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Spray treatments combined with climate modification for the management of *Leveillula taurica* in sweet pepper

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Abstract The effects of several spray and climate treatments on *Leveillula taurica* were tested under controlled and commercial greenhouse conditions either alone or combined with a climate treatment. *Ampelomyces quisqualis* AQ10 inhibited the germination of conidia on leaves, but not on glass. *Trichoderma harzianum* T39 inhibited germination on both surfaces. Neither the examined biological control agents (BCAs) nor the two tested mineral oils (AddQ and JMS Stylet-Oil) affected the viability of conidia. Sulphur drastically limited the germination and viability of *L. taurica*. In experiments at 15–25°C, AQ10 alone reduced hyphal leaf colonisation at 25°C. *T. harzianum* T39 significantly reduced leaf colonisation at all temperatures but significantly reduced disease only at 20–25°C. The oils significantly reduced leaf colonisation and sulphur reduced both leaf colonisation and disease at all temperatures. Results were confirmed in an experimental greenhouse. In a field experiment, azoxystrobin, polyoxin AL, neem extract, and T39 were effective; sulphur was superior to them. Under severe epidemic conditions the disease had a negative impact on yield; late fungicide treatments at spring-time were found unnecessary. Chemical sprays applied in alternation was compared with the 'friendly' spray regime (alternation of Heliosoufre, *T. harzianum* T39 + JMS Stylet oil, *A. quisqualis* AQ10+AddQ oil and Neemgard) in two climates i.e. (i.) day warm climate and (ii.) regular (cool) day climate regimes. In the warm climate, there was no significant difference in the performance of the 'friendly' spray regime and the chemical spray regime. However, in the cooler climate, the 'friendly' spray programme was not as effective as the chemical spray programme. It was concluded that a change in the greenhouse climate may affect the development of powdery mildew and, at the same time, promote the activity of BCAs and render a pathogen more vulnerable to these control agents, allowing for better disease suppression.

Keywords Biological control · Cultural practices · Integrated disease management · Plant extract

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Introduction

Sweet pepper (*Capsicum anuum*) is an important crop in Israel (2240 ha in greenhouses and net houses) (Elad et al. 2007). Powdery mildew, caused by

Leveillula taurica is a major problem in this crop; it attacks pepper in all cropping regions; farmers treat plants by spraying intensively, sometimes with low control efficacy. In Israel, this disease has been known for several decades. The disease first appears early in the growing season and control becomes increasingly difficult over the course of the season (Elad et al. 2007). *L. taurica* in pepper develops differently than the 'classical' powdery mildew fungi. Part of its life-cycle takes place inside the leaf, while other powdery mildew fungi grow only on the leaf surface, forming haustoria through which they feed on the plant. *L. taurica* conidia germinate and their germ tubes grow on the leaf surface until they encounter a stoma through which they can enter the plant (Kunoh et al. 1979).

Synthetic fungicides and sulphur are used to control powdery mildew in pepper. The current recommendation is for weekly-biweekly applications, beginning very early in the season (Reuveni et al. 1998; Tsror et al. 2003). In recent years, Israeli pepper growers have increased their use of sulphur sprays, which are applied alongside other chemical products. Sulphur may have an adverse side-effect on beneficial insects and therefore other control methods need to be developed. Several control agents, including plant extracts, may induce resistance (Dik and Van der Staay 1995) or otherwise directly affect powdery mildews. Bicarbonates (Fallik et al. 1997; Homma et al. 1980; Pasini et al. 1997; Ziv and Zitter 1992), biological control agents (BCAs) (Askary et al. 1997; Bélanger et al. 1994, 1997; Elad et al. 1996, 1998; Sztejnberg et al. 1989, 1990; Verhaar et al. 1996), and mineral oils (Bélanger et al. 1997; Elad et al. 1998; McGrath and Shishkoff 2000), have all shown potential in controlling powdery mildew, but most of this research has been done in crops other than pepper. Neem seed extract was found to be effective against *L. taurica* in pepper (Dik et al. 1999). A foliar spray of 1% mono-potassium phosphate (KH_2PO_4) on the upper surfaces of lower leaves of greenhouse-grown peppers has been shown to induce local and systemic resistance to *L. taurica* (Reuveni et al. 1974). $NaHCO_3$ controlled powdery mildew by 50–90% compared to an untreated control (Dik et al. 2003). In Brazil, pepper powdery mildew was affected by triadimenol, kresoxim methyl, sodium bicarbonate and cyproconazole (De Souza and Cafe Filho 2003). In Israel, in one experiment, sulphur agents, applied as foliar sprays or greenhouse fumigants, were very effective in controlling the disease and performed better than an aqueous extract from cattle manure compost, Kaligreen (potassium bicarbonate) and Rifol (fish oil). In the second year of that experiment, Neemgard, aqueous extract from grape marc compost, AQ10 (*Ampelomyces quisqualis*), Kaligreen and Rifol all significantly reduced the incidence of disease relative to an untreated control, but, none of these treatments performed as well as sulphur. All of the treatments, especially Neemgard, had yields significantly higher than those of the control (Tsror et al. 2003). Milsana, a formulated extract from *Reynoutria sachalinensis*, was tested against powdery mildew in one tomato cultivar. Results in various experiments with milsana were variable (Malathrakis et al. 2002).

In recent work it was found that *L. taurica* severity was negatively correlated with lengthy periods of temperatures >25°C. Increasing night-time temperatures by heating and day-time temperatures by closing the greenhouse side walls reduced disease in commercial greenhouse experiments (Elad et al. 2007). In this work, we tested potential control agents for powdery mildew of pepper under different climatic conditions and in combination with cultural methods of control such as greenhouse day-time passive heating for optimising disease suppression. A preliminary report of this research was published earlier (Brand et al. 2002).

Materials and methods

Pathogen and host plants

The laboratory and growth chamber experiments required placement of conidia on glass and leaf surfaces. The pathogen *L. taurica* was isolated from young leaves of sweet pepper plants grown in a commercial greenhouse at the Besor Research and Development Station, western Negev, Israel. Conidia of the pathogen were collected by rinsing leaves which exhibited typical symptoms with sterile water. The conidia in the rinse suspension were counted under the light microscope using a haemocytometer. For inoculations of pepper leaves, the concentration of conidia in the suspension was adjusted to 10^6 ml^{-1}. The suspension was sprayed onto plants at a volume

of 2 ml per plant, within 10–15 min after initial collection of the conidia.

Thirty to forty day-old pepper plants cv. Mazurka were obtained from a nursery (Shorashim, Moshav Ein Habesor, Israel). For the laboratory and growth chamber experiments, plants were transplanted into 1 l pots containing peat and vermiculite (1:1) growth mixture supplemented with 50 g 17:20:27 NPK slow-release fertiliser (Osmocot, Scotts-Sierra. Horticulture, Marysville, Ohio, USA). Plants were irrigated every 1–3 days, allowing for 30% drainage. Plants were kept at 20–25°C in a pest-free, disease-free greenhouse for 5–6 weeks prior to the initiation of experiments. Experiments were initiated when plants had reached the 5-node growth stage.

Control agents

The following products were used in our experiments: AQ10 (*A. quisqualis*, 10^9 conidia g^{-1}, WG), Ecogen Inc., PA, USA; Trichodex (*Trichoderma harzianum* T39, 10^9 conidia g^{-1}, P), Makhteshim Chemical Works, Beer Sheva, Israel; AddQ oil (96.5% mineral oil), Ecogen Inc., PA, USA; JMS Stylet-Oil (97.1% mineral oil), Flower Farms Inc., FL, USA; Heliosoufre S (Heliosulphur, 700 g l^{-1} Sulphur, FC), Action Pin, Castets, France; Neemgard (97% neem seed extract), Certis Columbia, MD, USA; Kaligreen (82% potassium bicarbonate, WP), Otsuka Chemicals Co. Ltd., Japan; Triton X-100 (990 g l^{-1} octyl phenyl polyether alcohol) Agan Cemicals, Ashdod, Israel; Polar (50% Polyoxin AL, FG), Kaken Pharmaceutical Co., Japan; Biofilm (997 g l^{-1} fatty acids glycol esters, CL), Colloidal Products, CA, USA; Amistar (250 g l^{-1} azoxystrobin, FC), Syngenta, UK; Dorado (480 g l^{-1} pyrifenox, CE), Aventis CropScience, Lyon, France; Sistan (125 g l^{-1} myclobutanil, CE), Dow Agrosciences LLC, Indianapolis, Indiana, USA. The rates of the different agents used in the experiments are detailed in each experiment below. Plants were sprayed with a hand sprayer in controlled condition experiments and with a Echo Kioritz DM-9 backpack motor sprayer (Tokyo, Japan) in the field experiment.

Effects of spray treatments on the viability of conidia and germination

For testing the effects of the spray treatments on the viability of conidia, the treatments were sprayed on glass slides, which were then left to dry for 1 h on the bench-top. The treatments (product concentration in brackets) were Heliosoufre (1%), *T. harzianum* T39 (0.4% Trichodex), JMS Stylet-Oil (1.0%), *A. quisqualis* (0.004% AQ10) or AddQ oil (0.3%); water served as the control. Conidia were then sprayed on the slides, as described above, and their viability was tested following 10 h incubation at 22±1°C, 85±3% relative humidity (RH) and 5150 lux light intensity. For the viability tests, the conidia were washed off of the slides with water and glucose was added to the rinse solution at a concentration of 200 mg glucose ml^{-1}. The suspension was then centrifuged for 5 min at 10,000 rpm. The conidia were then re-suspended in a solution of 200 mg glucose ml^{-1} with 160 μl of 10 μM Na-HEPES buffer, 10 mg ml^{-1} calcofluor in water and 40 μl of 1% FUN1 solution. The FUN1 solution consisted of 10 mM 2-chloro-4-(2,3-dihydro-3-methyl-{benzo-1,3-thiazol-2-yl}-methylidene)-1-phenylquinolinium iodide (Molecular Probes, Eugene, OR, USA) Na-HEPES and was kept in the dark. The suspensions were agitated at 50 rpm at 28°C in the dark for 90 min. Drops of the conidial suspensions were placed on glass slides and observed under the fluorescent microscope (480 nm). Live (respirating) conidia emit red radiation while dead conidia emit green-yellow radiation with no red dots (Millard et al. 1997). There were five slide replicates for each treatment. Three-hundred conidia were evaluated in each replicate.

