia that are 22 to 46 × 10 to 20 µm and lack fibrosin bodies, and double-lobed to multi-lobed appressoria that are rarely nipple-shaped. These conidia are occasionally found in short chains of two to six conidia. Oichi (29), who studied the formation of pseudochains of conidia by *O. neolycopersici* under the microscope, found that wind is required for the dispersal of progeny conidia from the conidiophores, and that the fungus produces conidial pseudochains when the wind is below a critical level, independent of relative humidity levels.

Symptoms of the disease caused by the ectoparasite *O. neolycopersici* include powdery white lesions on leaf blades and, in severe epidemics, similar lesions may also be observed on other organs, i.e., petioles, stems, and sepals, but not on fruit. This is in contrast to *L. taurica*, a hemiendophytic powdery mildew pathogen that causes symptoms only on leaves. In severe outbreaks, the lesions coalesce and the disease is debilitating. This disease is common in glasshouse tomatoes worldwide, and its importance on field-grown tomato crops is increasing (18). In Israel, *O. neolycopersici* epidemics occur in unheated greenhouses and net houses in the spring, summer, and early autumn (14,15).

The host range of the pathogen is broad and it is reported to attack over 60 species in 13 plant families, particularly members of the families Solanaceae and Cucurbitaceae (13,18). Resistance mechanisms of *Lycopersicon* spp. against *O. neolycopersici* were studied (24). During the early stages of *O. neolycopersici* infection, significant differences in conidial germ tube development on resistant and susceptible accessions were observed. A hypersensitive reaction was the most frequent defense response in *Ly-*

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copersicon spp. and involved significant changes in peroxidase and catalase activities during pathogenesis (24).

There has been limited research into the effects of different environmental conditions on *O. neolycopersici*. Conidia of this pathogen can germinate within 3 to 5 h, form appressoria within 6 to 8 h, and penetrate the host within 11 h of their germination (19). In a study of the effects of relative humidity (80 to 95% at a constant 19°C for 8 weeks) on the development of tomato powdery mildew, Whipps and Budge (36) found that disease severity was greatest at 80% relative humidity (RH). Disease decreased as RH increased to a minimum level at 95% RH on both inoculated plants, introduced to act as initial infection sources, and adjacent, uninoculated plants (36). These results indicate that high humidity may decrease the severity of this disease in glasshouses and may aid the management of this disease. However, a report from Connecticut claims that the disease develops at RH levels above 50% and that the optimum RH for disease development is above 90% with no free water (7). This same study found that the temperature range for development is 10 to 35°C, with maximal disease development at below 30°C (7).

A more detailed study regarding the effect of microclimate on pathogen ecology and disease etiology was carried out with another tomato powdery mildew pathogen, *L. taurica* (11). Temperatures of >30°C were deleterious for germination of the conidia, and disease development. Low RH levels (20 to 40%) reduced conidial germination and disease progress. Intermediate RH levels (50 to 70%) increased conidial germination and optimized disease development (11). A more detailed study with this pathogen was carried out in pepper (8). In the *L. taurica* pepper system, optimal conidial germination was observed at 20°C. Conidial viability declined as temperatures increased to 40°C for 6 h. Severe leaf infections occurred at 15 to 20°C and conidiation was suppressed at 20 to 25°C. The highest germination rates were observed at 75 to 85% RH. Disease severity was high for plants which were subjected to longer periods of temperatures between 10 to 15°C and daytime RH between 85 to 95%, and was negatively correlated with lengthy periods of temperatures above 25°C (8).

The objectives of the present work were to examine factors that influence *O. neolycopersici* powdery mildew in tomato. We wanted to identify strategies that can be used to manipulate growth conditions within commercial greenhouses to slow the progress of the disease and reduce the need for chemical control measures. Some preliminary data from this study were presented previously (14,15).

MATERIALS AND METHODS

Pathogen and host plants. *O. neolycopersici* was isolated from young leaves of tomato plants grown in a commercial greenhouse at the Besor Research and Development Station, western Negev Desert, Israel, during January 2005. Conidia of the pathogen were collected by rinsing infected leaves with sterile water (13). For the artificial infection of tomato leaves (laboratory and growth chamber experiments), the concentrations of these conidial suspensions were determined under a light microscope using a hemacytometer. All suspensions were adjusted to 10^4 /ml and then sprayed onto plants at a rate of 5 ml per plant. All suspensions were sprayed within 10 to 15 min of the initial conidia collection. Suspensions were applied with a hand-held spray bottle and plants were left to dry in an open greenhouse for up to 30 min.

Tomato plants were obtained from a commercial nursery (Hishtil, Ashkelon, Israel) at 40 to 50 days after seeding and transplanted into 1-liter pots, containing a peat/volcanic gravel (3:7, vol/vol) growth mixture. Plants were irrigated every 1 to 3 days, allowing for 30% drainage. Fertilization with 5 g/liter 20:20:20 of NPK fertilizer applied as 250 ml of fertilizer solution

per pot was started 1 week after transplanting. Plants were maintained at 20 to 25°C in a pest- and disease-free greenhouse for 2 to 3 weeks prior to the initiation of the experiments. Experiments were initiated after plants had reached the 5-node developmental stage. The tomato cv. 1402 (Hazera Genetics, Ltd., Brurim M.P. Shikmim, Israel) was used in most of the experiments of this study. Some experiments were performed on cultivars 189, 870, 662, and 1138 (Hazera Genetics, Ltd.), 1912 (Zeraim Gedera, Zeraim Farm, Gedera, Israel), and 1107 and 1125 (Top Seeds, Ltd., Kefar Vitkin, Israel).

Germination of conidia and formation of appressoria. A series of experiments were performed to determine the effects of temperature, RH, light intensity, cultivar, and leaf position on germination and germ tube elongation (to evaluate potential development). Germ tube length values were calculated for all conidia and for conidia germinated, since these are two different characteristics of germinated conidia, the germination data are presented separately in this publication. These experiments were performed using cultivar 1402. Conidia were spread on tomato leaflets by touching mildew-bearing leaves to the leaflet. Conidia were applied at a rate of approximately 10^3 conidia/cm², as counted under the light microscope after application.

