European Journal of Plant Pathology (2006) 114:283–292
DOI 10.1007/s10658-005-5804-6

Effect of climatic factors on powdery mildew caused by *Sphaerotheca macularis* f. sp. *fragariae* on strawberry

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Accepted 5 December 2005

Key words: environmental factors, *Fragaria* × *ananassa*, light, relative humidity, temperature

Abstract

Powdery mildew of strawberry is caused by the obligate pathogenic fungus *Sphaerotheca macularis* f. sp. *fragariae*. The disease affects the leaves, flowers and fruit of this crop. This study examined the effects of different environmental factors on disease cycle components (germination, conidiation and survival) in strawberry to determine which conditions limit the progress of the disease. The optimal environmental conditions for conidial germination and conidial germ tube length ranged between 15 and 25 °C with relative humidity (RH) higher than 75%, but less than 98%. High light intensity reduced germination and hyphal growth. The viability of conidia on infected leaves was examined at temperatures ranging from 15 to 35 °C at 80–85% RH. Conidia survival declined over time, but a certain percentage of conidia remained active after 5 months incubation. The rate of conidial germination was significantly higher on young leaves than on older leaves. This observation was consistent across all four tested cultivars. Conidiation at 70–75% RH was similar to that at 80–85%, but greater than that at ≥95% RH. The shortest time from inoculation to appearance of the first disease symptoms was 4 days, at 20 and 30 °C with RH above 75%. In growth chambers, temperatures of 10 and 30 °C, RH above 95%, radiation of 7000 lux and the use of a more tolerant cultivar were all detrimental to disease development. In general, the environmental conditions required for germination and dispersal of powdery mildew are conducive to disease progress under strawberry production conditions in Israel. Furthermore, viability and survival of the pathogen during and between seasons appears to be dependent on asexual inoculum production.

Introduction

Powdery mildew of strawberry (*Fragaria* × *ananassa*), caused by the obligate parasite *Sphaerotheca macularis* f. sp. *fragariae*, is one of the major fungal diseases of this crop worldwide (Spencer, 1978; Maas, 1998). The pathogen affects leaves, petioles, stolons, flowers and fruit, and appears to be specific to this crop. Serious damage to the foliage results in reduction of photosynthesis due to dense mycelium coverage, which can lead to necrosis and eventual defoliation (Maas, 1998). Yield losses may also be inflicted due to infection of flowers and fruit, organs which are susceptible to infection at all stages of development. Affected flowers may be deformed, produce low levels of

pollen or wilt and die, while infected green fruit fail to ripen and infected ripe fruit remain soft, have a shortened shelf life and possess small seeds (Spencer, 1978).

Conidia of *S. macularis* f. sp. *fragariae* remain viable for a short period of time and require 4–6 h of high relative humidity at approximately 25 °C for germination. Subsequent penetration and colonization of leaf tissue takes place within 24–48 h of germination (Peries, 1962; Jhooty and McKeen, 1965). Miller et al. (2003) showed a direct association between vapour pressure deficit (VPD, mmHg) and necrosis, caused by the pathogen on strawberry leaves. Optimal pathogen development occurred at 25 °C but germination percentages ranged between 6 and 36 °C at 17–27 mmHg VPD (Miller et al., 2003). Similarly, optimal germination rates and germ tube elongation was reported for *S. macularis* f. sp. *fragariae* under conditions of 20 °C, with 96% RH being recorded on the strawberry leaf surface (Jhooty and McKeen, 1965). However, disease incidence was reduced at temperatures of 10 and 30 °C. Peries (1962) also reported optimal disease progress at 20 °C whereas conidiation and infection did not take place below 13 and 5 °C, respectively. Furthermore, conidia remained viable for up to 5 weeks at 0 °C under saturated conditions. However, free moisture was the main factor causing conidial mortality and germination did not take place under these conditions.

Dispersal of *S. macularis* f. sp. *fragariae* conidia is usually windborne; however, free water may disrupt this process (Peries, 1962). Powdery mildews survive and proliferate well under shaded conditions, indicating that the conidia are sensitive to direct sunlight and UV radiation (Yarwood, 1957; Jordan and Richmond, 1972). It has also been reported that the sexual fruiting bodies, cleistothecia, are formed under shaded conditions, a mechanism that may be used by the pathogen when and where these structures are necessary for survival or for over-wintering (Peries, 1962; Maas, 1998).

The choice of cultivar is of utmost importance when considering resistance/susceptibility to powdery mildew in strawberry as losses may reach 50% in certain cultivars (Nelson et al., 1995). Although absolute resistance has not been reported, relative tolerance to the disease among certain cultivars has been reported in California (Nelson et al., 1996). Similarly, the inheritance of mildew resistance has been reported in ever-bearing and day-neutral strawberry seedlings in European cultivars and lines (Simpson, 1987). Leaf and plant phenology can also be an important factor affecting tolerance as reported by Okayama et al. (1995), whereby daughter runner plants and young leaves were more susceptible to disease than mature plants and leaves.