For the germination experiments, conidia were spread on glass slides or on detached leaves whose petioles were placed in test tubes filled with water. The tested agents (product concentration in brackets) were *T. harzianum* T39 (0.04 and 0.4% Trichodex), JMS Stylet-Oil (0.3%), *A. quisqualis* (0.004% AQ10) or AddQ oil (0.3%); water served as the control. Control agents were sprayed onto the leaves and the treated leaves were then left to dry for 1 h. Conidia were then applied at the rate of c. 10^3 cm^{-2} by agitating symptom-bearing leaves above the treated leaves. The inoculated leaves were then incubated for 12 h at 22±1°C, 85±3% RH and 5150 lux light intensity. Leaf samples (2×6 cm) were cut and placed on glass slides and drops of lacto-glycerin (lactic acid, glycerin, water (1:1:1 v:v:v) were placed on them. Subsequent conidial germination was observed using a light microscope. The lengths of the germ tubes and the percentage of germination were observed in ten leaf replicates with 50 conidia counted in each leaf. Cumulative germ tube

length was calculated for 100 conidia by multiplying percent germination by the germ tube length.

Hyphal colonisation inside leaf tissues was evaluated in leaves harvested from plants treated once, as mentioned above, by *T. harzianum* T39 (0.4% Trichodex), JMS Stylet-Oil (0.3%), *A. quisqualis* (0.004% AQ10) or AddQ oil (0.3%); water served as the control. The leaves were bleached in order to allow for the visualisation of hyphae. Sampled leaves were washed with tap water to remove dust and aerial detached pathogen thallus, and then submerged in a discolouration solution of formalin, acetic acid and ethanol (1:1:1 v:v:v, FAA) for 72 h at 50°C. The bleached leaves were then incubated in lacto-glycerin for 24 h at 50°C. Two 2×3 cm samples were taken from each of 10 leaf replicates, from each of five treated plants in each treatment, placed on glass slides and observed under the light microscope. All germination and colonisation experiments were repeated twice. Results of one representative experiment are presented.

Growth chamber experiments

The effects of control agents on powdery mildew development were tested on pepper plants in growth chambers (Conviron Products, Winnipeg, Canada). The agents (product concentration in brackets) *T. harzianum* T39 (0.4% Trichodex), JMS Stylet-Oil (1.0%), *A. quisqualis* (0.004% AQ10) or AddQ oil (0.3%) were sprayed on a bi-weekly basis; water served as the control. Three temperature treatments were set up in the growth chambers (15, 20 and 25°C). The RH in all three chambers was between 80 and 90%. All temperature × spray treatments received the same lighting. The growth chamber lights were turned on at 06:00 h and they increased in intensity in four steps until 09:00 h. The light declined in intensity from 16:00 h until it was completely turned off at 19:00 h. Temperature and RH were recorded hourly with a data logger (Hobo, Onset Computer Corp., Pocasset, MA, USA). Five groups of four plants each served as replicates in the growth chamber and the experiment was repeated twice. Results of a typical experiment are presented.

Experimental greenhouse

Preliminary field experiments were carried out in a 3.5 m high, polypropylene experimental greenhouse in central Israel. Day-time conditions were 20–28°C with 30–50% RH and night-time conditions were 10–15°C with 85–90% RH. Plants were grown in 10 l pots filled with sand, peat and vermiculite mixture (1:1:1 v:v) and fertilised as described above. Plants were hooked to a wire to allow growth to 2 m. A hand sprayer was used to apply control agents once every 2 weeks. Control agents (product concentration in brackets) were *A. quisqualis* (0.004% AQ10), AddQ oil (0.3%), *T. harzianum* T39 (0.4% Trichodex), JMS Stylet-Oil (1.0%) and Heliosoufre (1.0%); water served as the control. *L. taurica* conidia were dispersed in the greenhouse by shaking infected leaves at the beginning of the experiments. There were five replicates of five plants each.

Commercial greenhouses

For field experiments, 1–5 sweet pepper plants were planted between 1st and 5th September each year in sandy soil. The plants were grown to one stem and then attached to a rope hanging from the ceiling. The first bloom was removed as soon as it appeared. The plants were managed in accordance with local, commercial practices. Applications of 0.05% Vertimec (abamectin 18 g l^{-1} EC, Syngenta) were sprayed twice each season for the control of European red mite (*Panonychus ulmi*; Acari: Tetranychidae) and broad mite (*Polyphagotarsonemus latus*; Acari: Tarsonemidae). Once a year, there was also an application of 0.04% Tracer (spinosad 240 g l^{-1} SC, Dow Agrochemicals) for the control of Western flower thrips (*Frankliniella occidentalis*; Thysanoptera: Thripidae). Plants were sprayed with a back-carried motor sprayer (Echo DM-9).

Two types of polyethylene covered greenhouses were used at the Besor R&D Research Station located in the western Negev. (i.) One large 1000 m^2 structure that consisted of 12 bays. Three rows of plants were planted along each bay. A forced-air heater was placed along the southern wall of this greenhouse. The warm air was moved around the greenhouse by perforated polyethylene sleeves which carried the warm air along the gaps between every second row. The heating was turned on in mid-November of each year when night-time temperatures began to fall below 15°C. (ii.) Small greenhouse units (250 m^2) were each planted with six 18 m-long rows. An irradiative heating system, in the form of pipes carrying warm water around each row, was used

when night-warming of these greenhouses was necessary.

Powdery mildew infection occurred naturally every growth season. No fungicides were applied during the season, except for the experimental treatments. The first signs of the disease in the greenhouses usually appeared during October of each year. Disease progress was usually evaluated every 2–3 weeks, unless otherwise mentioned. There were 20 plants in each plot, unless otherwise specified, and ten centrally located plants in each plot were examined for disease severity.

Microclimate measurements

Air and leaf temperatures and RH values were recorded hourly using data-loggers (Campbell Scientific Inc., Logan, Utah, USA) with thermocouple and RH sensors. Dew presence and vapour pressure deficit (VPD) were deducted from these data.

Disease evaluation

In all experiments, leaves of sampled plants at different heights were evaluated for the percentage coverage with powdery mildew symptoms. The severity (percent) of leaf coverage (LC) in each plot was calculated by averaging the severity values at different plant heights over the ten sampled plants in each plot. The number of shed leaves (NSL) per plot was counted at each evaluation time and the fallen leaves were then removed. Total disease severity (TDS) was calculated as TDS = NSL/NLP×100 + (1-NSL/NLP) × LC, where NLP = number of leaves remaining on the plant. This formula was originally developed by Shtienberg and Dreishpoun (1991). Fruits were picked every 2 weeks, sorted (A = export quality, B = local market quality, C = distortions), counted and weighed.

Control of *L. taurica* under commercial greenhouse conditions

Effect of control agents on pepper powdery mildew (Field experiment 1, 1998-1999) Plots of pepper cv. Mazurka were planted in the large greenhouse. Day-time conditions were 16–32°C with 25–65% RH and night-time conditions were 13–19°C minima with 85–95% RH. Spray treatments were arranged in a randomised block design, with five replicates of each treatment. Treatments were applied using a backpack sprayer. The treatments (product concentration in brackets) were (1.) Untreated control; (2.) Kaligreen (0.1%) + Triton X-100 (0.025%); (3.) Neemgard (1.0%); (4.) Heliosoufre (1.0%); (5.) AQ10 (0.03%) + AddQ (0.3%); (6.) Trichodex (0.4%) + JMS Stylet-Oil (0.5%); (7.) Amistar (0.05%); (8.) Polar (0.25%) + Biofilm (0.05%). Treatments were sprayed once each week from 20.10.98 until 11.1.99. Disease severity at the beginning of the experiment was 0.01% LC. The effects of pepper powdery mildew on crop yield over the entire season were evaluated. The yields of the different treatment plots were compared with those of the control plots. In order to evaluate the specific effects of Heliosoufre over an extended time period, Heliosoufre was applied until mid-April 1999 every 2 weeks and disease levels and yields of those plots were compared with those of control plots which were also maintained until mid-April.

Effects of climate, cultivar and spray treatments on powdery mildew (Field experiment 2, 1999–2000) Plants of cvs Mazurka and Turkal were planted in five bays of the large greenhouse. Plants of each cultivar were planted in each bay. There were four climate regimes, characterised by different day/night temperatures. Night heating began 97 days after planting to reach the night-time minima of 13 (five west greenhouse bays) and 20°C (five east greenhouse bays); these two major treatment areas were separated by a transparent polyethylene film. Climate measurements during the growth season showed a difference in the day-time temperatures between the northern and southern halves of the greenhouse according to which high- and low-day temperatures were 19–32°C and 15–27°C, respectively. Thus the four climate regions created were: (1.) High day/min. night—13°C; (2.) low day/min. night—13°C; (3.) high day/min. night—20°C; (4.) low day/min. night—20°C.

Seven spray treatments were applied to each cultivar in each climate, for a total of 56 treatments. The spray treatments (product concentration in brackets) were applied weekly from 40–150 days after planting, as follows: (1.) Untreated control; (2.) Heliosoufre (1.0%); (3.) AQ10 (0.03%) + AddQ (0.3%); (4.) Trichodex (0.4%) + JMS Stylet-Oil (0.5%); (5.) Neemgard (1.0%); (6.) alternation of 'friendly' treatments 2 through to 5; (7.) alternation of Sistan (0.1%)/

Amistar (0.05%)/Polar (0.025%)/Heliosoufre (1.0%)/Neemgard (1.0%)/Dorado (0.025%). A split-plot design was used with a randomised block design, with four replicates of each spray treatment in each one of the four climate regions and cultivars.