The leaflets were incubated for 24 h at 5, 10, 15, 20, 25, 30, and 35°C and 99% RH and 5,150 lux light intensity, in closed transparent boxes (90 × 90 × 15 mm). Other leaflets were kept at a constant temperature ($22 \pm 1^\circ\text{C}$) and eight different RH levels. The different RH conditions were created by incubating the samples above different salt solutions (41). The infected leaves were placed in open 90 mm diameter petri plates above different saturated salt solutions in polyethylene covered boxes (20 × 15 × 30 cm) that were kept at $22 \pm 1^\circ\text{C}$. Light intensity in the boxes was 4,230 lux. The solutions used were (RH in parentheses) NaOH (7%), CH₃COOH (23%), MgCl₂ (33%), glucose (55%), NH₄NO₃ (65%), NaCl (75%), KCl (85%), KNO₃ (94%), and no salt (99%). Light intensities tested were 0 (dark), 480, 1,750, and 5,150 lux ($22 \pm 1^\circ\text{C}$, 99% RH). In all experiments, plants were kept at 12-h photoperiod. All tests were carried out with leaves positioned at nodes three to five out of eight nodes. In another set of experiments, the effects of leaf position and age were examined at 99% RH, 22°C, and 5,150 lux light intensity. Mature, fully expanded leaves from nodes one to two, medium-aged leaves (nodes 3 to 5), young leaves (nodes 6 to 8), leaves close to blossoms (nodes 6 to 8), and leaves close to developed fruits (nodes 4 to 6) were examined. A test of cultivar effect on germination was carried out with cvs. 1138, 662, 189, and 1912 at $22 \pm 1^\circ\text{C}$, 99% RH, and 5,150 lux.

Conidial germination was observed under a light microscope after 24 h of incubation. Appressorial formation was observed following 12 h of incubation at $22 \pm 1^\circ\text{C}$ and 99% RH and an additional 24-h incubation under the above-described conditions. The effects of leaf age and location were tested as described above. Cultivar 1402 was also used in this experiment. The length of the germ tubes, the extent of germination and the percentage of appressoria formed were recorded for 100 conidia per leaf (12 leaves per treatment). The germination and appressoria formation assays were repeated twice.

Formation of conidia. Plants were infected as mentioned above, incubated for 6 days (one day before the appearance of symptoms) at $22 \pm 1^\circ\text{C}$, 70 to 75% RH, and 5,150 lux light intensity, and then transferred to chambers with different temperatures (16, 20, and 26°C; 75 to 80% RH, 5,150 lux), RH levels (70 ± 3 , 85 ± 3 , $99 \pm 1\%$; $22 \pm 1^\circ\text{C}$, 5,150 lux), and light intensities (480, 1,750, and 5,150 lux; $22 \pm 1^\circ\text{C}$, $99 \pm 1\%$ RH). Plants were kept at 13-h photoperiod. Plants were also placed in a greenhouse compartment in which conditions fluctuated between 18 to 35°C and 55 to 85% RH. Conidiation on mature leaves was measured every 3 to 4 days for 16 days. In one set of experiments, conidia formation on leaves of two different ages (intermediate-

aged and mature) was tested at 24 and 26°C. In order to measure conidiation, leaflet pieces (3 × 5 cm each) from 10 different leaves were each placed in an individual vial with 1 ml of distilled water and shaken for 1 min using a vortex. A 100-µl sample was taken from each of the 10 wash suspensions and these samples were combined to yield 1 ml of conidial suspension. A 10-µl sample of this pooled conidial suspension was placed on a hemacytometer and all conidia were counted under a light microscope. Experiments were repeated twice and each of the treatments was replicated six times in each experiment.

Conidial survival. Tomato leaves with powdery mildew symptoms were stored in boxes (20 × 15 × 30 cm) for 1 week, either under summer (25 to 37°C, 45 to 75% RH, 3,100 to 7,100 lux) or winter (10 to 26°C, 57 to 87% RH, 1,700 to 3,800 lux) conditions, followed by 143 days at 22 ± 4°C, 45 to 65% RH, and 1,500 to 1,800 lux. At each sampling date (i.e., every 30 days), conidia were transferred to fresh tomato leaves by rubbing the sampled leaf on the surface of the fresh leaf. The freshly inoculated leaves were then transferred to a closed, 90 mm empty petri dish and incubated for 24 h at 22 ± 1°C, 99 ± 1% RH, and 5,150 lux light intensity to allow germination of the conidia. Conidial germination was evaluated as described above. Leaf samples were replicated 12 times. That is, each month six old leaves were selected and each of these six leaves was rubbed against two new leaves.

Growth chamber experiments. The effects of temperature, RH, and light intensity on powdery mildew development were tested on tomato plants incubated in walk-in growth chambers under the following conditions: the effects of cultivar and leaf location on severity of powdery mildew were tested at 24 ± 1°C, 5,150 lux and 70 ± 3% RH; the effect of temperature (16 to 28°C) was tested at 5,150 lux and 70 ± 3% RH; the effect of relative humidity (70 to 99%) was tested at 22 ± 1°C and 5,150 lux; and the effect of light intensity was tested at 22 ± 1°C and 70 to 75% RH. Treatments were replicated 10 times, in each of two experiments. All treatments received the same light intensity (5,150 lux), unless otherwise noted. The lights were turned on at 06:00 and turned off at 19:00. Relative humidity in the temperature experiments was kept between 70 and 75%. RH experiments were conducted at 22 ± 1°C. Temperature and RH were recorded hourly using data loggers (Hobo, Onset Computer Corp., Pocasset, MA). Cultivars used were 1107 and 1125 (leaf age, temperature, RH, and light intensity experiments) and 662, 870, 1402, and 1912 for the temperature experiments. All of these cultivars were included in the cultivar comparison experiments. Four groups of five plants each served as replicates in the growth chamber experiments. Disease severity as percent leaf coverage was evaluated using a pictorial key. Severity was evaluated at three different plant heights and averaged for the entire plant. The disease severity values for the mature and intermediate leaves and for the

entire plant are described separately. Most of the disease symptoms were observed on the leaves and not on other plant parts, thus we chose to monitor leaf infection. The areas under the disease progress curves (AUDPC values) were calculated.

Experiments in commercial-like greenhouses. Tomato plants were planted in sandy soil at the Besor R&D Research Station located in the northwestern part of the Negev Desert (southern Israel). Cultivar 1402 was planted on 15 August 2005 for the autumn crop and cv. 870 was planted on 19 February 2005 and 3 March 2006 for the spring crops. The plants were grown to one stem and then attached to ropes hanging from the ceiling of the greenhouses, drip irrigated, and fertilized. The plants were maintained according to local commercial standards. No fungicides were used during autumn, whereas the following fungicides were applied to control late blight in the spring crops (all products applied once per experiment): Acrobat WG (9% dimethomorph + 60% mancozeb; BASF, Ludwigshafen, Germany), Sandomyl WP (7.5% metalaxyl + 56% mancozeb; Dow Agrosiences, Indianapolis, IN), and FolioGold SC (3.75% mefenoxam + 50% chlorothalonil; Syngenta, Basel, Switzerland). Eight walk-in tunnel greenhouses (30 m²) were each planted with three 6-m-long double rows of tomato plants. Plants were planted 40 cm apart in rows spaced 60 cm apart. In order to achieve variability in climatic conditions, the greenhouses were different from each other in their roofing and the materials used for their front and back openings, as well as soil cover and their internal humidity sources. Roofing and front and back door materials included polyethylene, insect-proof netting, and shade netting (Table 1).