Since strawberry in Israel is cultivated completely under plasticulture, which is conducive to disease, it was of utmost importance to study the environmental conditions that are favourable for disease development in order to formulate a plan for pathogen control. In a related study, at least four powdery mildew populations from strawberry originating from different geographic regions and in Israel were examined for genetic diversity by various molecular tools (ap-PCR, RAPD-PCR and ITS sequence analyses) and these subpopulations were found to be homogeneous (Amsalem et al., 2004). No difference in virulence or disease incidence was detected between the various subpopulations when inoculated on strawberry in individual growth chambers to separate the inoculum (subpopulations) from different sources (pers. comm.).

In this study, we report on the effect of certain environmental factors such as temperature, relative humidity, light regime and cultivar on conidiation, germination, germ tube elongation, pathogen survival and disease severity of *S. macularis* f. sp. *fragariae* on strawberry.

Materials and methods

Pathogen, plants, inoculation procedures and disease severity

Sphaerotheca macularis f. sp. *fragariae* used in this study was obtained from naturally infected leaves (cv. Tamar, susceptible to disease) from a strawberry production field located in the Sharon region of central Israel. The pathogen was cultured and maintained throughout this study on strawberry plants (cv. Tamar) grown in a greenhouse chamber at the Volcani Center, Bet Dagan, at respective day/night temperatures of 22–25 °C (day) and 15–18 °C (night). The plants were cultivated in 13 cm diam pots in a coconut and styrofoam (3:1;

v:v) soil-less medium and were watered every, 1–3 days, according to season.

For all experiments, an artist's paint brush was used to dust inoculum from conidiating lesions onto non-infected leaves. Disease symptoms appeared on leaves 7–10 days after inoculation. Disease severity was rated from 0 to 100% according to mycelium coverage of infected leaves. In some experiments, disease severity was monitored at different time periods and used to calculate the area under the disease progress curve (AUDPC).

Assessment of conidial germination and germ tube length

The effects of various treatments on conidial germination and germ tube elongation were evaluated on detached strawberry leaves (cv. Tamar). Three- to four-week-old leaves were picked on the same day the experiment was conducted. Leaves were placed on saturated sterilized filter paper in Petri dishes and inoculated as described above. Inoculated leaves were incubated at 20 ± 1 °C for 24 h (or as otherwise described). Conidial germination on leaf surfaces was determined according to the method described by Peries (1962), with minor modifications. A piece of 'cellotape' (2 cm×4 cm) was used to remove the conidia and germlings from the leaf surfaces. The recovered conidia and germlings were subsequently stained with lactophenol blue before microscopic observation. Each treatment was replicated four times, 50 conidia were counted per replicate, and these observations were used to calculate a percentage of germinated conidia. These experiments were repeated twice.

Effects of relative humidity, temperature and light regime on germination

Conidial germination and germ tube length were monitored under different levels of relative humidity (RH), temperatures and light regimes. The effect of RH was determined by placing inoculated leaves in Petri dishes (without filter paper or lids), and exposing the dishes to different RH conditions, at a constant temperature of 20 °C. RH levels were manipulated through the use of different saturated salt and sugar solutions, as described by Young (1967). The solutions used were as follows (RH percentage in brackets): NaOH (7%), CH_3COOH (23%), $MgCl_2$ (33%), Glucose (55%), NH_4NO_3 (65%), NaCl (75%), KCl (85%), KNO_3 (94%), K_2SO_4 (97%) and H_2O (100%). The effect of temperature in combination with RH was determined by incubating leaves at 10, 20 and 30 °C. The effect of light was studied under a mixture of cool-white, day-light fluorescent and incandescent lamps (36 fluorescent, 40 W each, and six incandescent lamps spread along 270 cm) by placing inoculated leaves on water saturated filter paper in covered Petri dishes and exposing these dishes to 12 h day/night or 24 h dark (dishes wrapped in aluminum foil), at a constant temperature of 20 °C. The experiments were repeated twice.

Survival of conidia over time

Naturally infected leaves (cv. Tamar) were collected in a field in the Sharon region of central Israel. In order to mimic mild winter commercial cultivation conditions, the leaves were kept in a paper bag in a shaded walk-in greenhouse. Microclimate conditions were recorded hourly with temperatures and RH monitored through the use of computerized Hobo equipment (H8 Pro Series, Onset Computer Corp. Miami, FL, USA). Temperatures ranged between 15 and 30 °C and RH ranged between 55 and 97%, without exposure to rainfall. At each sampling date (14 to 35 days) during a 5-month winter period (mid-November to mid-April), the dried inoculum from leaves was dislodged with an artist's paintbrush over detached fresh leaves in order to transfer the conidia. The inoculated leaves were incubated for 24 h in conditions described above until germination was observed and continuously monitored until percentage declined to zero or to values close to this.