The effects of foliar-applied fungicides on the development of powdery mildew in the spring (Field experiment 3, 2000) Pepper plots treated with control agents during field experiment 2, were assigned to three different groups according to their respective levels of TDS (i.e. high, medium and low). A fourth group consisted of the control plots of experiment 2. There were 4–18 plots in each of the treatments with initial disease severities of low, medium and high, each located in the west side (low night minimum) or east side of the greenhouse (high night minimum). Plots allocated to each of the severity levels were either assigned to fungicide treatment or not treated during the period of spring 2000 experiment 2. In this experiment, we did not distinguish between the two cultivars since we saw no difference in disease severity (P=0.231) between them in experiment 2. Plots were located in a randomised manner in the greenhouse. Half of the plots of each of the six (climate × disease level) treatments were sprayed with Heliosoufre (1%) three times between 180–270 days after planting. The other half of the plots was not sprayed. The control plots from field experiment 2 were also left untreated during this field experiment.

The combined effects of climate and spray regimes on powdery mildew

Field experiment 4, 2000–2001 This experiment was carried out in the small greenhouses with pepper cv. Selika. We used a split-plot design with climate as the primary factor and spray treatment as the secondary factor. Each of the spray treatments was applied in each of the climate treatments in randomised plot locations. The experiment was replicated in four different greenhouses. Two climates were maintained in each of the four greenhouses with no significant gradient across the greenhouse, as follows: (1.) Warm climate: day-time temperatures of 25–32°C were maintained by rolling down the side polyethylene walls during the day and a night-time temperature of 18°C was ensured by heating during the cold season (January through to March). (2.) Cool climate: day-time temperatures of 15–25°C were maintained by opening the side walls during the day and night-time heating was used from January through to March in order to maintain a night-time temperature of 15°C. The bi-weekly spray treatments (product concentration in brackets) in each of the climates were (1.) Untreated control; (2.) 'friendly' spray regime: alternation of Heliosoufre (1.0%), Trichodex (0.4%) + JMS Stylet-Oil (0.5%), AQ10 0.03%) + AddQ (0.3%) and Neemgard (1.0%); (3.) Chemical spray regime: alternation of Heliosoufre (1.0%) + Dorado (0.025%), Heliosoufre (1.0%) + Polar (0.25), Heliosoufre (1.0%) + Sistan (0.1%) and Heliosoufre (1.0%) + Amistar (0.05%).

Field experiment 5, 2001–2002 This experiment was carried out in the small greenhouses. This experiment included a climate factor (one greenhouse = one climate replicate, four replicates each climate), a spray treatment factor and a cultivar factor. Each of the spray treatments was applied in each of the climates and each of the cvs Cubi and Selika, six randomised replicates, each. Two climates were maintained as follows: (1.) warm day/cool night climate: day-time temperatures of 25–30°C were maintained by rolling down the side polyethylene walls during the day and a night-time temperature of 13°C was maintained by heating during the cold season of January through to March 120–210 days after planting; (2.) cool day/warm night climate: day-time temperatures were maintained at 15–25°C by opening the polyethylene side walls during the day and a night-time temperature of 16°C was maintained by heating the greenhouse from 120–210 days after planting. The bi-weekly spray treatments in all greenhouses were (1.) untreated control; (2.) 'friendly' spray regime: alternation of Heliosoufre, Trichodex + JMS Stylet oil, AQ10 + AddQ oil and Neemgard in rates as mentioned for experiment 4; (3.) Chemical spray regime: alternation of Heliosoufre, Dorado, Polar, Sistan and Amistar in rates as mentioned for experiment 4. Grey mould (*Botrytis cinerea*) incidence was evaluated by counting dead plants from the disease.

Statistical analysis

Experiments under controlled conditions were repeated twice and results of a representative experiment were presented when the experimental factor was not found significant ($P \geq 0.05$). Powdery mildew severity (LC)

was averaged per plant and then per plot. Leaf shedding was counted per plot and related to a single plant. Total disease severity (TDS) was calculated in percentage as detailed above. Data in percentages were arcsin-transformed before analysis. Progress curves were drawn and in some cases the area under the disease progress curve (AUDPC) or area under progress curve (AUPC) were calculated (Fry 1978)). Data were analysed using ANOVA and Fisher's protected LSD tests. Treatment means were compared using Fisher's protected LSD test. One-way analysis of variance was performed to determine the treatment effect in most of the experiments and two-way analysis of variance was used to determine the effect of coupled treatment combinations in field experiment 2. Least significant differences (LSD) are marked in figures using bars. Standard errors (SE) of the mean yields in field experiment 1 were calculated. Statistical analyses were performed using JMP software (SAS Institute, Cary, NC, USA).

Results

Effects of spray treatments on the germination and viability of *L. taurica* conidia

Conidial germination and the cumulative germ tube length on glass were both inhibited by all of the spray treatments, except for the low rate of Trichodex (*T. harzianum* T39) and AQ10 (*A. quisqualis*). Germination and cumulative germ tube length on leaves were reduced by all treatments, except for *T. harzianum* T39 at the lower rate. Germ tube elongation was not affected by any of the BCAs. Sulphur was superior to all control agents in inhibiting germination and germ tube elongation (Table 1).

The viability of *L. taurica* conidia was tested following a 10 h incubation period on glass slides with Heliosoufre (1.0%), *T. harzianum* T39 (0.4% Trichodex), JMS Stylet-Oil (1.0%), *A. quisqualis* (0.004% AQ10) or AddQ oil (0.3%). Seventy percent of the conidia, treated with water only, remained viable. None of the conidia treated with sulphur survived. None of the other treatments affected the viability of conidia differently from the water control treatment.

Effect of temperature on the efficacy of spray treatments

The BCA, mineral oil and sulphur treatments were applied to pepper plants artificially inoculated with *L. taurica* and incubated in growth chambers for 78 days at temperatures of 15, 20 and 25°C and 85% RH. LC and the growth of hyphae inside the leaves were expressed as AUDPC values (Fig. 1). Although AQ10

Table 1 Germination of *Leveillula taurica* conidia on glass and sweet pepper leaves pre-treated with biocontrol agents, oils, their combinations and sulphur

Control agent and product concentration (%)			Test on glass			Test on leaves		
			Germination (%)	Germ tube length (μm)	Cumulative germ tube length (μm/100 conidia)	Germination (%)	Germ tube length (μm)	Cumulative germ tube length (μm/100 conidia)
1	Water control	–	50.1 a[a]	36.5 a	1828.6 a	40.1 a	38.6 ab	1547.9 a
2	*Ampelomyces quisqualis* AQ10	0.004	48.2 a	37.1 a	1788.2 a	15.8 bc	44.1 a	696.8 bc
3	AddQ oil	0.3	20.3 cd	20.2 b	410.1 c	16.1 bc	25.1 c	404.1 bcd
4	2+3		16.8 cd	21.0 b	352.8 c	16.5 bc	31.1 abc	513.1 bc
5	Trichodex (*Trichoderma harzianum* T39)	0.04	42.2 ab	35.1 a	1481.2 a	41.2 a	34.2 abc	1409.0 a
6	Trichodex	0.4	28.4 bc	33.2 a	942.9 b	20.1 b	32.1 abc	645.2 b
7	JMS Stylet-Oil	0.3	15.2 cd	18.9 b	287.3 c	15.2 c	28.1 bc	427.1 bc
8	5+7		5.6 de	19.2 b	107.5 c	9.5 cd	24.5 c	232.7 bcd
9	6+7		9.1 de	19.1 b	173.8 c	7.9 d	29.9 bc	236.2 bcd
10	Heliosoufre	1.0	0 e	0 c	0 c	0 e	0 d	0 d

[a] Numbers in each column followed by a common letter are not significantly different according to Fisher's protected LSD test ($P \leq 0.05$).

A. quisqualis significantly reduced the accumulation of hyphal biomass inside the leaf tissue at temperatures 20–25°C, it did not significantly affect the development of symptoms at 15–25°C. AddQ significantly suppressed the disease, with and without the *A. quisqualis* AQ10 preparation. All agents were effective at 25°C (Fig. 1a, b). Trichodex (*T. harzianum* T39), reduced hyphal growth inside the tissue at 15–25°C but disease suppression was observed only at 20–25°C. JMS Stylet-Oil, applied alone or with Trichodex, was effective at all tested temperatures (Fig. 1c, d). Sulphur effectively suppressed the accumulation of hyphal biomass and disease symptoms at all temperature levels. In most cases, this control was better than that provided by the BCAs alone (Fig. 1a–d).