Disease development. In order to ensure the even availability of *O. neolycopersici* inoculum in the greenhouses, nine pots of 2-month-old tomato plants with 40 to 60% powdery mildew severity were placed in each greenhouse, 21 days after the planting of each experiment. Three pots were placed in each of three rows (nine pots per greenhouse), evenly scattered in the greenhouse. Conidia spread naturally in the greenhouse. No fungicides against powdery mildew were applied during the entire growth cycles. AUDPC values were calculated. Ten centrally located plants were rated for disease severity every 2 to 4 weeks. Leaves from nodes 3 to 4, 7 to 9, and 12 to 14, corresponding to low, intermediate, and high heights, were evaluated for disease severity. Disease severity (percentage of the leaf surface covered with powdery mildew symptoms) was calculated for each plant height and for the entire plant by averaging the percent severity values for the three heights.

Microclimate measurements. Air temperature and RH values were recorded hourly in the greenhouses by data loggers (Hobo, Onset Computer Corp., Pocasset, MA) positioned 1 m above the ground. The duration (h) of temperature in 5°C intervals and that of RH levels (in 10% intervals) were analyzed on a weekly basis.

TABLE 1. Greenhouse structures used in experiments during autumn 2005 and spring 2006

Greenhouse number	Roofing material	Material used for the front and back door-flaps	Soil cover	Humidity source	Relative climate ^y	
					Temperature	RH
Y1	Polyethylene	Insect-proof 50 mesh	Bare soil		Medium	Medium
Y2 ^z	Insect-proof 50 mesh	Insect-proof 50 mesh	Bare soil		Low	Low
Y3	Polyethylene + 45% shade netting	Insect-proof 50 mesh	Bare soil		Low	Medium
Y4	Polyethylene	Insect-proof 50 mesh	Transparent polyethylene		Medium	Medium
Y5	Polyethylene	Insect-proof 50 mesh + 2/3 polyethylene cover	Bare soil		High	High
Y6 ^z	Insect-proof 50 mesh (Optinet)	Insect-proof 50 mesh (Optinet)	Bare soil		Low	Low
Y7	Polyethylene	Insect proof 50 mesh	Bare soil	Wetted back open, 2 × 3 × 0.6 m water pools	Medium	High
Y8	Polyethylene	Insect-proof 50 mesh net	Bare soil		Medium	Medium

^y Daytime conditions were typically as follows: RH 50 to 75% (low), 70 to 90% (medium), and 85 to 100% (high) with temperatures 15 to 22°C (low), 20 to 30°C (medium), and 25 to 40°C (high).

^z Greenhouse not included in the spring experiments.

Correlations between the above-mentioned climate parameters and the powdery mildew levels over different periods during the growing season were calculated. Two greenhouses (Y2 and Y6) were excluded from the analysis of the spring crops because of late blight infections.

Statistical analysis. The effects of temperature, RH, and light intensity on germination, appressorial formation, and conidial viability were evaluated using regression analysis. Powdery mildew severity (leaf coverage) was averaged per leaf level (node), plant, and plot, and AUDPC values were calculated. Data in percentages were arcsin-transformed before further analysis. Disease severity and AUDPC data were analyzed using ANOVA and Fisher's protected least significant difference (LSD) test. Standard errors (SE) of the means were calculated and disease levels were statistically separated following a one-way ANOVA. The SE are marked in the figures (with error bars) and stated in the tables.

Linear regression was used to evaluate the relationships between disease severity and temperature and RH data. Nonlinear regression analyses were also carried out, but they did not result in a better description of the relationships between parameters, as compared with linear regressions. Correlation results are presented when significant. Coefficient values and whether the relationships between parameters are positively or negatively correlated are presented. Statistical analysis was done using JMP software (SAS Institute, Cary, NC).

RESULTS

Effects of temperature, RH, leaf age, cultivar, and light intensity on conidial germination. Conidial germination and germ tube elongation on tomato leaflets were evaluated at 5 to 35°C (at 99% RH) and 7 to 99% RH (at 22°C), with light inten-

Fig. 1. Effects of temperature (A, C, D), relative humidity (B, E, H), and light intensity (C, F, I) on germination (A to C), germ tube length of all conidia (D to F), and of germinated conidia only (G to I) for *Oidium neolycopersici* conidia on leaves of tomato cv. 1402 following 12 h of incubation. Bars represent the standard error (SE) of each mean.

sities of 0 to 5,150 lux, in four tomato cultivars and five leaf locations. The highest rate of germination was observed at 25°C. The rate of germination declined at temperatures below 15°C and between 30 to 35°C (Fig. 1A). With temperature held constant at 22°C, germination was highest at 99% RH and declined as RH decreased, down to no germination at 7% RH (Fig. 1B). Germination declined as light intensity increased and germ tube development was lowest at 1,750 lux (Fig. 1C). Percent germination on leaves of four cultivars was 29.5 to 31.0, while average germ tube lengths calculated for all conidia and for the germinated conidia only were 16.6 to 18.6 and 22.5 to 28.8 µm; the plant cultivar did not significantly affect germination or germ tube elongation. Conidia from leaves adjacent to fruits had lower germination rates and less germ tube growth than those collected from other leaves (Table 2).

Effects of temperature, RH, leaf age, cultivar, and light intensity on appressoria formation. Appressoria were formed at

TABLE 2. Effects of leaf age and leaf position on germination of *Oidium neolycopersici* on tomato (cv. 1402)

Leaf age and position	Germination (%)	Germ tube length (µm)	
		All conidia	Germinated only
Mature	32.3 ab ^z	14.3 ab	44.4 a
Intermediate	38.4 a	16.5 a	43.3 ab
Young	32.7 ab	11.7 b	35.1 abc
Under blossom	29.3 b	10.7 b	34.7 bc
Under fruit	15.0 c	3.8 c	25.6 c

^z Numbers in each column followed by a common letter are not significantly different according to Fisher's protected least significant difference test ($P \leq 0.05$).

all temperatures (5 to 35°C; 99% RH) with maximal formation at 25°C and minimal formation at 35°C (Fig. 2A). A higher rate of appressoria formation was observed at 33 to 99% RH, as compared with 7 to 23% RH (Fig. 2B). Maximal appressoria formation was observed at 1,750 lux light intensity (Fig. 2C). The cultivar affected appressoria formation only on leaves growing under fruit. Leaf age affected the formation of appressoria on two cultivars (i.e., being lower on young leaves of all cultivars) (Table 3). The interaction between cultivar and leaf position significantly affected the formation of appressoria ($P = 0.0178$) (Table 3).