Effect of cultivar and plant phenology on conidial germination and germ tube length

Four leading commercial cultivars (Tamar, Hadas, Gaviota and Mala'ach) with a history of different disease severities claimed by extension specialists and growers alike, and two phenological stages of plants were tested for their effects on conidial germination and germ tube length. Two stages of plant phenology were considered, immature plants

with 3 to 4 leaves and those bearing flowers and fruit. Fully developed leaves, one per plant, were sampled from 10 plants of each cultivar at each phenological stage. Experiments were repeated once. The experiments were conducted in a factorial design with main effects of cultivar and phenology.

Effect of RH on conidiation

Infected plants (cv. Tamar) were incubated in walk-in growth chambers at 20 °C with 12 daylight hours, at three different RH levels. Three different polyethylene coverings provided the different humidity levels. The treatments were as follows: transparent polyethylene covering (RH ≥ 95%), transparent polyethylene covering punctured with 20/m^2 10-cm long holes (RH from 80 to 85%) and transparent polyethylene covering punctured with 50/m^2 10-cm long holes (RH from 70 to 75%). RH was monitored with the computerized Hobo unit which was situated within the plant canopies. Three leaves were sampled from each RH treatment at different time periods. Each sampled leaf was weighed and disease severity was assessed as described previously. Percent disease incidence multiplied by leaf area was used to measure unit infected area in cm^2. Subsequently, the mycelium was brushed from infected leaves into 1 ml volume of water and conidial concentrations were determined using a haemocytometer. The experiment was repeated twice.

Effect of temperature, RH and light intensity on disease severity

All plants used in these experiments were maintained in controlled environment chambers (Conviron, Winnipeg, Manitoba, Canada) with 12 h of daylight. Different RH conditions (at 20 °C) were achieved under transparent polyethylene covering (RH ≥ 95%), transparent polyethylene covering punctured with 20/m^2 10-cm long holes (RH from 80 to 85%) and transparent polyethylene covering punctured with 50/m^2 10-cm long holes (RH from 70 to 75%) and monitored with the computerized Hobo unit which was situated in plant canopies within each of the three chambers. The effect of light intensity was studied under conditions of 20 °C and 70–75% RH. Light intensity was adjusted to 1200, 3800 and 7200 lux according to the distance of plants from a light source on the ceiling of the growth chamber, a mixture of cool-white, day-light fluorescent and incandescent lamps (36 fluorescent, 40 W each, and six incandescent lamps spread along 270 cm). The light intensity at leaf level was measured with a digital lux tester (Y-F-1065, Yu Fing, Taiwan). Each treatment consisted of 10 plants in five replicates. Plants were inoculated with an artist's paintbrush, as previously described, with dry inoculum originally recovered from diseased leaves; the inoculation procedure was repeated four times within 10 min in order to ensure uniformity. Disease symptoms and severity in all treatments and experiments were evaluated every 3–4 days over a 30-day period by sampling 10 leaves, one per plant, at each sampling time. The experiment was repeated twice.

Data analyses

Since the results of repeated experiments were, in general, similar, results of representative experiments are presented. Statistical analyses of data were performed using the JMP-in software, version 3 for Windows (SAS Institute, Cary, NC, USA). Standard errors (SE) of the means were calculated. For some analyses, multiple regressions were employed and these results are presented in the graph legends. Analysis of variance was used to determine the relative influences of the different treatments. One-way analysis of variance was performed to determine the influence of temperature, RH and light on disease severity. Two-way analysis of variance was used to determine the influence of cultivar and plant age on disease severity.

Results

Effects of temperature and relative humidity on germination and germ tube elongation of S. macularis *f. sp.* fragariae

The effects of different temperatures, humidity levels and combinations of these two parameters on germination and conidial germ tube length were evaluated on detached strawberry leaves. A maximum of 15% conidial germination rate was observed at temperatures between 15 and 25 °C with only 1% germination observed at 5 and 35 °C (Figure 1a). Average germ tube length (of