Control of pepper powdery mildew by BCAs and oils

Experimental greenhouse conditions Control agents were tested in an experimental greenhouse in order to evaluate their potential for *L. taurica* control. LC reached 64, 52 and 25% coverage on leaves of the lower, middle and upper levels of the plants and 47% on whole plants at 130 days after planting (Fig. 2a–b). All agents (1. *A. quisqualis* AQ10 (0.004%) 2. AddQ oil (0.3%); 3. 1+2; 4. Trichodex (0.4%) *T. harzianum*;

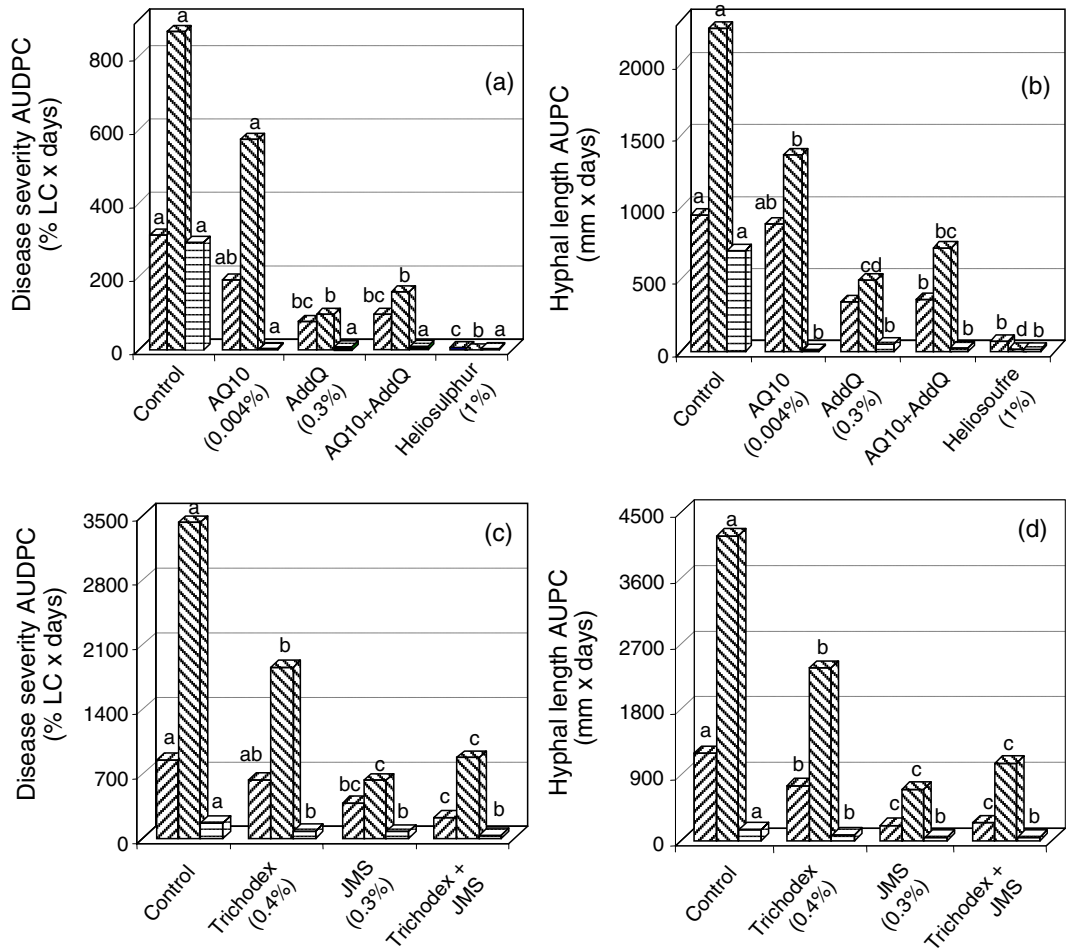

Fig. 1 Powdery mildew of sweet pepper (cv. Mazurka) described as AUDPC, and hyphal colonisation of leaves described as area under the progress curve (AUPC), each through to 78 days after inoculation. Severity of disease on leaves (LC) (**a**,**c**) and total length of hyphae inside the tissue (**b**,**d**). These results were derived from two different sets of experiments: (**a**) and (**b**) vs. (**c**) and (**d**). Plants were treated with the control agents, artificially inoculated and then incubated in growth chambers at 15 ( ), 20 ( ) and 25°C ( ). Columns of each treatment in each graph bearing a common letter at their top are not significantly different according to Fisher's protected LSD test ($P \leq 0.05$)

5. JMS Stylet-Oil (0.3%); 6. 4+5; and 7. Heliosoufre (1%) suppressed the disease on leaves at the three plant heights, except for Trichodex which did not control the disease on the younger leaves (Table 2). The two BCAs, the two oils and their combinations significantly reduced LC over the whole plant (Table 2). Most of the agents (except for *T. harzianum* alone) significantly reduced the number of shed leaves (Fig. 2b). For each BCA × oil combination, the oils were significantly more effective than the microorganisms and the disease control provided by the combinations was not any better than that provided by the oils alone (Table 2).

Control of L. taurica under commercial greenhouse conditions (Field experiment 1, 1998–1989) The effects of the foliar-applied different treatments on the progress of the epidemic in cv. Mazurka for 150 days are described in Fig. 3a–c and Table 3. A severe powdery mildew infection developed on leaves in the untreated control treatment, reaching 95% LC severity at 105 days after planting (Fig. 3a). Plants began to shed leaves at 75 days after planting and, by 150 days after planting, leaf shed levels reached >60 leaves/plant (Fig. 3b). TDS scores remained >90% until 150 days after planting (results not shown). The sulphur treatment provided significantly better control than the other treatments. The effects of polyoxin AL, neem extract, azoxystrobin and *T. harzianum* T39 + JMS Stylet-Oil were not significantly different from each other and all of these treatments provided significant disease control (between 40 and 80%). Disease levels in the potassium bicarbonate and *A. quisqualis* AQ10 + AddQ treatments were not significantly different from those of the control (Fig. 3a–b, Table 3).

After the last of the foliar applications, when plants had 19–20 nodes, leaves at the 14th and 15th nodes were sampled and the viability of powdery mildew thallus recovered from those leaves was evaluated. Leaf coverage and *L. taurica* thallus viability on the untreated lower leaves were 94 and 82%, respectively. Leaf coverage and thallus viability scores were reduced by all of the treatments, except for potassium bicarbonate and *A. quisqualis* AQ10 + Add Q. Coverage of the untreated upper leaf surface was 23.3% and the same trend of control was observed (Table 3).

In order to study the effect of powdery mildew on yield accumulation, we compared the yields and disease levels of the untreated plots with those of the Heliosoufre plots (Fig. 3c, Table 4). For this experiment, Heliosoufre was applied until 235 days after planting, so that it would be possible to evaluate its effect on disease and yield over the entire growing season. A decline in TDS was observed in the control plots from 150 days after planting, from 92% down to 40%, 235 days after planting. In the Heliosoufre plots, TDS levels did not exceed 18%. Up to 44–59% increase in total yield and export quality yield, respectively, were observed in the Heliosoufre treatments compared to the untreated control. Significant increase in export quality fruits was obtained at all sampling dates (Table 4).

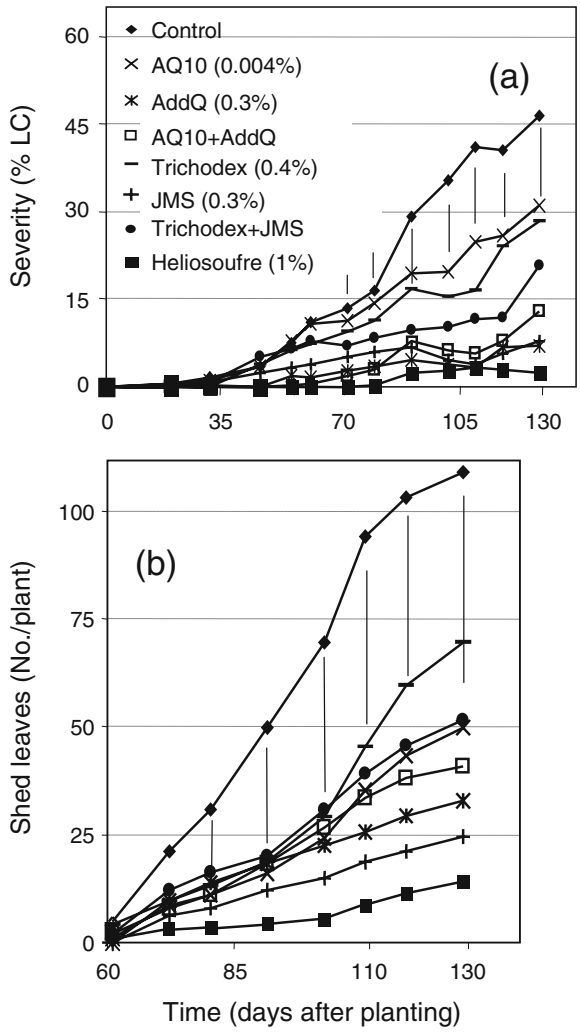

Fig. 2 Powdery mildew of sweet pepper (cv. Mazurka) grown in an experimental greenhouse. Disease severity on leaves (LC) in the whole plant (**a**), and the number of shed leaves (**b**). Bars represent the least significant differences (at $P \leq 0.05$) for each date

Table 2 Powdery mildew on sweet pepper (cv. Mazurka) grown in an experimental greenhouse

Treatment and product concentration (%)			Leaf level (node)			
			General	1–3	6–8	11–13
1	Water control	–	2103 a[a]	2920 a	2436 a	963 a
2	*Ampelomyces quisqualis* AQ10	0.004	1468 b	2077 b	1584 b	750 b
3	AddQ oil	0.3	305 e	435 cd	354 de	127 b
4	2+3		392 e	492 cd	506 de	177 b
5	Trichodex (*Trichoderma harzianum* T39)	0.4	1207 bc	1826 b	1174 bc	623 a
6	JMS Stylet-oil	0.3	449 de	733 cd	467 de	148 b
9	5+6		854 cd	1004 c	847 cd	713 a
10	Heliosoufre	1.0	114 e	186 d	132 e	24 b

[a] Numbers in each column followed by a common letter are not significantly different according to Fisher's protected LSD test ($P \leq 0.05$). Severity of disease leaf coverage (LC) by *L. taurica* symptoms on lower, middle and upper leaves and calculated whole plant disease severity (LC). Results are presented as area under the disease progress curves (AUDPC, %×days), as described in Fig. 2

Combined effects of climate, cultivar and spray regimes on powdery mildew (Field experiment 2, 1999–2000) The potential powdery mildew suppression effect of spray treatments under different climatic conditions and with different pepper cultivars was tested. In this experiment we used the pepper cvs Mazurka and Turkal. Since the results from the two cultivars were similar ($P \geq 0.7213$), only the results with cv. Mazurka are described (Fig. 4). Only two climates are presented in these graphs—low and high night-time minima carried out in the lower day climate regions. Leaf coverage in the low night-time treatment reached 9% 67 days after planting, increased to 55% 122 days after planting and declined after February, when new leaves developed (Fig. 4a, b). Leaf shedding began 85–105 days after planting and reached 31 and 22 leaves plant^{-1} in the most severely infected control plots of the high and low night-time climates, respectively (Fig.