Conidia formation. Conidia were first observed 7 days after inoculation. Maximal conidia production under controlled conditions reached a level of $5.75 \times 10^4/\text{cm}^2$ leaf (Fig. 3). In the greenhouse, it reached a similar level at 16 days after inoculation in spite of the fluctuation in the microclimatic conditions during each day and suboptimal conditions during part of the day (results not shown). Under controlled conditions, more conidia were formed at 20°C, lower RH levels (70%), and higher light intensity (5,150 lux) (Fig. 3). Conidial formation rates per square centimeter of leaf area 16 days after infection on the mature and intermediate-aged leaves of tomato cv. 1402 were $55,240 \pm 17,881$ and $25,480 \pm 4,621$ at 24°C and $13,000 \pm 2,980$ and $9,420 \pm 2,364$ at 27°C, respectively. The temperature effect on conidiation was significant ($P = 0.0044$), whereas neither leaf age (mentioned before) nor cultivar (data not shown) significantly affected conidiation.

Survival of conidia. The viability (ability to induce symptoms on tomato leaves) of conidia that were collected from leaves in the summer and winter was tested. The conidia that were produced and tested during the summer survived 1 month of incubation. The germination of conidia tested during autumn and

Fig. 2. Effects of temperature (A), relative humidity (B), and light intensity (C) on the formation of *Oidium neolycopersici* appressoria (at the tip of germ tubes) on leaves of tomato cv. 1402 after 12 h of incubation. Bars represent the standard error (SE) of each mean.

TABLE 3. Effects of leaf age and position on the formation of *Oidium neolycopersici* appressoria on tomato leaves of different cultivars^y

Leaf age and position	Cultivar				<i>P</i> values for significance of major treatment factors and their combinations		
	662	870	1402	1912	Leaf age	Cultivar	Leaf age × cultivar
					$P = 0.0001$	$P = 0.0727$	$P = 0.0178$
Mature	20.1 ± 2.8 A a ^z	18.4 ± 4.7 AB a	30.6 ± 3.5 A a	16.3 ± 3.4 A a	A	n.s.	n.s.
Intermediate	25.0 ± 4.2 A a	19.7 ± 2.9 AB a	26.3 ± 4.5 AB a	20.6 ± 3.2 A a	A		
Young	12.1 ± 5.1 A a	7.9 ± 3.3 B a	14.7 ± 2.9 B a	13.7 ± 3.0 A a	B		
Under blossom	11.4 ± 3.0 A b	30.6 ± 3.7 A a	19.3 ± 2.3 AB ab	12.4 ± 2.7 A b	AB		
Under fruit	15.0 ± 2.7 A a	15.4 ± 4.9 AB a	22.4 ± 1.9 AB a	24.6 ± 4.6 A a	AB		

^y Conditions were kept at $24 \pm 1^\circ\text{C}$, 5,150 lux, and $70 \pm 3\%$ relative humidity. Results are means ± SE.

^z Treatments in each column followed by a common capital letter and treatments in each row followed by a lowercase letter are not significantly different according to Fisher's protected least significant difference test; n.s. = not significant.

winter drastically declined within the first month of incubation followed by a slower, further decline over 4 months of incubation (Fig. 4A). The growth of the germ tubes of the germinating conidia declined over time. Further incubation resulted in the total loss of viability (Fig. 4B).

Effects of leaf age, temperature, RH, cultivar, and light intensity on disease severity. Disease was more severe on mature leaves than on younger leaves that were infected at the same time (Fig. 5A and B; Table 4). Severity of powdery mildew on tomato plants (AUDPC, % $\times$ days; through 29 days after infection) on cvs. 1125 and 1107, respectively, was 156.2 ± 70.0 and 642.0 ± 24.7 on mature leaves and 64.0 ± 28.6 and 232.8 ± 26 on intermediate-aged leaves. The cultivar effect was insignificant ($P = 0.1561$), whereas the effect of leaf age was significant ($P = 0.0001$), and the interaction of leaf age $\times$ cultivar was insignificant ($P = 0.3817$).

Since a cultivar effect on susceptibility was observed in some cases (Tables 5 to 7), a set of experiments was conducted with four commercial cultivars. Small, yet statistically significant, differences were observed between mature leaves of the different cultivars and between cultivars (when evaluated on a whole plant basis) (Fig. 5B; Table 4). Significant differences in the responses to the different microclimate parameters were observed. We also observed a significant difference between cv. 1125 and cv. 1107 in one of the three sets of experiments (Tables 5 to 7).

In two sets of experiments, plants were incubated at temperatures of 18 to 28°C and later at a narrower range of 20 to 26°C to identify the differential temperature effect more precisely. Disease symptoms did not develop at 28°C. The most severe disease was observed on the plants kept at 22 and 24°C, being significantly higher at the later temperature (Fig. 5C and D; Table 5). Lower disease severity was observed at 99% RH than at RH levels of 70 to 85% (Fig. 5E; Table 6). Disease severity was positively correlated with light intensity (Fig. 5F; Table 7). In most cases, there were no significant differences between cvs. 1107 and 1125. However, cultivar 1107 exhibited significantly lower disease severity at 18°C (Table 5).

Effect of greenhouse climate on disease. Different microclimatic conditions were established in greenhouses in southern Israel by varying the roofing material, front and back door material, soil cover, and humidity source for each greenhouse (Table 1). In the autumn crop, we observed no disease at 7 days after the introduction of inoculum plants to the greenhouses. The first disease was noticed and rated at 10 days after inoculation (DAI) on the lower leaves (Fig. 6A). At 16 DAI, disease was first observed on midlevel leaves in some of the greenhouses (Fig. 6B) and infection was observed on the young leaves in most of the greenhouses only at 44 DAI (Fig. 6C). Disease severity reached more than 60% in greenhouse Y4 and 55% in greenhouses Y7 and

Y8 at 44 DAI (Fig. 6D). Epidemics in greenhouses Y4, Y7, and Y8 were also more severe in terms of AUDPC, whereas the least severe epidemic, in terms of AUDPC values, developed in greenhouse Y5 (Table 8).