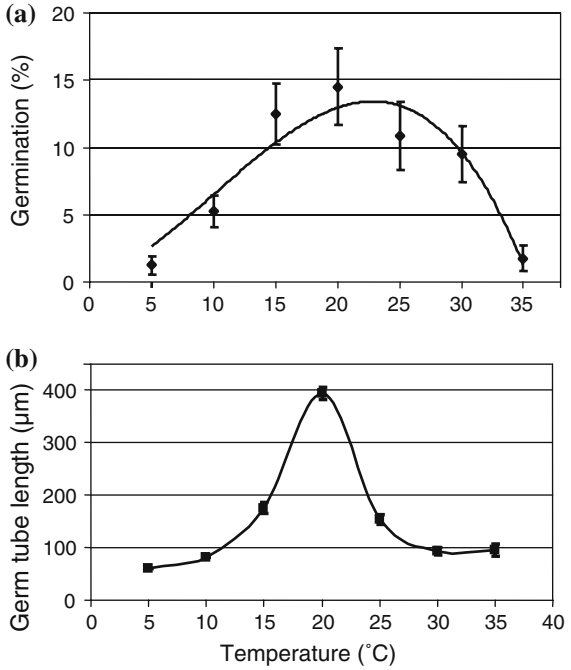

Figure 1. Effect of temperature (10–35 °C) on (a) percent germination and (b) germ tube elongation (μm) of conidia of *Sphaerotheca macularis* f. sp. *fragariae* inoculated on detached leaves of the susceptible strawberry cv. Tamar. Regression equation for percent germination: $y = 0.016x^3 + 0.048x^2 + 0.327x$; $R^2 = 0.9033$. Vertical bars denote standard error of the mean.

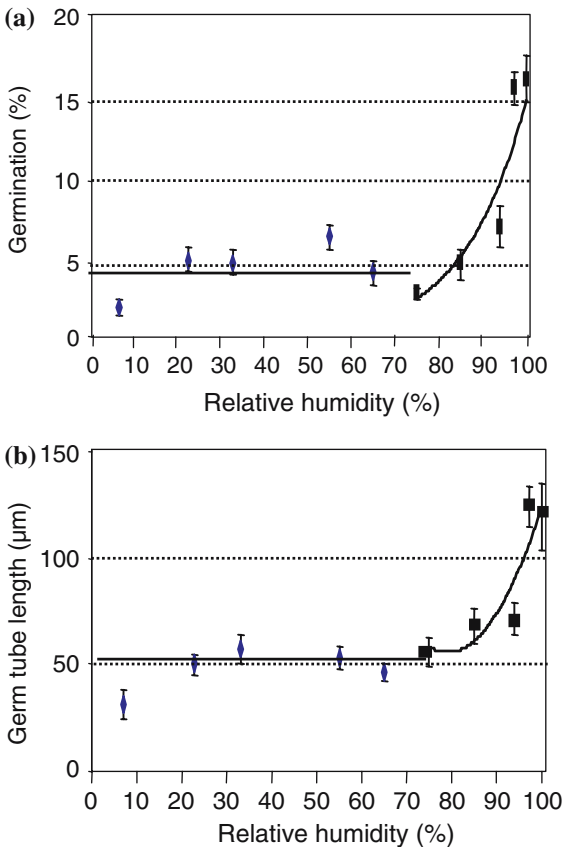

Figure 2. Effect of relative humidity (RH) on (a) percent germination ($y = 0.031e^{7x}$; $R^2 = 0.91$; $P \leq 0.05$), and (b) germ tube elongation (μm) ($y = 1545.1x^2 - 2441.9x + 1020$; $R^2 = 0.82$; $P \leq 0.05$) of conidia of *Sphaerotheca macularis* f. sp. *fragariae* inoculated on detached leaves of the susceptible strawberry cv. Tamar incubated at 20 °C. RH of 33–100% was achieved by using different saturated salt and sugar solutions, according to Young (1967). Regression equations of each graph are presented in brackets and denote the range from 75 to 100% RH. Vertical bars denote standard error of the mean.

germinated conidia) was highest (ca. 400 μm) at 20 °C. Germ tube length decreased at both higher and lower temperatures (Figure 1b).

The effect of relative humidity (at 20 °C) on germination and conidial germ tube length was also evaluated on detached strawberry leaves (Figure 2). An average of 5% conidial germination was recorded at RH levels below 75%, whereas an increase, reaching 17%, occurred between 97 and 100% RH (Figure 2a). A maximum germ tube length of 100 μm was recorded at 97 to 100% RH (Figure 2b).

In the factorial experiment combining three different temperatures (10, 20 and 30 °C) with three different levels of RH (33, 55, 75 and 97%), the main effects of both temperature and RH were significant ($P \leq 0.05$). Within each humidity treatment, germination was greater at 10 and 20 °C (8–10% germination) and decreased significantly ($P \leq 0.05$) to 5% at 30 °C (Figure 3). RH of 97% induced maximal germination of ca. 10%, decreasing with reduction in RH (Figure 3). Similar effects of RH and temperature on germ tube length were also observed (data not shown).