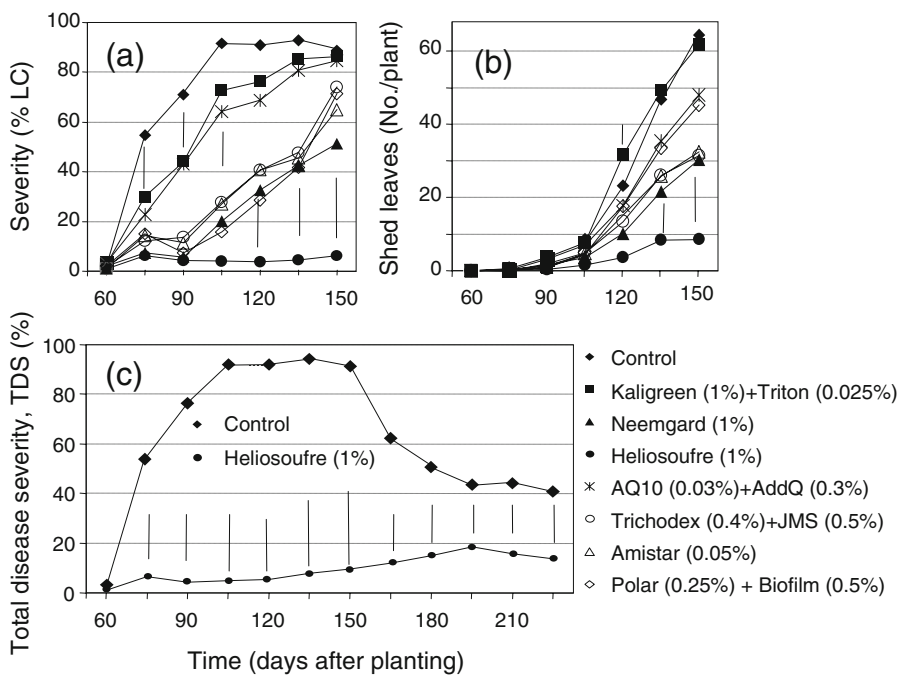

Fig. 3 Effects of spray treatments applied through to 150 days after planting (**a**–**b**) and of sulphur applied over the whole growing season (**c**) on sweet pepper powdery mildew under commercial greenhouse conditions. Severity of disease on leaves (LC) (**a**), incidence of leaf shedding (NSL) (**b**) and total disease severity (TDS) (**c**) (Field experiment 1, 1998–1989). Bars represent the least significant differences (at $P \leq 0.05$) for each date

Table 3 Effects of spray treatments on sweet pepper powdery mildew (field experiment 1), AUDPC as described in Fig. 3, leaf coverage (LC) and thallus viability at 150 days after planting

Treatment and product concentration (%)		AUDPC through to 150 days after planting			Leaf coverage and thallus viability at 150 days after planting			
		Leaf cover (% coverage × days)	Leaves shed (No/plant × days)	Total disease (% severity × days)	Upper leaf surface		Lower leaf surface	
					Coverage (%)	Viability (%)	Coverage (%)	Viability (%)
Control		6725 a[a]	1719 a	6865 a	93.6 a	82.1 a	23.3 a	78.9 a
Kaligreen (potassium bicarbonate) + Triton X-100	0.1+0.025	5314 ab	1854 a	5573 ab	89.5 a	78.7 a	12.6 a	54.7 b
Ampelomyces quisqualis AQ10 + AddQ oil	0.03+0.3	4885 b	1309 b	5086 b	84.4 a	71.9 a	12.0 a	52.1 b
Amistar (azoxystrobin)	0.05	2592 c	947 b	2897 c	49.1 b	28.7c	1.1 c	0 c
Trichodex (*Trichoderma harzianum* T39) + JMS Stylet-Oil	0.4+0.5	2719 c	932 b	2963 c	52.7 b	32.2 bc	1.5 c	0 c
Polar (polyoxin AL) + biofilm	0.25+0.05	2193 c	1202 b	2518 c	35.2 c	28.2 c	0.6 c	0 c
Neemgard (neem extract)	1.0	2041 c	786 bc	2272 c	47.0 b	26.1 c	1.4 c	0 c
Heliosoufre	1.0	406 d	276 c	517 d	10.9 d	21.7 c	0.5 c	0 c

[a] Numbers in each column followed by a common letter are not significantly different according to Fisher's protected LSD test ($P \leq 0.05$).

4c, d). Total disease peaked at 50% in plots of the low night-time temperatures (results not shown).

AUDPC values for leaf coverage, leaf shed and TDS for the different cultivar, climate and spray treatment levels are listed in Table 5. The spray × cultivar, spray × night temperature, cultivar × night temperature and cultivar × sub-climate (combinations of day- and night-time temperatures) interactions were not significant. Therefore, the effects of the main treatments could be analysed. A significant interaction was found between the sub-climate and spray treatments.

Unlike earlier results (data not shown here, see Elad et al. 2007), no cultivar effect was noticed, except for one evaluation of leaf coverage. Night-time temperature significantly affected the disease leaf coverage and shedding. LC was 24–59% more severe in the plots with night-time lows of 13°C than in those with night-time lows of 20°C. Similarly, the plots with the lower day-time temperatures had levels of LC which were 23–67% lower than those of the plots with the higher day-time temperatures. Spray treatments decreased LC severity. Sulphur and the

Table 4 Accumulated sweet pepper yields in sulphur-treated and untreated plots in the spring (field experiment 1)

	Yield (kg 1000 m^{-2} ± SE)								
	Days after planting								
	205			235			270		
Treatment	Overall	Grade A	Grade B	Overall	Grade A	Grade B	Overall	Grade A	Grade B
Control	2835±259	2393±239	441±040	3817±329	3312±342	506±036	7009±161	5913±172	1099±050
Heliosoufre (1.0%)	4087±502	3806±394	282±114	4902±391	4484±272	418±120	7514±413	6468±193	1046±231
Yield increase by treatment (%)[a]	44	59	36	N.S.[b]	9.4	N.S.	N.S.	N.S.	N.S.

[a] Percent yield increase in the sulphur treatment compared with the control treatment. Only significant increases were calculated.

[b] N.S. = Yield difference between control and treatment not significant according to Fisher's test ($P \leq 0.05$).

standard chemical treatments were the most effective. Neemgard and Trichodex + JMS oil were less effective than the other treatments.

When the leaf coverage was at its peak 120 days after planting, we sampled leaves from nodes 10 through to 12. The LC data and the fungal thallus viability data are described in Table 6. Heliosoufre and the standard chemical alternation were the most effective treatments for reducing powdery mildew leaf coverage and thallus viability. The 'friendly' spray programme resulted in a similar reduction in thallus viability in the warmer night environment in the Mazurka plants and in both climate treatments in the Turkal plants. The 'friendly' spray programme was less effective than the chemical programme in reducing the appearance of symptoms in Mazurka in both climates and in Turkal at the higher night-time temperatures. In all cases, the efficacy of the BCA preparations AQ10 + AddQ and Trichodex + JMS oil was similar to that of Neemgard and inferior to that of Heliosoufre. On the Mazurka plants, the BCAs were more effective at the warmer night-time temperatures. On the Turkal plants, the temperature treatments did not affect the performance of the BCAs (Table 6).

Yields (results not shown) of the control plots with the cooler night-time temperatures were lower than those of the control plots with the warmer night-time temperatures. In the low night temperature treatments, yields were higher at the lower day temperature. The plots that received the spray treatments had higher yields of grade A fruit and this effect was greater in the cooler day temperature treatments than in the warmer day temperature treatments.

The effects of foliar-applied fungicides on the spring-time development of powdery mildew (Field experiment 3, 2000) After a build-up of powdery mildew in the first half of the growth season (autumn) it usually

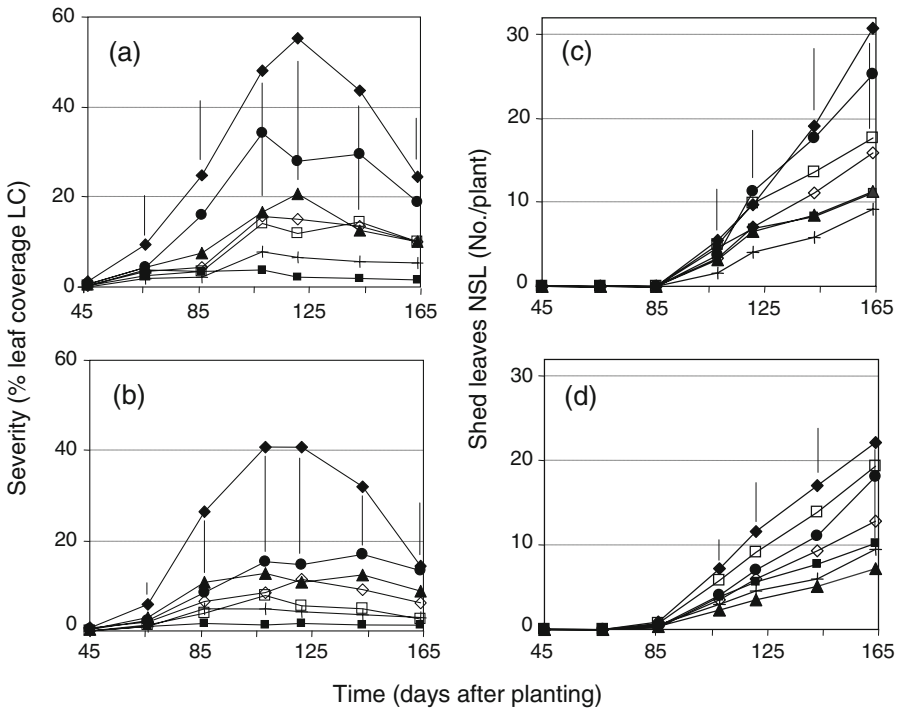

Fig. 4 Effects of spray treatments (agents applied alone or as part of larger alternation schemes) on powdery mildew of sweet pepper (cv. Mazurka) in a commercial greenhouse under conditions of lower (13°C) (**a**,**c**) and higher (20°C) (**b**,**d**) night-time low temperatures. Severity of leaf infection (LC) (**a**,**b**) and incidence of leaf shedding (NSL) (**c**,**d**). Treatments and product concentrations were water control (♦); Neemgard, 1% (▲); Heliosoufre, 1% (■); *Ampelomyces quisqualis* AQ10, 0.03% + AddQ oil, 0.3% (□); Trichodex (*Trichoderma harzianum* T39), 0.4% + JMS Styley-oil, 0.5% (●); alternation of Amistar, 0.05%/ Sistan 0.1%/ Polar 0.25%/ Heliosoufre 0.1%/ Neemgard 0/1%/ Dorado 0.025% (+); and alternation of Trichodex, 0.4%/ Heliosoufre, 0.1%/ Neemgard, 0/1%/ AQ10 0.03% (◊). Bars represent the least significant differences (at $P \leq 0.05$) for each date