The greenhouses that harbored severe epidemics were characterized by medium temperature conditions during the day. The least severe epidemics developed where temperature and RH values were highest (Tables 1 and 8).

In the spring of 2005, epidemics developed before 14 DAI. Lower disease severity on lower leaves during the growing season (Fig. 7), on the whole plant at 57 DAI, and lower AUDPC values (Table 9) were observed in greenhouse Y5 (Table 9; Fig. 7A). This greenhouse was warmer than the others (Table 1). Powdery mildew epidemics were less severe in the second spring crop (2006) than in the first spring crop (2005) (Fig. 7B).

Correlations between the levels of disease severity and microclimates of the greenhouses in the different growing seasons are summarized in Tables 10 and 11. Powdery mildew severity was positively correlated with RH levels of 60 to 90 at 1 to 4 weeks

Fig. 4. Survival of *Oidium neolycopersici* conidia on leaves of tomato plants (cv. 1402) with established disease symptoms. Leaves were incubated for 1 week in the shade, either under summer (25 to 37°C, 45 to 75% relative humidity [RH]) or autumn-winter (10 to 26°C, 57 to 87% RH) conditions, followed by 143 days at $22 \pm 4^\circ\text{C}$ and 45 to 65% RH. Conidia were then transferred onto fresh tomato leaves and their subsequent germination was observed. Bars represent the standard error (SE) of each mean.

Fig. 3. Effects of temperature (A), relative humidity (B), and light intensity (C) on the formation of *Oidium neolycopersici* conidia on leaves of tomato cv. 1402. Infected leaves were first incubated for 5 days at $22 \pm 1^\circ\text{C}$ (70% relative humidity [RH], 5,150 lux) and then transferred to chambers with the different conditions. Bars represent the standard error (SE) of each mean.

before disease evaluation and 50 to 60% RH during the week preceding the evaluation. Disease severity was negatively correlated with the persistence of RH levels of 40% or less at 1 to 4 weeks before evaluation, and with 50 to 60% RH during the third week before evaluation. High RH (90 to 100%) was also negatively correlated with disease severity (Table 10).

Durations of temperatures in the ranges of 5 to 15°C and 35 to 40°C during 1 to 4 weeks before evaluation were negatively correlated with disease severity. Temperatures between 15 and

25°C 1 to 4 weeks before evaluation were positively correlated with disease severity. There was also a positive correlation between disease severity and temperatures up to 35°C in parts of the periods preceding disease evaluation (Table 11).

DISCUSSION

The life cycle of a powdery mildew pathogen, such as *O. neolycopersici*, includes both stages that take place on plant surfaces,

Fig. 5. Powdery mildew severity expressed as leaf coverage of the indicated cultivars grown under different environmental conditions. One group of tomato plants was incubated at 70 ± 3% relative humidity (RH), 24 ± 1°C, and 5,150 lux and disease severity was evaluated on two leaf stages (A) or on mature leaves (B). Other plants were incubated at 18 to 28°C (C) or 20 to 26°C (D) with 70 ± 3% RH and a light intensity of 5,175 lux. Additional groups of plants were incubated at 24 ± 1°C, 70 to 99% RH, and 5,175 lux (E) and 24 ± 1°C, 70 ± 3% RH, and 450 to 5175 lux (F). Disease severity on the whole plants was calculated for the treatments described in panels C-F. Bars represent the standard error (SE) of each mean.

TABLE 4. Severity of powdery mildew (whole tomato plants) on four cultivars grown in a growth chamber^y

Cultivar	Leaf age		P values for significance of major treatment factors and their combinations		
	Mature	Intermediate	Cultivar	Leaf age	Cultivar × leaf age
			P = 0.0037	P = 0.0001	P = 0.0014
662	1,145.5 ± 37.9 bc ^z	775.5 ± 12.5 a	ab	Mature a	
870	1,280.6 ± 47.2 ab	736.5 ± 26.8 a	a	Intermediate b	
1402	1,040.6 ± 36.5 c	738.3 ± 40.3 a	b		
1912	1,378.1 ± 64.6 a	802.5 ± 17.1 a	a		

^y Results are presented as areas under disease progress curves (% × days) through 24 days after infection. Growth chambers were kept at 24 ± 1°C, 5,150 lux, and 70 ± 3% relative humidity. Results are means ± SE.

^z Treatments in each column followed by a common letter are not significantly different according to Fisher's protected least significant difference test.

such as leaves, and a phase that takes place inside the host tissue. In the present work, we studied parameters related to key components of the development of *O. neolycopersici* on tomato leaves and to the development of tomato powdery mildew. The various microclimatic conditions tested may affect the behavior of the pathogen on the plant surface (i.e., conidial germination, germ tube growth, and appressorial formation) during infection, the growth of the fungus within plant tissue, and/or the formation and survival of conidia. Although germination of *O. neolycopersici* was first observed 3 to 5 h after its introduction to the plant surface (18), maximal germination was observed in *O. lycopersici* after 24 h of incubation (9). In the present work, *O. neolycopersici* conidia that were incubated for 24 h germinated over a wide range of microclimatic conditions (5 to 35°C, 23 to 99% RH, and 0 to 5,150 lux) and on leaves from all tested nodes and cultivars (Fig. 1).

Optimal germination of conidia of many powdery mildew pathogens occurs between 15 and 25°C (1,33,40). Optimal germination rates of *S. macularis* (17,28,32) and *L. taurica* (8) conidia have been observed at 20°C. Our findings are similar to those of Fletcher et al. (9), who found that 25°C is the optimal temperature for *O. lycopersici* germination. Our results are also similar to those of Celio and Housbeck's (4) study of poinsettia powdery mildew and those of Guzman-Plazola et al. (11), who worked with another powdery mildew pathogen of tomato (*L. taurica*). Guzman-Plazola et al. (11) reported that temperatures >30°C were deleterious for conidial germination, germ tube elongation, and disease development. A 30°C temperature has also been shown to be too warm for conidial germination and germ tube growth of grape (6) and rose powdery mildews (35). Interestingly,

the optimal germination temperature (25°C) observed in our study corresponds to the conditions that promote strong growth of the tomato host plant. This shows that the pathogen is environmentally adapted to parasitize its host.

The dependence of powdery mildew conidia on external humidity is comparably lower than that of conidia of many other fungi (16). According to Fletcher (9) and Whipps and Budge (37), conidia of *O. lycopersici* germinate well at 65 to 100% RH and best at 95%; similar to the 99% RH optimum reported in the present work. However, we report here that conidial germination is evident at RH levels of 33% and above. Nevertheless, surface condensation inhibits germination (37). Our findings are similar to those reported for the powdery mildew pathogens of poinsettia (4), strawberry (1), tomato (9), and pepper (8,11), for which high RH is associated with higher germination rates and a film of water inhibits germination.