Effect of light regime on germination of conidia

Incubation of conidia on strawberry leaves for a period of 24 h in complete darkness resulted in 14.8% germination, which was significantly higher ($P \leq 0.05$) than that under an alternating 12 h dark/light regime (8.7%). Similarly, germ tube length increased in the dark as compared

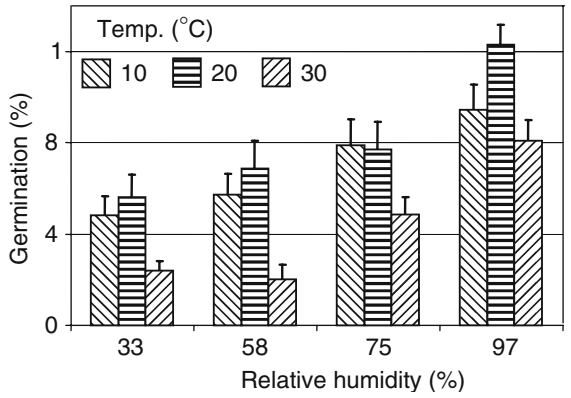

Figure 3. Effect of combined relative humidity (RH) and temperature on percent germination of conidia of *Sphaerotheca macularis* f. sp. *fragariae* inoculated on detached leaves of the susceptible strawberry cv. Tamar. RH ranged from 33 to 97% (at 20 °C) combined with temperatures of 10, 20 and 30 °C. Vertical bars denote standard error of the mean.

to the alternating regime, with mean lengths of 100 and 15 μm, respectively.

Survival of conidia over time

The viability of conidia was examined over a 5-month period. Germination declined over time, from 18% to levels close to zero after 5 months incubation (Figure 4a). A similar decline in germ tube length was observed over time (data not shown). The mean length of the germ tubes of germinated conidia declined from 90 μm after 1 month of incubation to 40 μm after 5 months (Figure 4b).

Effect of cultivar and plant phenological stage on germination

The effects of four cultivars and plant age on conidial germination were evaluated. Four cultivars and two plant ages were tested in a factorial design. The two-way analysis revealed significant ($P \leq 0.05$) effects between the two factors (leaf age and cultivars) in their effects on conidial germination. Leaves of young plants on all cultivars were conducive to germination resulting in 24–32% which was significantly different ($P \leq 0.05$) from germination of approximately 10% on leaves of older plants. Variable results were obtained for germ tube length on the different cultivars (Table 1). When leaves of the same plant were compared for susceptibility to

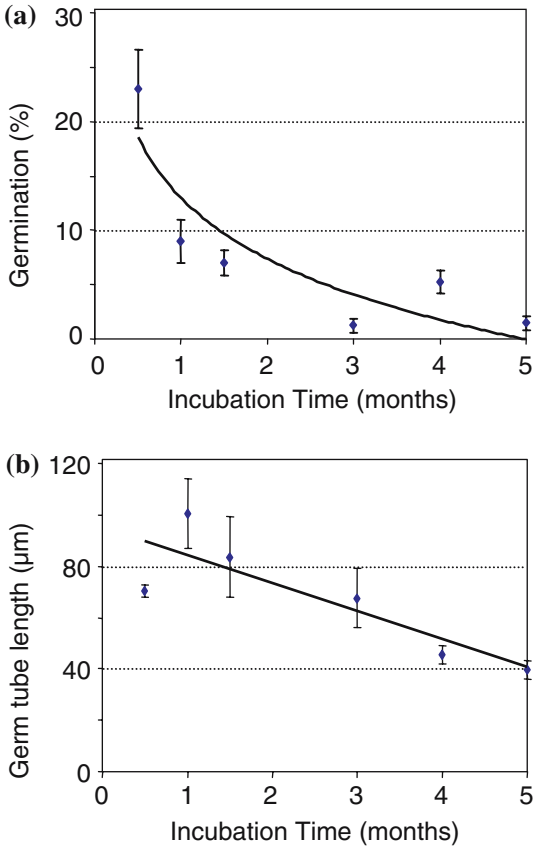

Figure 4. Viability of conidia of *Sphaerotheca macularis* f. sp. *fragariae* over a 5-month period as determined by (a) percent germination ($y = -8.06\ln(x) + 12.95$; $R^2 = 0.8$; $P \leq 0.05$), and (b) germ tube elongation (μm) ($Y = -10.92x + 95.14$; $R^2 = 0.73$; $P \leq 0.05$). Conidia were inoculated on detached leaves of the susceptible strawberry cv. Tamar, incubated in a shaded greenhouse at min/max temperatures (15–30 °C) and 55–97% RH, and sampled periodically. Regression equations of each graph are presented in brackets. Vertical bars denote standard error of the mean.

powdery mildew it was found that younger leaves were more susceptible than older leaves (results not shown).

Effect of RH on conidiation

Infected leaves were incubated at 20 °C at RH levels of 70–75%, 80–85% and ≥95% to examine the effect of RH on conidial production. A significant increase ($P \leq 0.05$) in conidial production was observed at RH levels of 70–75% and 80–85%, compared to that at ≥95% (Figure 5).

