European Journal of Plant Pathology **107:** 883–894, 2001.

The effect of soil moisture and cabbage amendment on the thermoinactivation of *Phytophthora nicotianae*

L. Coelho[1], D.J. Mitchell[2] and D.O. Chellemi[3]
[1]*Departamento de Biologia, FCAV, UNESP, Jaboticabal, SP 14870, Brazil (E-mail: lisias@fcav.unesp.br);* [2]*Plant Pathology Department, University of Florida, Gainesville, FL 32611, USA;* [3]*US Department of Agriculture, Agricultural Research Service, 2199 S. Rock Road, Fort Pierce, FL 34945, USA*

Accepted 5 August 2001

Key words: field capacity, non-chemical control

Abstract

The analysis of the effect of soil water matric potential and temperature regimes on the inactivation of chlamydospores of *Phytophthora nicotianae* in cabbage amended soils was evaluated using three matric potentials (0, −10, and −30 kPa), temperature regimes of 1.5 h at 44 °C, 5 h at 41 °C and 8 h at 35 °C, or 3 h at 47 °C, 5 h at 44 °C and 8 h at 35 °C, with a baseline temperature of 25 °C during the rest of the day. The results indicated that survival of *P. nicotianae* was lowest in saturated soil; and as temperature increased, survival of the pathogen decreased at all soil water matric potentials evaluated. Cabbage amendments can enhance the effect of the heat treatment, further decreasing the pathogen population. The soil water matric potentials evaluated represent optimum levels for the study of thermal inactivation. However, under field conditions lower potentials may be found. Extending the range of soil water matric potentials and the treatment time would allow better comparisons with the field data. There is a clear indication that one irrigation period prior to solarization would provide enough moisture to inactivate the primary inoculum of *P. nicotianae* in the top soil under field conditions; however, other factors may affect the effectiveness of solarization, reducing or enhancing its potential.

Introduction

Soil solarization is a hydrothermal process in which moist soil is covered with transparent plastic and exposed to sunlight, allowing it to heat to temperatures under favorable conditions that are lethal to many plant pathogens, pests, and weeds (Souza, 1994). The effectiveness of soil solarization depends on soil color and structure, soil moisture, air temperature, length of day, and intensity of sunlight (Souza, 1994). Solarization has reduced populations of *Fusarium* spp. (Chellemi et al., 1994; Ramirez-Villapudua and Munnecke, 1987; 1988), *Phytophthora* spp. (Barbercheck and Von Broembsen, 1986; Chellemi et al., 1994), *Pythium ultimum* (Gamliel and Stapleton, 1993a,b; Kulkarni et al., 1992), *Verticillium dahliae* (Ghini et al., 1993; Hartz et al., 1993), and *Rhizoctonia* sp. (Gamliel et al., 1993; Grooshevoy et al., 1941). Success of solarization for the control of plant diseases is closely associated with a combination of high ambient temperatures, maximum solar radiation, and optimum soil moisture (Souza, 1994).

Soil solarization alone may not be effective or consistent for the control of soil-borne pathogens, especially in regions where the rainy season occurs simultaneously with the warmer months of the year. In such cases, the use of soil amendments may enhance the performance of solarization (Coelho, 1997; Coelho et al., 1999; Gamliel and Stapleton, 1993a; Keinath, 1996; Ramirez-Villapudua and Munnecke, 1988). Cruciferous residues, due to their high content of isothiocyanates and aldehydes, have been suggested as amendments for use in combination with solarization (Mayton et al., 1996); cabbage is the primary

amendment that has been studied in combination with soil solarization.

Although soil solarization is a hydrothermal process, depending on moisture for maximum heat transfer throughout the soil profile and to soil-borne organisms (DeVay, 1991; Mahrer et al., 1984), very little is known about the influence of moisture on the inactivation of soil-borne pathogens. Moisture has been provided during soil solarization by different methods. Kulkarni et al. (1992) flood-irrigated solarized plots once a week, removing the plastic tarp. These authors found that recontamination of the solarized plots could occur with either contaminated water or soil movement with the irrigation water. Furrow irrigation of level fields has been suggested as an alternative to periodically replenish moisture to the soil under solarization (Pullman et al., 1979; Stapleton and DeVay, 1986). However, a single irrigation before the plastic is laid down can provide the same control of soil-borne plant pathogens as several irrigation events (Grinstein et al., 1979a,b; Jacobsen et al., 1980; Katan, 1980; Pullman et al., 1979).

Studies of thermal inactivation of pathogens can yield important information on survival of specific types of propagules and, more importantly, when simulating field conditions, can serve as the basis for estimation of the time needed for soil solarization to be an effective strategy for management of soil-borne plant pathogens. Relationships between the effectiveness of soil solarization in the field and thermal inactivation *in vitro* have been studied with several pathogens (Benson, 1978; Myers et al., 1983; Pullman et al., 1981). However, there was a lack of quantification of the inoculum added or recovered after the heat treatment. Additionally, the propagules used in some studies for heat treatment were not the same as the propagules normally found in the soil, or the detection techniques did not allow the quantification of the surviving population (Ramirez-Villapudua and Munnecke, 1987; 1988). Katan (1985) indicated the need for caution in the interpretation of the significance of heat mortality curves obtained under laboratory conditions. Potential problems that need to be addressed include inoculum type, moisture level, medium containing the inoculum, and the procedure for heating the samples.