An effect of light intensity on the germination of other powdery mildew pathogens was rarely reported. We report here that light intensity affected germination. Specifically, low light intensity was associated with optimal germination of *O. neolycopersici* (Fig. 1). Similar results were obtained in a study of strawberry powdery mildew (1).

During the process of fruit development, plants direct metabolites to the developing fruits, which act as sinks (16). As obligate parasites, powdery mildew pathogens depend on their hosts for necessary nutrients. In 1957, Horsfall and Dimond (12) categorized powdery mildew-causing fungi as "high sugar" pathogens. Therefore, we expected that the location of the leaf, among other host parameters, would affect conidial germination rates. Indeed, we found that conidia germinated better on leaves located close to developing fruits than on other leaves, but the exact mechanism behind this phenomenon is not clear and must be investigated further. A similar effect of leaf location was mentioned regarding *L. taurica* by Palti (31).

The information currently available on the optimal conditions for appressorial formation and the formation and survival of

TABLE 5. Effect of temperature on the severity of powdery mildew (whole tomato plants) on two cultivars grown in growth chambers^y

Temperature (±1°C)	Cultivar		Temperature (±1°C)	Cultivar 1402
	1125	1107		
18	132.0 ± 19.1	91.9 ± 14.7	20	242.8 ± 9.4
22	511.0 ± 42.8	460.5 ± 19.2	22	496.5 ± 37.2
28	0	0	24	622.4 ± 22.8
			26	512.2 ± 27.5

P values for significance of major treatment factors and their combinations

Temperature	Cultivar	Temp. × cultivar	Temperature
<i>P</i> < 0.0001	<i>P</i> = 0.0638	<i>P</i> = 0.388	<i>P</i> < 0.0001
18 b ^z	1,125 a	n.s.	20 a
22 a	1,107 a		22 b
28 c			24 c
			26 b

^y Results are presented as areas under disease progress curves (AUDPC, % × days) through 29 days after infection. Growth chambers were kept at 5,150 lux and 70 ± 3% relative humidity. Results are means ± SE.

^z Treatments in each column followed by a common letter are not significantly different according to Fisher's protected least significant difference test; n.s. = not significant.

TABLE 7. Effect of light intensity on the severity of powdery mildew (whole tomato plants) on two cultivars grown in growth chambers^z

Light intensity (lux)	Cultivar		<i>P</i> values for significance of major treatment factors and their combinations		
	1125	1107	Light	Cultivar	Light × cultivar
			<i>P</i> = 0.0001	<i>P</i> = 0.0338	<i>P</i> = 0.4331
480	109.9 ± 20.8	98.8 ± 15.4	a	1125 a	n.s.
1,750	235.9 ± 29.9	146.9 ± 26.5	b	1107 b	
5,150	511.7 ± 42.8	460.5 ± 19.2	c		

^z Results are presented as areas under disease progress curves (% × days) through 29 days after infection. Growth chambers were kept at 22 ± 1°C and 70 to 75% relative humidity. Results are means ± SE. Treatments in each column followed by a common letter are not significantly different according to Fisher's protected least significant difference test; n.s. = not significant.

TABLE 6. Effect of relative humidity (RH) on powdery mildew severity (whole tomato plants) on two cultivars grown in growth chambers^y

RH (% ± 3)	Cultivar		<i>P</i> values for significance of major treatment factors and their combinations		
	1125	1107	RH	Cultivar	RH × cultivar
			<i>P</i> = 0.001	<i>P</i> = 0.3598	<i>P</i> = 0.07
70	511.7 ± 42.8	460.5 ± 19.2	a ^z	1,125 a	n.s.
85	394.1 ± 28.9	296.2 ± 91.1	b	1,107 a	
99	104.7 ± 21.1	91.7 ± 24.0	c		

^y Results are presented as areas under disease progress curves (% × days) through 29 days after infection. Growth chambers were kept at 22 ± 1°C and 5,150 lux. Results are means ± SE.

^z Treatments in each column followed by a common letter are not significantly different according to Fisher's protected least significant difference test; n.s. = not significant.

O. neolycopersici conidia is very limited. In this study, we observed the formation of appressoria at a range of temperatures, RH levels, and light intensities, on leaves at several different positions in a number of different cultivars (Fig. 2). Optimal conditions for appressorial formation were 25°C, RH levels of 33 to 99%, and 1,750 lux (Fig. 2). Similar to our findings, it was reported that in the *Oidium* spp. that incites disease in poinsettia, the formation of appressoria was inhibited at 30°C (4). In laboratory tests, the conidia of the mango powdery mildew-causing pathogen, *O. mangiferae*, formed appressoria at 10 to 30°C, with maximum appressorial formation occurring at 25°C and 92% RH (34). Unlike the findings presented here, in a study of *Erysiphe* spp. on rhododendron, it was found that more appressoria formed on plants kept in the dark than on plants kept in the light (21).

Powdery mildews survive and proliferate well under shady conditions, indicating that their conidia are sensitive to direct sunlight and UV radiation (20,40). However, the differences observed between shady and sunny environments may reflect differences in temperature and RH conditions in the different environments. Peries (32) did not observe any effect of RH on conidiation when testing an RH range of 12 to 100% at several temperatures. Elad et al. (8) also reported that the formation of conidia on leaves

infected by *L. taurica* at RH 85/95% (day/night) was not different from the conidiation observed at 60/85% day/night RH. However, in that study, mycelial density was suggested to be the sole discerning parameter, as opposed to conidiation. In comparison, Amsalem et al. (1) reported an effect of RH on conidiation of *S. macularis*. In that study, RH levels of 70 to 85% were conducive to conidiation, while RH above 95% resulted in a significant decrease in the production of conidia (1). In the present work, an effect of microclimatic conditions on conidiation was also observed. The largest amounts of conidia were formed at 16 to 26°C, 70 to 85% RH, and the highest light intensity (5,150 lux) (Fig. 3). These conditions may have affected conidiation by affecting the host, as well as the pathogen. Similarly, Byrne and Hausbeck (3) reported effects of air movement (speed), rain, temperature, RH, and irradiation intensity on the production and release of conidia of *Oidium* spp. on poinsettia in a greenhouse. In the present work, we did not allow for the accumulation of visible condensation on the tomato leaves, but we would expect that the amount of conidia released from powdery mildew conidiophores would decrease in the presence of water (16).