Table 1. Germination of *Sphaerotheca macularis* f. sp. *fragariae* conidia on leaves of strawberry plants of four cultivars

Cultivar	Germination (%)		Germ tube length (μm)	
	Young plants	Older plants	Young plants	Older plants
Tamar	23.5b	9.8c	62.5bc	86.5a
Hadas	26.8ab	10.3c	77.3a	82.9ab
Mala'ach	26.9ab	9.9c	75.0ab	73.6abc
Gaviota	32.3a	9.7c	77.5a	50.0c

Numbers in each parameter, followed by a common letter are not significantly different ($P \leq 0.05$).

Effects of temperature, RH and light intensity on disease severity

Artificially inoculated plants were incubated at 10, 20 and 30 °C (RH between 75 and 85%) and symptom development was assessed over a period of 15 days (Figure 6a). At 20 °C, disease symptoms and severity were significantly higher ($P \leq 0.05$) (ca. 40% leaf coverage) than those at both 10 and 30 °C, where very low levels of disease incidence (<5%) were detected.

Likewise, disease incidence was evaluated in artificially inoculated plants incubated at 20 °C under different RHs of 75–80%, 85–90% and ≥95% over a period of 21 days (Figure 6b). Disease severity increased to approximately 55% leaf coverage at 85–90% RH, which was significantly higher ($P \leq 0.05$) than that of ca. 30 and 8% at 75–80% RH and ≥95% RH, respectively.

Three different light intensities (1200, 3800 and 7000 lux) were evaluated for their effect on disease incidence over a period of 28 days (Figure 7).

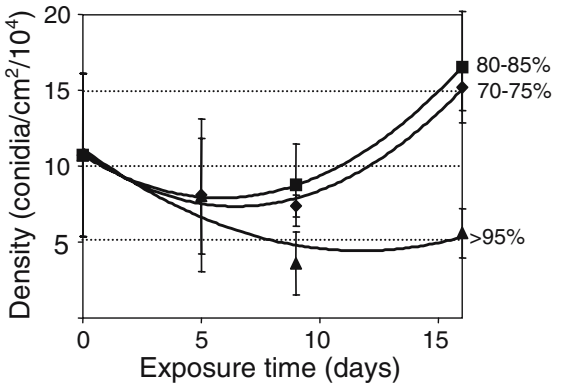

Figure 5. Effect of relative humidity (RH) on conidiation of *Sphaerotheca macularis* f. sp. *fragariae* inoculated on the susceptible strawberry cv. Tamar. Plants were incubated at 20 °C with 12 daylight hours. Leaves were removed periodically and inoculum density was determined per cm^2. Regression equations for each RH value are as follows: 70–75% ($y = 852.7x^2 - 11{,}040x + 109{,}083$; $R^2 = 0.983$; $P \leq 0.01$), 80–85% ($y = 832.5x^2 - 9692x + 107{,}320$; $R^2 = 1$; $P \leq 0.01$) and ≥95% ($y = 488.5x^2 - 11{,}452x + 111{,}519$; $R^2 = 0.875$; $P \leq 0.01$). Vertical bars denote standard error of the mean.

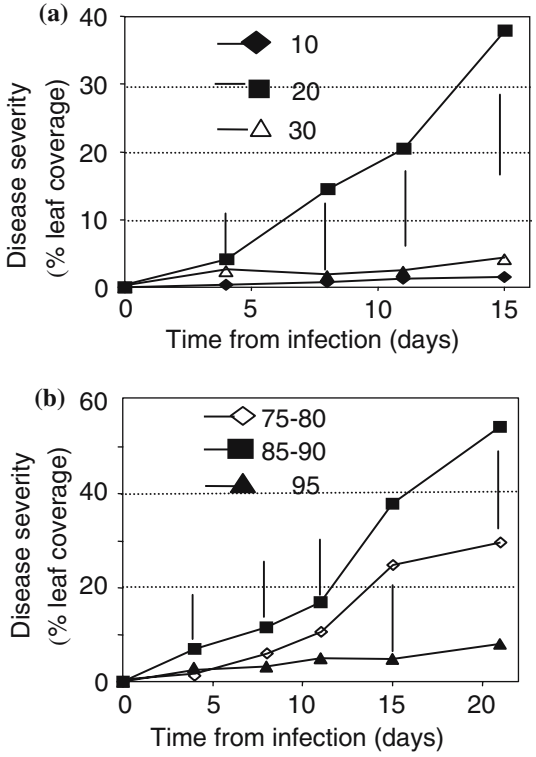

Figure 6. Effect of (a) temperature and (b) relative humidity (RH) on disease severity of *Sphaerotheca macularis* f. sp. *fragariae* inoculated on the susceptible strawberry cv. Tamar. All plants were maintained in controlled environment chambers exposed to 12 daylight hours. Temperatures ranged from 10 to 30 °C (at 75 to 85% RH). RH conditions ranged from 75 to ≥95% (at 20 °C). Disease symptoms and severity were evaluated every 3–4 days over a 15 to 20-day period by sampling five leaves, one per plant, at each sampling time. Vertical bars denote LSD at $P \leq 0.05$.