Juarez-Palacios et al. (1991) found that the determination of the heat sensitivity of isolates of *Phytophthora* spp. in the laboratory closely reflected their inactivation in solarized soil, and the results supported the possible use of soil solarization for management of these pathogens. These authors found that an isolate of *P. megasperma* tolerant to high temperatures survived exposure for 30 min at 45 °C in a heat sensitivity study, but that the number of leaf discs infected by the pathogen after solarization for 4 weeks declined. In contrast *P. cinnamomi* and a low-temperature isolate of *P. megasperma* did not survive either treatment.

Bollen (1985) noted that different types of propagules have different sensitivities to heat. Oospores of *P. capsici* were more thermotolerant than mycelium from either mating type of this pathogen. The difference in tolerance was more than 5 °C; oospores survived at 50 °C for 30 min, but mycelium was eliminated at 42.5–45 °C for 30 min. Differences in the survival of *Fusarium oxysporum* were also observed; survival of this pathogen in soil cultures was greater at higher temperatures than survival of the pathogen in soil infested before the heat treatment. The difference may have been due to the presence of chlamydospores in the soil culture. However, the system used did not reflect field conditions, since soil was continuously flooded, which rarely occurs for extended duration in any field. Bollen (1985) did not analyze the relationship of time to temperature, and the temperature used, 50 °C, is reached most commonly under soil solarization only in arid or tropical climates.

Phytophthora nicotianae Breda de Haan (syn. = *P. parasitica* Dastur) has been reported on more than 170 plant hosts in Florida (Alfieri Jr. et al., 1994). Soil-borne diseases caused by *P. nicotianae* have limited production of several important crops, such as citrus, tobacco, ornamentals, and tomato.

Low levels of inoculum of *P. nicotianae* in the field can result in severe epidemics (Ferrin and Mitchell, 1986a; Kannwischer and Mitchell, 1981; Mitchell, 1978). Kannwischer and Mitchell (1981) found that 0.13 chlamydospore of *P. nicotianae* per gram of soil or 42 zoospores per plant were sufficient to cause 50% mortality on a susceptible cultivar of tobacco in a controlled environment. Residual population densities of 0.005–0.67 propagules per gram of soil were found in a tobacco nursery; mortality of a susceptible cultivar transplanted to this field reached 80% at the end of the growth season (Ferrin and Mitchell, 1986a).

Moisture plays an important role in the formation of sporangia, zoospore release, and subsequent epidemics. Sporangia of *P. nicotianae* are produced over a range of soil matric potentials (−4 to −1500 kPa), with the greatest number of sporangia being produced at the higher end of the range (−4 to −25 kPa) (Bernhardt and Grogan, 1982; Sidebottom and Shew, 1985a). Although flooding does not favor the formation of

sporangia, it enhances zoospore release (Bernhardt and Grogan, 1982).

Lutz and Menge (1991) observed that populations of *P. nicotianae* increased from 17 propagules per gram of soil before irrigation to 70 propagules per gram 2 days after a 24 h furrow irrigation event in a citrus grove. The highest proportion of propagules at that time was comprised of sporangia and zoospores; chlamydospores increased 4 days after the irrigation event, and reached a maximum on the seventh day. When the citrus grove was irrigated with a drip system, the soil matric potential was maintained close to −10 kPa, and the highest proportion of propagules consisted of sporangia and zoospores, with populations ranging from 71 to 93 propagules per gram of soil.

Ristaino et al. (1988) analyzed the effect of irrigation frequency and duration on the development of Phytophthora root rot of tomato and found that an irrigation regime in which plants were irrigated every 14 days, either for 4–8 h or for 24 h, increased root infection and decreased tomato yield. A less frequent irrigation schedule, such as 4–8 h every 28 days, stressed the plants and also led to severe root infection. Zoospores of *P. nicotianae* can be carried in irrigation water and infect tomato plants more than 60 m from inoculum sources (Neher and Duniway, 1992). In tomato, earlier infection led to higher disease intensity, and lower yield (Neher and Duniway, 1991; Neher et al., 1993). Infection of tobacco was favored by flooding of potted plants, or by saturating soil in Buchner funnel tension plates (Shew, 1983; Sidebottom and Shew, 1985b), and coincided with periods of high moisture levels in field trials (Ferrin and Mitchell, 1986b), indicating that zoospore movement is enhanced in saturated soils.

Even though extensive studies have been done on the relationships of inoculum density and disease, water status of the soil and disease, and temperature and increased recovery of chlamydospores in the soil (Ferrin and Mitchell, 1986b; Lutz and Menge, 1991; Ristaino et al., 1988; Shew, 1983; Sidebottom and Shew, 1985a,b), there is a lack of information about the effects of interactions of moisture and temperature on the inactivation of *P. nicotianae*.