Conidia survived and maintained their ability to germinate for a long period of time when initially incubated at lower temperatures and higher RH, as compared with their rapid decline under more extreme, warm conditions (Fig. 4). Similarly, in a study of *S. macularis*, Amsalem et al. (1) found that conidial survival declined exponentially over time, but a certain percentage of conidia remained active after 5 months of incubation. This finding emphasizes the importance of sanitation during the growing season, to limit the accumulation of inoculum.

The effect of powdery mildew pathogens on their hosts may be mediated by leaf age and position. For example, daughter strawberry runner plants and young leaves have been found to be more susceptible to *S. macularis*-incited powdery mildew than mature plants and leaves (30). Another study also found that *S. macularis* conidial germination and disease severity were both higher on young leaves as compared with older leaves (1). In the present

Fig. 6. Severity of powdery mildew symptoms on tomato (cv. 1402) grown as an autumn crop in commercial-like, walk-in structures covered by various combinations of nets and polyethylene as described in Table 1. Disease was evaluated on leaves at nodes 3 and 4 (A), 7 through 9 (B), and 12 through 14 (C), and calculated for the entire plant (D). Bars represent the standard error (SE) of each mean.

Fig. 7. Severity of powdery mildew symptoms on tomato (cv. 870) grown as early (A) and late (B) spring crops in commercial-like, walk-in structures covered by various combinations of nets and polyethylene as described in Table 1. Disease was evaluated on leaves at nodes 3 and 4. Bars represent the standard error (SE) of each mean.

TABLE 8. Development of powdery mildew epidemics in tomato (cv. 1402) in greenhouses with different microclimates (autumn 2005)

Greenhouse	Disease severity (% × days ± SE) ^z			
	Leaf location (nodes)			Overall disease
	Low (3–4)	Intermediate (7–9)	High (12–14)	
Y1	693.4 ± 75.2	274.2 ± 40.5	22.0 ± 6.8	1,142.3 ± 110.2
Y2	1,810.4 ± 124.8	220.6 ± 34.9	20.6 ± 9.8	752.4 ± 49.5
Y3	902.1 ± 91.4	161.2 ± 26.7	2.8 ± 1.5	358.4 ± 33.3
Y5	260.3 ± 55.3	27.1 ± 7.9	0.0 ± 0.0	20.6 ± 3.8
Y6	277.1 ± 13.2	29.9 ± 3.9	0.0 ± 0.0	105.9 ± 5.8
Y7	2327.1 ± 171.8	847.9 ± 124.7	222.6 ± 55.8	1,191.1 ± 78.9

^z Area under disease progress curve values (Fig. 1) were calculated for leaves at three plant heights and for the total plant.

study, leaf position had some effect on the germination of *O. neolycopersici* conidia and there were slight effects of leaf age and cultivar on appressorial formation. Leaf age did not affect conidial formation. In their review of powdery mildew epidemiology, Jarvis et al. (16) suggested that flower and fruit development affect host susceptibility to powdery mildew infection by changing sink-source relationships. The susceptibility of a host to a powdery mildew appears to be dependent on available carbohydrates and, in certain plant tissues, high concentrations of carbohydrates appear to facilitate disease development (10).

We found that some of the tomato cultivars that we tested were more resistant to disease than others. Differences between cultivars were up to 60% in some cases, but these differences were

mild compared with cultivar differences in a crop like strawberry (1), for which different resistance sources are available. None of the current tomato cultivars are not marketed as being powdery mildew resistant, nevertheless, host resistance to powdery mildew, once found for tomato, could play an important role in management of this disease.

Disease development is the cumulative effect of various parameters on the host and pathogen. In various studies, temperatures allowing for powdery mildew development have been shown to range from 15 to 25°C, with an optimum of approximately 20°C, i.e., in strawberry (1,30) or 22 to 23°C in rose (38,39). Temperatures of 10 and 30°C and above have been shown to be detrimental to the pathogen and disease incidence was significantly reduced under these conditions (1,8,17,32). In our growth chamber experiments, disease did not develop at 28°C (Fig. 4; Table 5), but the pathogen itself was capable of developing at this temperature (Figs. 1 and 2). Disease did not develop at temperatures higher than 30°C in studies of rose or grape powdery mildews either (6,35). It may be speculated that high temperatures affected the tomato host plant, rendering it more resistant to the pathogen (8). These results contrast with those of Douglas (7), who observed tomato powdery mildew development at 10 to 35°C. Nevertheless, inoculum viability is also affected at the high temperatures.

Optimal RH for disease severity ranged from 80 to 85% and a significant reduction was recorded at RH ≥ 95% in strawberry powdery mildew (1). Whipps and Budge (36) found that tomato powdery mildew was greatest at 80% RH and decreased as RH increased, to a minimum level at 95% RH. In another study of tomato powdery mildew, Douglas (7) observed disease develop-

TABLE 9. Development of powdery mildew epidemics on tomato (cv. 870) during spring 2006 in greenhouses with different microclimates

Greenhouse (No.)	AUDPC ^y , total disease severity (% × days ± SE)	
	Crop 1 ^z (57 days after planting)	Crop 2 ^z (45 days after planting)
Y1	2,512.7 ± 355.0	744.0 ± 204.1
Y3	1,187.0 ± 160.8	819.0 ± 190.3
Y4	2,410.3 ± 380.5	984.0 ± 216.3
Y5	391.5 ± 99.1	318.03 ± 92.5
Y7	5,348.8 ± 448.0	1,754.3 ± 276.0
Y8	3,230.8 ± 344.8	1,281.5 ± 207.9

^y Area under disease progress curve (AUDPC) values were calculated for the total plant.

^z Crop 1 was planted on 19 February 2005 and crop 2 was planted on 3 March 2006.

TABLE 10. Correlations of temperatures during the 4-week period before evaluation of the tomato powdery mildew with disease severity in greenhouse experiments

Week before disease evaluation	Temperature range (°C)									
	5–10	10–15	15–20	10–20	20–25	15–25	20–30	25–30	30–35	35–40
1	/	/	0.8827 + ^y ***	/	/	0.9583 + ***	/	0.9519 + ***	/	0.7675 – *
2	0.9679 – *	0.9815 – *	/	0.8085 + *	/	0.9465 + ***	/	/	0.9319 + ***	/
3	0.9622 – *	/	0.9614 + *	0.7526 – *	0.9759 + *	0.9918 + ***	0.9672 + *	0.9425 + ***	/	0.857 – **
4	0.9502 – *	/	0.9523 + *	/	0.9566 + *	0.955 + ***	/	/	0.7923 + *	0.9129 – **

^y (+) = positive correlation, (–) = negative correlation, and / = no significant correlation as obtained using a series of *t* tests.