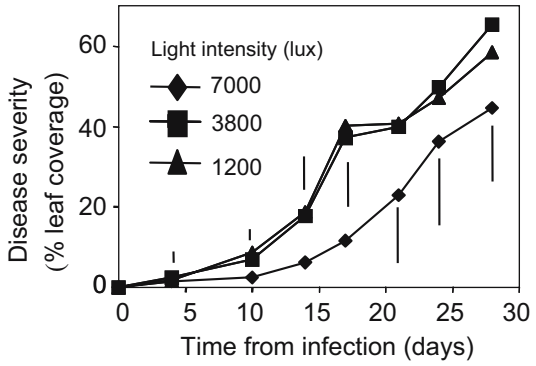

Figure 7. Effect of light intensity on disease severity of *Sphaerotheca macularis* f. sp. *fragariae* inoculated on the susceptible strawberry cv. Tamar. All plants were maintained in controlled environment chambers exposed to 12 daylight hours. Light intensity ranged from 1200 to 7200 lux. Disease symptoms and severity were evaluated every 3–4 days over a 30-day period by sampling five leaves, one per plant, at each sampling time. Vertical bars denote LSD at $P \leq 0.05$.

Significantly lower levels ($P \leq 0.05$) of disease severity were recorded at the highest light intensity of 7000 lux, compared to those at 1200 and 3800 lux, which were very similar and not significantly different ($P > 0.05$) in value (Figure 7).

Latent period

Latent period was measured from initial inoculation to the time secondary conidia were formed in necrotic zones. The shortest time of 4 days was measured at temperatures of 20 and 30 °C with RH above 75% (Figure 6). The longest latent period of 10 days was recorded under conditions of light intensity of 7000 lux (Figure 7).

Discussion

This study was conducted to assess environmental factors that could affect the biology and epidemiology of powdery mildew infections of strawberry. The parameters of temperature, relative humidity, light intensity, cultivar and leaf phenology were found to affect *S. macularis* f. sp. *fragariae* conidial germination, germ tube elongation, conidiation and disease severity.

Germination of conidia of *S. macularis* f. sp. *fragariae*, determined after 24 h incubation, reached 10–15% which was similar to that reported by Peries (1962) and Jhooty and McKeen (1965). However, Miller et al. (2003) reported increased germination of up to 25% after 48 h incubation. These variations may be dependent upon age of conidia, isolate and population variability, and/or interaction between different strawberry cultivars and the pathogen. In this study, conidial germination and germ tube elongation occurred over a wide temperature range (from 5 to 35 °C) with an optimal range of 15 to 25 °C (Figure 1). Similarly, conidial germination rates were highest at 20 °C (Peries, 1962; Jhooty and McKeen, 1965). Germination occurred at temperatures of 4–36 °C, but decreased significantly at both 10 and 30 °C (Figure 1; Miller et al., 2003). This wide range indicates that the pathogen may be able to adapt to varying environmental conditions worldwide.

Percent germination was highest at RH of 97–100%, while a significant increase was observed from 75% (Figure 2). Similar results were reported by Peries (1962). Furthermore, Schnathorst (1965) grouped the powdery mildews into three categories based on percent conidial germination at different RH conditions and associated *S. macularis* f. sp. *fragariae* with those exhibiting highest germination rates at 96–99% RH. The combination of temperature and RH is of paramount importance for conidial germination and germ tube elongation. An RH of 97% combined with temperatures of 10 and 20 °C is optimal for conidial germination (Figure 3). Similar results were recorded by Jhooty and McKeen (1965) whereas at 75% RH, there was less of an effect of temperature on germination (Peries, 1962).

In this study, highest germination rates and germ tube lengths were recorded under complete darkness, whereas Mitchell and McKeen (1970) reported positive phototropism under these conditions. Peries (1962) did not find any effect of light regime on these parameters. Variability may therefore be attributed to the indirect effects of photosynthesis stress, host–pathogen interaction and/or interactions of these factors with the light regime (Jarvis et al., 2002).