slows down during winter and further develops during spring time. In order to evaluate the effect of late season spray application on the late developing powdery mildew, the plots from experiment 2 were kept for a continuing experiment (experiment 3) in which they were placed into three groups according to their levels of disease severity at the end of experiment 2. Within each of these three groups (low, medium and high disease severity), half of the plots were sprayed with Heliosoufre and half were left untreated. In the plots that, during winter, were assigned to the higher night-time temperature, the increase in disease severity was not so pronounced and disease levels were kept low by the Heliosoufre treatments (results not shown). The spring results of the previously assigned low night-time temperature are presented in Fig. 5. Powdery mildew levels in the untreated plots declined during the spring and then increased again by the last sampling day (300 days after planting) (Fig. 5a–c, left). In the low night temperature plots of the medium and high disease level groups, the severity of powdery mildew on leaves declined until 250 days after planting. Significant increases of LC were only seen in the untreated plots at the last scoring date (300 days after planting) (Fig. 5a). Intensive leaf shedding occurred in the high disease level plots and leaf shedding was significantly suppressed by Heliosoufre from 200–300 days after planting (Fig. 5b). At the last rating date (300 days after planting), the total disease severity scores of the medium and high disease plots were significantly higher in those plots that had not been treated (Fig. 5c).

The combined effects of climate and spray treatments on powdery mildew

The purpose of the experiment (field experiment 4, 2000–2001) was to test the efficacy of two spraying programmes under the two climate regimes, i.e. warm days or cool days. The climate treatment was applied after the initial establishment of the disease in all greenhouses. At this stage, the disease severity was c. 20% LC in all greenhouses. Once the climate regimes were in place, we noticed a difference in the development of disease. The warmer plots had less severe disease. In the warm climate treatment, LC reached 30% and TDS reached 33%. At the same time in the cool climate, we saw 88% LC and 91% TDS (Fig. 6). In the cool climate greenhouses, the chemical spray programme was more effective than the 'friendly' spray programme. However, in the warmer greenhouses, there was no significant difference between the two programmes (Fig. 6). The number of flowers per plant was affected by both the climate regime and the spray scheme. In the warmer climate, there were similar amounts of flowers in the two spray treatments (3.4–3.8 and 5.4–5.8 flowers/plant, 145 and 174 days after planting, respectively) and these amounts were significantly higher than those of the untreated control (2.7 and 4.1 flowers/plant, 145 and 174 days after planting, respectively). In the cooler climate, the 'friendly' spraying scheme was inferior in flower numbers (0.9 and 1.5 flowers/plant, 145 and 174 days after planting, respectively) to the full chemical treatment (1.8 and 2.3 flowers/plant, 145 and 174 days after planting, respectively) but there were still more flowers on these plants than on the untreated control plants (0.2 and 0.8 flowers/plant, 145 and 174 days after planting, respectively).

The winter sweet pepper crop is harvested in waves. The first wave is characterised by high numbers of fruits picked in December and January and originate from the flowers of nodes 3 through to 8. After the first wave, the flowers of nodes 9 and 10 are aborted and the flowers of nodes 11 and 12 produce fruit in a second wave in March. Fewer fruits are harvested in this second wave. The flowers of the third wave begin to develop in March, from nodes 13 through to 17. This third wave is harvested during May and June and is characterised by high numbers of fruits. We compared the yields of the treatments in the warm temperature climate regime at the different harvest times (Table 7). Yields in the cooler climate were significantly lower and, within the cooler environment, the differences between the spray treatments were not significant (results not shown).

All of the spray treatments resulted in major yield increases, with no significant differences between the treatments. The majority of this yield increase came between February and March (second wave). For the first part of the first wave and the last part of the third wave, there were no significant yield differences between treatments (Table 7).

The effect of greenhouse climate on the efficacy of two spraying programmes in powdery mildew suppression was tested in a final experiment (field experiment 5, 2001–2002). The disease was more severe in the cool

Table 5 AUDPC values for powdery mildew severity of leaf coverage (LC), leaf shedding (NSL) and total disease severity (TDS) over the course of the epidemic in field experiment 2

Treatments		Days after planting and disease parameters											
		132			154			173			193		
		LC	NSL	TDS	LC	NSL	TDS	LC	NSL	TDS	LC	NSL	TDS
Cultivar	Mazurka	955	308	1071	1257	693	1474	1444	1319	1817	1622	1974	2172
	Turkal	723	287	819	1011	643	1193	1209	1327	1530	1444	1743	1897
	LSD	181	26	381	212	54	112	362	154	331	246	250	243
Microclimate-night	13°C (west)	985	329	1087	1337	745	1543	1577	1504	1954	1884	1869	2420
minimum	20°C (east)	693	266	802	932	591	1124	1076	1142	1392	1183	1848	1650
	LSD	71	16	81	92	34	112	122	54	131	146	150	143
Sub- microclimate (Night/day temp.)	a min night 13°C/high day	829	296	929	1165	683	1362	1387	1327	1736	1675	2174	2212
	b min night 13°C/low day	1140	362	1245	1508	807	1723	1768	1688	2172	2093	1565	2628
	c min night 20°C/high day	357	198	452	464	515	641	561	781	826	621	1607	1023
	d min night 20°C/low day	1030	334	1153	1398	667	1606	1592	1504	1959	1744	2100	2278
	LSD	114	23	114	159	48	159	185	77	185	206	214	202
Day microclimate (temp.)	High (south)	593	247	690	815	599	1001	974	1054	1281	1148	1891	1618
	Low (north)	1085	348	1199	1453	737	1663	1680	1596	2066	1919	1833	2453
	LSD	111	19	112	121	43	157	142	108	217	193	132	143
Spray treatment	Control	2377	405	2477	3162	1041	3369	3609	1991	4010	4094	2919	4710
	Heliosoufre 1.0%	191	255	305	230	498	430	262	966	581	320	1460	771
	AQ10 0.03%	453	216	535	656	437	806	809	857	1058	986	1208	1340
	Trichodex 0.4%	1119	341	1233	1559	810	1778	1825	1604	2221	2094	2037	2658
	Neemgard 1.0%	819	369	968	1127	849	1399	1306	1604	1759	1480	1985	2100
	'Friendly' agents - alternation	606	278	709	806	643	1009	976	1378	1334	1131	2079	1670
	Standard alternation	308	190	386	398	399	543	503	882	751	627	1344	997
	LSD	151	31	148	201	64	210	225	101	245	272	280	267
P values for significance of major treatment factors and their combinations.													
Cultivar		0.1283	0.3082	0.0831	0.0461	0.3733	0.0312	0.2097	0.9193	0.1276	0.3919	0.2903	0.1795
Microclimate-night minimum		0.0136	0.0023	0.0108	0.0132	0.0089	0.0154	0.0091	<0.0001	0.0037	0.0012	0.9300	0.0003
Sub microclimate		0.0002	0.0206	0.0001	0.0001	0.0001	<0.0001	0.0005	<0.0001	0.0001	0.0006	0.0398	0.0001
Day temperature		0.0097	0.0024	0.0079	0.0065	0.0075	0.0111	0.0032	<0.0001	0.0022	<0.0001	0.8999	0.0002
Spray treatment		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0011	<0.0001
Cultivar × Spray treatment		0.9599	0.7430	0.9545	0.9025	0.7881	0.9052	0.9829	0.0318	0.9578	0.9951	0.8313	0.9831
Microclimate-night minimum × Spray		0.9063	0.2228	0.8830	0.9311	0.2902	0.9316	0.8623	0.3296	0.7864	0.7411	0.0030	0.5592
Sub microclimate × Spray		0.0158	0.7862	0.0188	0.0188	0.6550	0.0197	0.0421	0.2614	0.0471	0.0462	0.7232	0.0327
Microclimate-night minimum × Cultivar		0.6239	0.5544	0.7623	0.5794	0.5635	0.6093	0.8105	0.1927	0.9193	0.9809	0.9846	0.8866
Sub microclimate × Cultivar		0.9599	0.2658	0.6957	0.5794	0.9046	0.6093	0.6526	0.0990	0.7688	0.5969	0.6491	0.6519

Table 6 *Leveillula taurica* leaf coverage and thallus viability in plants of two cultivars in two minimal night temperature environments at 120 days after planting (field experiment 2)

Treatment; control agents and their concentrations		Cultivar							
		Mazurka				Turkal			
		Minimum night-time temperatures							
		13°C		20°C		13°C		20°C	
		Leaf coverage (%)	Thallus viability (%)	Leaf coverage (%)	Thallus viability (%)	Leaf coverage (%)	Thallus viability (%)	Leaf coverage (%)	Thallus viability (%)
1	Control	83 a[a]	65 a	84 a	61 a	83 a	29 a	81 a	39 a
2	Heliosoufre (1.0%)	18 c	7 d	8 c	2 e	15 d	7 c	9 d	3 e
3	Ampelomyces quisqualis AQ10 (0.03 %)	60 b A[b]	28 c A	35 b B	17 c A	51 b A	13 bc A	22 c B	9 de A
4	Trichodex (*Trichoderma harzianum* T39) 0.4%	52 b A	36 bc A	39 b B	21 c B	39 bc A	12 bc A	42 b A	18 cd A
5	Neemgard (Neem extract) 1.0%	52 b A	39 b A	37 b B	28 bc A	38 bc A	18 ab A	29 c A	29 bc A
6	'Friendly' agents—alternation[c]	58 b A	23 c A	24 b B	13 cd A	31 c A	11 bc A	29 c A	12 d A
7	Chemical alternation[d]	23 c	10 d	11 c	11 de	10 d	4 c	20 cd	9 de

[a] Numbers in each column followed by the same lower case letter are not significantly different according to Fisher's protected LSD test $P \leq 0.05$.