^z Positive correlation: the higher the microclimate parameter, the more severe the disease. * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.

TABLE 11. Correlations of relative humidity levels during the 4 weeks before evaluation of the tomato powdery mildew with disease severity in greenhouse experiments

Week before disease evaluation	Relative humidity range (%)								
	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
1	/	/	0.9284 – ^y * ^z	/	0.9392 + *	0.9984 + **	/	0.9711 + *	/
2	0.8612 – **	/	0.9511 – *	/	/	0.9411 + *	/	/	0.9713 – **
3	0.8093 – *	/	/	/	0.9396 – *	0.9391 + *	0.9193 + *	/	0.7564 – *
4	0.7520 – *	/	0.9854 – *	/	/	0.9476 + *	0.9532 + *	0.9943 + **	0.9517 + *

^y (+) = positive correlation, (–) = negative correlation, and / = no significant correlation obtained using a series of *t* tests.

^z Positive correlation: the higher the microclimate parameter, the more severe the disease. * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.

ment at RH levels above 50% and reported optimal disease development at RH levels above 90% (with no free water). In contrast to this, within the range of 70 to 99% RH, the disease was less severe at higher RH levels than at lower RH levels (Fig. 4; Table 6). It was also less severe at lower light intensities (Fig. 4), but under these conditions the physiology of the tomato leaf tissue is changed. Therefore, an indirect effect on the host plant should also be considered. In contrast to these findings, the incidence of powdery mildew on apple was reduced with increasing levels of light radiation (5).

The results discussed so far have dealt with experiments conducted under controlled conditions. It is important to validate these findings under commercial growing conditions. Data collected in three experiments conducted in greenhouses similar to those used by local commercial growers, in which various climatic regimes were maintained, were used to draw conclusions regarding the effects of temperature and RH on disease development. Summarizing the significant correlations over the three field experiments, it can be concluded that the severity of powdery mildew is positively correlated with persistence of temperatures in the range of 15 to 25°C and RH levels of 60 to 90%. This is similar to the results from the experiments we conducted under controlled conditions, in growth chambers. Conversely, disease severity was negatively correlated with temperatures between 5 and 15°C, and 35 and 40°C and with the persistence of RH levels of 40% and below and 90 to 100% RH (Tables 10 and 11). The negative correlation between conditions of high temperature and low relative humidity and disease development can be attributed to the effects of these conditions on pathogen activity.

Since powdery mildew in tomato is a polycyclic disease, the period prior to evaluation, in which a certain microclimatic condition was observed, may point to the disease cycle stage that is affected by this parameter. The disease stages may be sequenced from germination and penetration through establishment in the host tissue up to conidiation, corresponding to different time periods before evaluation (i.e., from weeks 3 and 4 to week 1 before evaluation). A different effect was induced by 90 to 100% RH during week 4 than by the same humidity level during weeks 2 and 3 (Table 11), shifting from a positive to a negative correlation with disease severity. This may reflect a change in the disease cycle stage that is affected, for example, a change from the initial stages to the later stages of disease development. A reverse effect was observed at 50 to 60% RH. This humidity level encouraged conidiation and symptom development at the later stages of the disease, but had a negative effect on earlier stages of disease development.

These results are corroborated by the results obtained under controlled conditions (Figs. 1 through 4) and results from a study of *L. taurica* on pepper (8). In contrast to this, high RH levels (80 to 90%) encouraged the germination of *L. taurica* conidia, but continued exposure to these conditions limited lesion growth and disease progress, as described by Guzman-Plazola et al. (11). In their work under controlled conditions, RH had a similar effect on both conidial germination and disease development. That is, low RH levels (20 to 40%) reduced conidial germination and reduced disease progress, whereas intermediate RH levels (50 to 70%) increased germination of conidia and optimized disease development, as long as temperatures were kept within a certain range (11).

The effect of temperature on disease severity observed in our greenhouse experiment was similar to that reported in Douglas's (7) study, and also to those of our own growth chamber studies. Nevertheless, in our greenhouse study, the temperature associated with low disease severity was higher than that associated with low disease severity in our growth chamber experiments (35 and 28°C, respectively). There are several possible explanations for this difference. (i) In the greenhouse, temperatures were measured in the air around the plants, but not directly on the leaves. Within

the range of temperatures above 25°C, the leaf temperature during the day is significantly lower than the surrounding air temperature due to evaporative cooling achieved by the plant's transpiration. In the growth chamber, air movement at a constant temperature results in leaf temperatures similar to the surrounding air temperature. (ii) RH levels in the growth chambers were kept fairly constant ($70 \pm 3\%$), whereas in the greenhouse there was more variation in RH. This variation in RH may have partially compensated for the negative effect of high temperature.

The negative correlation of disease severity with the duration of low RH levels observed in our greenhouse study corresponds to the results of our growth chamber studies, the results reported by Douglas (7), and the fact that minimal disease is generally observed in greenhouses during the hot, dry summers of the western Negev Desert. The lower disease levels observed in the second spring experiment compared with those of the first spring experiment may also be due to high temperatures and low RH, since as the spring season progresses, the temperature increases and the RH decreases. Furthermore, in a fourth experiment carried out during the summer of 2005 (at the same location), no powdery mildew disease was observed on a susceptible cultivar, despite repeated introductions of inoculum-bearing plants into the greenhouses (data not shown), emphasizing the importance of environmental conditions for disease development.

In the present study, various abiotic factors were found to affect different aspects of the tomato powdery mildew disease cycle. Growers' choices of cultivar may also affect epidemic development. Our results show that the conditions that prevail in both unheated and heated greenhouses promote the disease and present a major challenge for growers attempting to control the disease by cultural means. Nevertheless, it is expected that in greenhouses where temperatures are kept high, disease severity will be kept low. Under appropriate climatic conditions, this can be done by closing the side polyethylene walls during the daytime and letting the temperature inside the greenhouse rise up to 28 to 35°C. This idea has also been suggested for the control of powdery mildew in pepper (8) and has been used successfully by some Israeli pepper farmers (Y. Messika, extension agent, Gilat, Israel and Y. Elad, *personal communication*). It should be noted that partial aeration to release humidity is essential in daytime-heated greenhouses, in order to prevent outbreaks of diseases encouraged by high humidity. In tomato greenhouses, additional measures to ensure pollination and fruit set should be taken as these are negatively affected by high temperatures. It is hoped that other diseases of tomato like gray mold and late blight will also be negatively affected by the high temperature treatment.

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