A reduction in viability of conidia of *S. macularis* f. sp. *fragariae* was recorded over a 5 month period (Figure 4). At a suboptimal temperature of 0 °C, conidia remained viable for up to 30 days. However, these conidia were unable to survive at higher temperatures due to germination (Peries,

1962; Jhooty and McKeen, 1965). Strawberry is grown all year round in Israel while field nurseries are planted in May and maintained until September producing daughter plants for production fields that in turn are cultivated for berries throughout the winter until June the following year. Powdery mildew is detected on leaves of nursery plants in the summer and in the production fields, mainly in autumn and spring. It should be noted that throughout this study (over a 4 year period), no cleistothecia were observed on leaves or other strawberry plant debris in Israel. This indicates that the survival strategy of powdery mildew on strawberry in Israel from the nursery to field crops and back to the nursery may be dependent solely on asexual propagation, either *via* dormant mycelium or viable conidia. During the cold winter months, for three consecutive winter seasons, we did not observe powdery mildew on leaves but the disease was observed mainly on fruits.

In this study, RH levels of 70–75% and 80–85% were found to be conducive to conidiation 15 days post-inoculation, while RH above 95% resulted in a significant decrease in the production of conidia (Figure 5). In comparison, Peries (1962) did not observe any effect of RH on conidiation when testing an RH range of 12–100%. However, in that study, mycelium density was the sole discerning parameter, which was not based on enumeration of conidial density. Latent period, which was measured from initial inoculation to the time that secondary conidia were formed in necrotic zones, lasted 4 days at 20 and 30 °C with RH above 75% (Figure 6). Previous studies conducted at 15–27 °C, high RH and short daylight conditions documented shorter latent periods of 5–6 days (Peries, 1962).

Disease severity was affected by temperature, RH, light intensity and cultivar. In various studies, temperatures allowing for disease development have been shown to range from 15 to 25 °C, with an optimum of approximately 20 °C (Figure 6a; Okayama et al., 1995). Temperatures of 10 and 30 °C have been shown to be detrimental to the pathogen and disease incidence was significantly reduced under these conditions (Figure 6a; Peries, 1962; Jhooty and McKeen, 1965). Optimal RH for disease severity ranged from 80 to 85% and a significant reduction was recorded at RH ≥ 95% (Figure 6b). Condensation may have occurred on the leaves at RH ≥ 95% which could have affected conidiation. Similarly, Jarvis et al. (2002) reported that free moisture can affect conidial viability.

In this study, radiation of 7000 lux was detrimental to disease progress and disease severity increased as light intensities decreased (Figure 7). Similarly, the disease incidence of powdery mildew of apple was reduced with increasing light radiation (Cimanowski et al., 1975). Different shading techniques have resulted in varying disease responses; under glass and coloured polyethylene, the incidence of disease caused by *S. macularis* f. sp. *fragariae* has been shown to be higher than under clear plastic (Jordan and Richmond, 1972). It has also been shown that shading of plants facilitates selection for powdery mildew resistance in squash (Leibovitch et al., 1996).

Leaf age and cultivar can have great influence on crop tolerance to powdery mildew disease. Susceptibility of a host to powdery mildews appears to be dependent on available carbohydrates and when in excess, in certain plant tissue, facilitates development of disease (Grainger, 1968; Schoeman et al., 1995). Powdery mildew of strawberry can survive on all foliar and fruit tissues, and perennate on green tissue of all ages (Jarvis et al., 2002). An interaction between leaf phenology and cultivar (as examined on detached plant parts) was shown to affect conidial germination. Therefore, conclusions on the effects of individual factors could not be made. Enhanced germination was observed on leaves of younger plants of all cultivars compared with older leaves (Table 1). These results correlate with our findings of higher disease incidence on younger leaves similar to the results reported by Okayama et al. (1995), who observed that stolon-derived daughter plants were more susceptible to infection than mature plants. Field observations revealed that the four tested cultivars differed in their respective susceptibilities to powdery mildew (data not shown), and although complete resistance was not observed, certain cultivars, such as Gaviota, were more resistant than Tamar in terms of germination on leaves of mature plants. Germination on leaves of the four cultivars further demonstrated the association between cultivar and disease incidence (Table 1). Variation to powdery mildew tolerance/resistance exists, as has been shown previously for 47 strawberry cultivars in California (Nelson et al., 1996).

In summary, this study demonstrates that temperature, RH, light intensity, phenology and cultivar can all significantly affect the development of powdery mildew in strawberry. Since powdery mildew is a disease that is routinely controlled with a range of different fungicides, reduction of pesticide applications is crucial for strawberry production worldwide. Therefore applying the knowledge gained in this research for the alternative control of powdery mildew in Israel will certainly have a positive impact on the reduction of chemical usage in this crop.

Acknowledgements

This work is a cooperative research project funded by SafeCrop Center (Fondo per la ricerca, Provincia Autonoma di Trento; No. SCVC1), the Chief Scientist at the Israeli Ministry of Agriculture (Grant No. 132-1104) and the Board of Vegetable growers. The authors thank Ms. Rebecca Bierman for her assistance in editing the English manuscript. Contribution No. 509/05 from the ARO, Institute of Plant Protection.

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