[b] Two larger means comparisons tests were performed on the leaf coverage data from all dates and the viability data from all dates, within each of the two cultivars. Values in each parameter (viability or coverage) in each cultivar, followed by a common capital letter are not significantly different according to Fisher's protected LSD test $P \leq 0.05$. No indication of significance was made when all paired comparisons in certain rows were found to be insignificant.

[c] Alternation of treatments 2 through to 5.

[d] Alternation of Sistan (0.1%) (myclobutanil)/Amistar (0.05%)/Polar (0.025%)/Heliosoufre (1.0%)/Neemgard (1.0%)/Dorado (0.025%).

day-warm night climate than in the warm day-cool night climate. For instance, in cv. Selika plants, disease severity reached 60–70% LC in the cool day/warm night climate as opposed to 25–40% LC severity in the warm day/cool night climate. The warm day-cool night greenhouses were characterised by long periods of high RH. Also, Botrytis grey mould appeared in those greenhouses, resulting in 15–50% mortality. Powdery mildew results are summarised as AUDPC values (Table 8). Both spraying programmes effectively controlled powdery mildew in both the warm day/cool night greenhouses and the cool day/warm night greenhouses, in both cultivars. The chemical spray scheme was superior to the 'friendly' spray scheme in cv. Selika in terms of leaf shedding in both climates and leaf infection in the cooler day climate (Table 8).

Yield was evaluated from December 2001 to March 2002. Neither of the two spray programmes significantly affected total yield. This may be due to low disease severity in the control plots until February 2002, 10–30% in Selika. A significant increase in disease was observed during April and May 2002 but, unfortunately, yield was not measured during this late part of the season. The yields in the two climate regimes were similar. Therefore, we could conclude that the switch from night warming to day warming did not result in yield losses but did provide for significant energy savings.

Discussion

The life-cycle of a powdery mildew pathogen, such as *L. tauricai*, includes both stages that take place on leaf surfaces, and a phase that takes place inside the host tissue. In the present work, we followed key components of the development of *L. taurica* on sweet pepper leaves and inside the leaves. We studied the effects of BCAs, mineral oils, a plant extract and chemical fungicides on *L. taurica* under controlled conditions in greenhouses. BCAs have already been

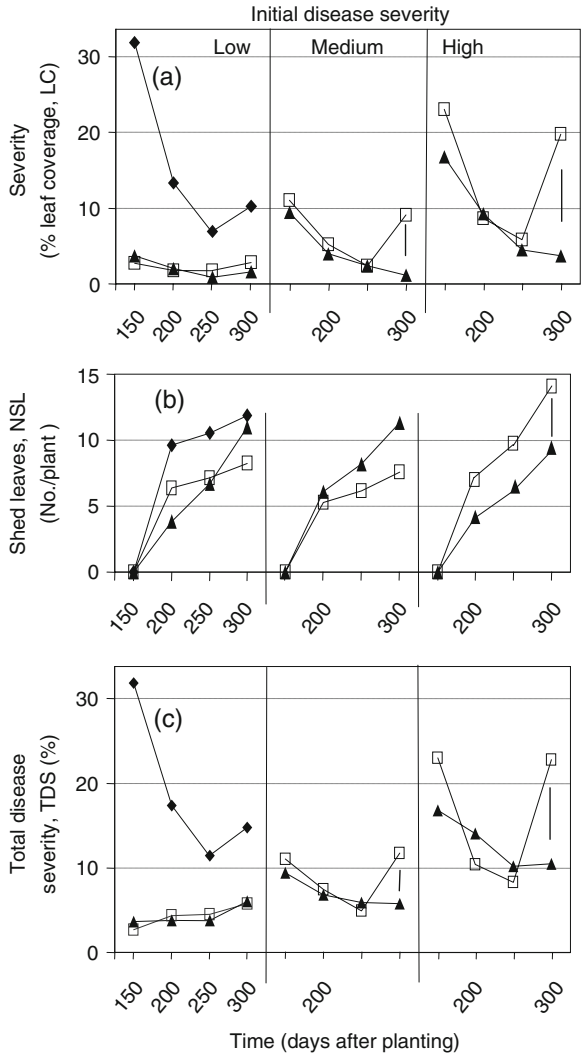

Fig. 5 Development of powdery mildew on sweet pepper (cv. Mazurka grown in a greenhouse under commercial conditions (field experiment 3). Severity of disease coverage on leaves (LC) (**a**), leaf shedding (NSL) (**b**) and total disease severity (TDS) (**c**). Low night temperature plots were divided into three groups: low (*left*), medium (*middle*) and high disease severity at the beginning of the experiment (Table 3). Plots within each of these groups were either sprayed with Heliosoufre, 1.0% (▲) or left untreated (□). (⧫) = Whole season untreated control. Bars represent the least significant differences (at $P \leq 0.05$) for each date

suggested as antagonists, parasites and control agents of *L. taurica* (Benuzzi et al. 2006; Kasselaki et al. 2006; Sztejnberg et al. 1989). In the present work *A. quisqualis* AQ10 inhibited conidial germination on leaves, but not on glass, while the higher rate of *T. harzianum* T39 inhibited germination on both surfaces (Table 1). Both BCAs may have affected the conidia indirectly by inducing changes in the leaf, but *T. harzianum* may also have induced a change in the germination process. *Ampelomyces quisqualis* is a mycoparasite (Sztejnberg et al. 1989) but its activity is usually observed when the host thallus is exposed to its conidia over a longer time period. Thus, in the light

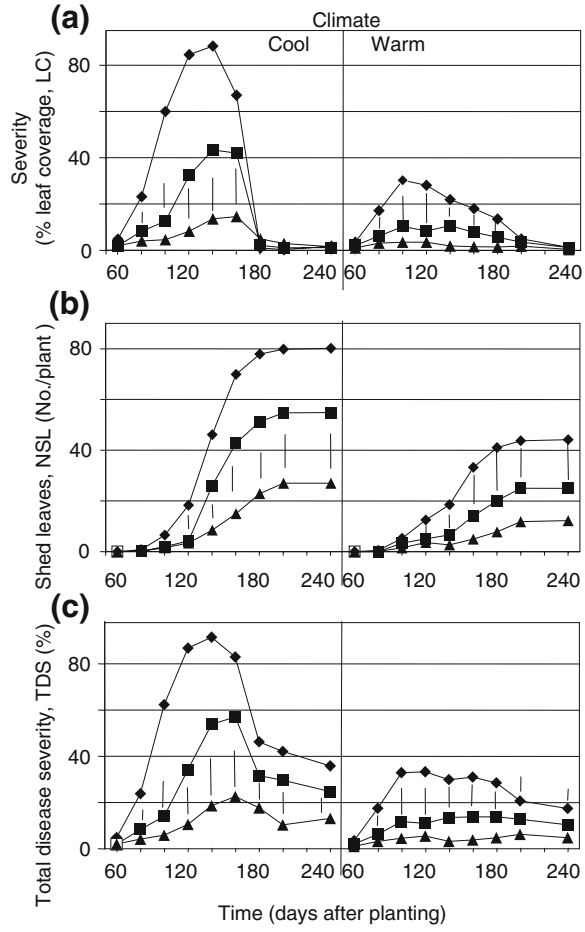

Fig. 6 Development of powdery mildew of sweet pepper (cv. Selika) grown in greenhouses under commercial conditions (field experiment 4). Severity of disease coverage on leaves (LC) (**a**), leaf shedding (NSL) (**b**) and total disease severity (TDS) (**c**). 1. Cool climate - day temperatures 15–25°C and night heating to 15°C from January through to March (left). ii. Warm climate - day temperatures of 25–32°C and minimal night temperature of 18°C from January through to March (right). Spray treatments in each of the greenhouses were: Untreated control (⧫); 'Friendly' spray programme: alternation of (product concentration in brackets) Heliosoufre (1.0%), Trichodex (0.4%), AQ10 0.03%) and Neemgard (1.0%) (■); Chemical spray programme: alternation of Heliosoufre (1.0%) + Dorado (0.025%), Heliosoufre (1.0%) + Polar (0.25), Heliosoufre (1.0%) + Sistan (0.1%) and Heliosoufre (1.0%) + Amistar (0.05%) (▲). Bars represent the least significant differences (at $P \leq 0.05$) for each date

Table 7 Sweet pepper fruit yield[a] (kg 1000 m^{-2}) in the warm climate greenhouses as affected by the spray treatments during the season (field experiment 4)

Period	Spray rotation		
	Untreated	Chemical[c]	'Friendly'[d]
November	1302 a[b]	662 b	421 b
December–January	2188 a	2702 a	2659 a
January–February	810 b	4009 a	3519 a
February–March	0 b	472 a	352 a
March–April	86 b	1332 a	1212 a
April–May	1810 a	2069 a	1997 a
Overall	6196 b	11246 a	10160 a

[a] General yield = harvested fruits of A and B grades; kg m^{-2}

[b] Numbers in each row followed by a common letter are not significantly different according to Fisher's protected LSD test ($P \leq 0.05$).

[c] 'Friendly' spray regime = alternation of (product concentration in brackets) Heliosoufre (1.0%), Trichodex (0.4%) + JMS Stylet-Oil (0.5%), AQ10 (0.03%) + AddQ (0.3%) and Neemgard (1.0%);

[d] Chemical spray regime = alternation of Heliosoufre (1.0%) + Dorado (0.025%), Heliosoufre (1.0%) + Polar (0.25), Heliosoufre (1.0%) + Sistan (0.1%) and Heliosoufre (1.0%) + Amistar (0.05%).

of the *A. quisqualis* effect on conidial germination on leaves, a new mode of action should be considered in addition to mycoparasitism. *T. harzianum* T39 has been found to be effective against cucumber powdery mildew (Elad et al. 1998); here, the mode of action was considered to be induced resistance. However, since it has been shown that this BCA does not produce antibiotics (Elad and Freeman 2002), the possibility of another mode of action should be considered and studied further. Similar to the activity of the mycoparasite *A.*

Table 8 Powdery mildew (AUDPC) on two cultivars of sweet pepper plants kept at two climate regimes and treated with two different spray programmes (field experiment 5)

Spray treatment	Cultivar			
	Selika		Cubi	
	Day/night temperature (°C)			
	25–30/>13	15–25/>16	25–30/>13	15–25/>16
AUDPC Leaf coverage (% severity, LC × days)				
Untreated control	1737 a[a]	2734 a	1725 a	3996 a
'Friendly' spray rotation [b]	721 b	1920 b	322 b	723 b
Chemical spray rotation [c]	376 b	822 c	625 b	818 b
AUDPC Leaf shedding (incidence, NSL × days)				
Untreated control	8540 a	10450 a	4650 a	9120 a
'Friendly' spray rotation	2974 b	6121 b	1844 b	3220 b
Chemical spray rotation	857 b	3998 c	1920 b	2654 b
AUDPC Total disease severity (% severity, TDS × days)				
Untreated control	1994 a	3354 a	1720 a	4008 a
'Friendly' spray rotation	746 b	1286 b	328 b	636 b
Chemical spray rotation	412 b	1026 b	622 b	786 b

[a] Within each disease parameter, numbers in each column followed by a common letter are not significantly different according to Fisher's protected LSD test ($P \leq 0.05$).

[b] Friendly' spray regime: alternation of Heliosoufre, Trichodex + JMS oil, AQ10 + AddQ and Neemgard in rates as mentioned for experiment 4.

[c] Chemical spray regime = alternation of Heliosoufre, Dorado, Polar, Sistan and Amistar in rates as mentioned for experiment 4.

quisqualis in the present work, spores of the hyperparasite *Acremonium alternatum* reduced powdery mildew infection by *L. taurica* on greenhouse tomato. The effect was slightly increased when spores were applied killed, and therefore not due to direct parasitism. The effect was systemic, protecting untreated leaves above the treated ones (Kasselaki et al. 2006).

The BCAs did not affect the viability of the conidia; and neither did the two mineral oils tested. Similarly, McGrath and Shishkoff (2000) reported that JMS Stylet-Oil did not affect the viability of *Podospheaera xanthii* conidia. However, in the present work, the oils significantly inhibited conidial germination when applied alone or together with the BCAs. Nevertheless, adding the BCAs to the oils provided no additional benefit, relative to the oils alone. Sulphur significantly inhibited the germination and viability of *L. taurica* conidia. Potassium bicarbonate was ineffective.

Under controlled conditions and temperatures of 15–25°C, *A. quisqualis* did not affect disease when applied alone at the low rate but it did reduce hyphal colonisation in the leaves at 25°C. *T. harzianum* T39 significantly reduced leaf colonisation at all three temperatures but significantly reduced disease only at 20–25°C. Similarly, it has been reported that this BCA (applied without oil) provides more effective control of cucumber grey mold at warmer temperatures (Elad et al. 1993). The oils significantly reduced leaf colonisation. However, combining them with the BCAs did not provide any additional benefit. Applications of combinations of these oils and BCAs have been shown to control cucumber powdery mildew better than applications of the individual agents (Elad et al. 1998).

Sulphur suppressed leaf colonisation and disease at all temperatures tested. Sulphur is regarded as an effective control agent of powdery mildews and was reported effective against *L. taurica* pepper powdery mildew (Tsror et al. 2003). In general, in the present work, the results of the single application treatments under controlled conditions were confirmed in the experimental greenhouse, where microclimate conditions fluctuated during the experiment and each treatment was applied several times. These results encouraged us to proceed with field experiments under commercial conditions.

In the first field experiment, we tested the above mentioned control agents alongside registered fungicides including a strobilurin (azoxystrobin), an antibiotic (polyoxin AL) and a plant extract (Neemgard). Potassium bicarbonate was also tested and found to be ineffective in the present work. This compound was reported as effective in other systems (Jamar and Lateur 2007; Matheron and Porchas 2007) including open field pepper infection by *L. taurica* (Fallik et al. 1997) and ineffective in others (McGrath 2007). The *A. quisqualis* AQ10 + AddQ mixture was found to be effective in a whole experiment calculation but not at 150 days after planting (in terms of leaf coverage and pathogen thallus viability tests). All other treatments, including the BCAs and plant extract, were effective in the present work, but sulphur was significantly superior to all of them. Indeed, sulphur is an old and effective control agent of powdery mildews (Spencer 1998) including *L. taurica* (Palti 1988; Tsror et al. 2003). Similar to the present work, sulphur was found most effective as a preventive fungicide (Smith et al. 1999).

There are two ways to demonstrate a negative effect of disease on yield. One way is to test the correlations between disease levels and yield in plots with no chemical intervention. In the previous work with pepper powdery mildew (Elad et al. 2007), high disease levels were positively correlated with low quality yield. Disease was associated with yield losses when severe epidemics occurred. This was due to significant loss of photosynthetic ability of the plants when a vast amount of leaves was shed. Palti (1988) generalised the *L. taurica*—yield relationship saying that yield losses in pepper occur when severe disease occurs in pepper. The second way to demonstrate negative effect of a disease on yield is to compare yields of treated and untreated plants. Utilising sulphur's ability to significantly suppress the disease over the whole season (Fig. 3d), we were able to show how the disease causes a significant decrease in crop yield (Table 4). This is probably the case only when disease severity is very high, as was observed during the middle part of this crop cycle. However, late season fungicide sprays may not provide any additional benefit, as was observed in field experiment 3 (Fig. 5). Following the winter, when disease severity declined, disease severity increased only from 250–300 days after planting and only in those plots which had been severely infected earlier in the season. This late season disease is not expected to cause yield losses. Therefore, although late season applications of Heliosoufre may provide effective disease control, they may not be economically justified.

Host resistance to *L. taurica* could play a role in management of this disease. In previous work in pepper, differences in susceptibility to *L. taurica* were found (Elad et al. 2007). Lafortune et al. (2005) worked with double-haploid progeny from a cross between a parental line and a cultivar of pepper and found variability in susceptibility to *L. taurica*. Resistance to *L. taurica* of an African pepper (*Capsicum annuum*) inbred line was found to be stable in the parental and haplodiploid lines and was high and stable in Mediterranean countries (Daubèze et al. 1995). Smith et al. (1999) found four experimental varieties that were significantly less susceptible to powdery mildew than the standard commercial variety. In tomato we found that some of the cultivars were more resistant to *O. neolycopersicy* than others (Jacob et al. 2008). In a crop such as strawberry (Amsalem et al. 2005) different resistance sources are available. On the contrary, in the present work there was no significant difference in resistance.

In various studies, temperatures allowing for powdery mildew development have been shown to range from 15–25°C, with an optimum of approximately 20°C in strawberry (Amsalem et al. 2005; Okayama et al. 1995) or 22–23°C in rose (Xu 1999a,b). Temperatures of 10°C and 30°C and above have been shown to be detrimental to the pathogen and disease incidence was significantly reduced under these conditions (Amsalem et al. 2005; Elad et al. 2007; Jhooty and McKeen 1965; Peries 1962). In tomato disease did not develop at 28°C (Jacob et al. 2008) Disease also did not develop at temperatures >30°C in studies of rose or grape powdery mildews (Delp 1954; Wheeler 1978).

Guzman-Plazola et al. (2003) found that short daily periods (two or three daily exposures of at least 2 h) of high temperatures (35°C) suppressed disease development by 70–92% in tomato. Similarly, high temperature treatment by non-ventilation of greenhouses (6 h, reaching 45°C) drastically reduced powdery mildew and downy mildew in summer cucumber production compared with constant ventilation (Sato et al. 2003). This concurs with our observation that long periods of high temperatures can suppress powdery mildew in pepper. Since high greenhouse temperatures were also found effective as a cultural means of control of pepper powdery mildew (Elad et al. 2007), it was essential to test the effect of climate on the efficacy of control agents under both controlled and commercial conditions. The effect of microclimate on the effectiveness of powdery mildew control agents is not reported in the literature. In the present study, under commercial conditions, all spray treatments were found effective when evaluated during the different periods of the season. But, at 120 days after planting, minimal night-time temperatures affected the efficacies of the BCAs with oils, neem extract and the 'friendly' spray rotation. In cv. Mazurka, these treatments did a better job of suppressing the disease in the warmer night-time temperature treatments. The *T. harzianum* T39 + JMS oil -temperature interaction had a similar effect on the viability of *L. taurica* thallus. The effects of *A. quisqualis* AQ10 also varied with temperature in cv. Turkal. From this, we conclude that temperatures >18°C enhance the activity of these agents under field conditions. Sulphur was very effective under all tested temperature conditions.

In the warm climate, there was no significant difference in the performance of the 'friendly' spray regime and the chemical spray regime. However, in the cooler climate, the 'friendly' spray programme was not as effective as the chemical spray programme (Fig. 6, Table 8). This phenomenon may be attributed to the inclusion of control agents that are affected by temperature in the 'friendly' spray rotation. A change in the greenhouse climate may affect the development of plant diseases such as powdery mildew and, at the same time, promote the activity of BCAs and render a pathogen more vulnerable to these control agents allowing for better disease suppression, as we have shown in this paper, supporting theories presented in earlier works (Elad and Freeman 2002).

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