Due to the demands on time and equipment, thermal inactivation studies very seldom explore extensive combinations of both time and temperature ranges. Thus, the full benefits that can be derived from such experiments are often not realized. The objectives of this study were to determine the relationships of time of exposure to temperature, soil water matric potential and cabbage amendment on the thermal inactivation of propagules of *P. nicotianae* and its pathogenicity in tomato.

Materials and methods

Production of chlamydospore inoculum of P. nicotianae

Chlamydospores of *P. nicotianae* were produced in V8 broth (Mitchell and Kannwischer-Mitchell, 1992). Four, 5 mm diameter V8 juice-agar plugs of a culture with actively growing mycelium of isolate Pn21 were transferred to a 325 ml prescription bottle containing 25 ml of clarified V8 broth. After incubation at 25 °C in the dark for 24 h, the bottle was shaken vigorously to fragment the mycelial mats. The hyphal fragments adhering to the walls were resuspended by slowly rotating the bottle. The bottle was incubated horizontally as a stationary culture at 25 °C for 6 days. One hundred milliliters of sterile deionized water were added to submerge the mycelial mat, and the culture was further incubated at 18 °C, vertically, for a minimum of 3 weeks.

The mycelial mats were rinsed in deionized water on a 400 mesh sieve, transferred to a blender with enough water to make a slurry, and blended on high for 1 min. The resulting slurry was ground about 30 times in a glass mortar and pestle and then subjected to two, 30 s cycles of sonication at 100 W (Model 450 Sonifier, Branson Ultrasonics Corporation, Danbury, CT). The total number of chlamydospores in the suspension was estimated with a hemacytometer, and the suspension was immediately used to infest soil to a density of 500 chlamydospores per gram of soil.

The effect of soil water matric potential, temperature regimes, and cabbage amendments on the thermal inactivation of chlamydospores of P. nicotianae

One-kilogram lots of moist soil from Decatur County, Georgia were pasteurized in a microwave at 700 W for 4 min in plastic bags. The soil was a loamy fine sand with pH 6.6 and 1.1% organic matter. After pasteurization the soil was infested with 500 chlamydospores per gram and moisture was adjusted to 0, −10, and −30 kPa using a pressure plate apparatus equipped with a 3 bar ceramic plate (Soilmoisture Equipment Corp., Santa Barbara, CA). These potentials were selected due

to their importance on the life cycle of the pathogen. One half of the soil was amended with 0.125% cabbage (Coelho, 1997; Coelho et al., 2000). Thirty grams of infested soil were dispensed into a test tube, which was loosely closed with a plastic cap to allow exchange of air.

A set of test tubes was placed in each of six water baths held at each of the following temperature regimes 1.5 h at 44 °C, 5 h at 41 °C and 8 h at 35 °C, or 3 h at 47 °C, 5 h at 44 °C and 8 h at 35 °C, with a baseline temperature of 25 °C during the rest of the day for 1, 2, 3, and 6 days. These temperatures were maintained with circulation heaters in water baths. Temperatures were monitored using a CR10 datalogger (Campbell Scientific, Inc., Logan, UT). Three tubes were removed at each date and part of the soil (15 g) was diluted with soft agar (2.5 g of Difco agar per liter of deionized water) and plated on a medium selective for pythiaceous fungi within 24 h. The selective medium (PARP) consisted of 17 g of cornmeal agar (Difco) in 1 l of deionized water amended with 5 mg of pimaricin, 250 mg of ampicillin, 10 mg of rifampicin, and 100 mg of pentachloronitrobenzene (Mitchell and Kannwischer-Mitchell, 1992). The soil overlay was removed after 48 h by gently washing the agar surface with tap water. The total number of colonies formed on PARP after 72 h of incubation was recorded as an estimation of the number of chlamydospores surviving the heat treatment. The experiment was repeated once.

At the end of the experiment, the other part of the soil (15 g), from all samples, was transferred to 50 ml tripour plastic beakers and one 1-month-old tomato seedling, cultivar solar set, was transplanted into the soil in each beaker. A small amount of vermiculite was poured on the top of the soil to prevent the roots from desiccating. All plants were kept in an growth chamber at 27 °C for 30 days. As plants died, the root systems were rinsed in water, surface disinfested for 30 s in 70% ethanol, rinsed twice in sterile water, and plated on PARP. At the end of the experiment, all plants were cut and the root systems plated on PARP for determination of infection by the presence of mycelium typical of *Phytophthora* spp.

Statistical analysis

The results of each experiment were analyzed individually. Whenever statistical analysis of the residues indicated that the results could be pooled due to the lack of variation, a final analysis was done with the pooled data.

The experiments on the determination of the effects of soil water matric potential on survival of *P. nicotianae* were analyzed using PROC GLM of SAS for the analysis of variance. The determination of the effect of each individual factor was calculated as the average of that factor across all other factors; the analysis of each interaction was done by calculating the average for the secondary factor within the main factor across all other factors.

Results

The effect of soil water matric potential and temperature regimes on the thermal inactivation of chlamydospores of P. nicotianae

The temperature regimes evaluated in these tests simulated either average daily periods or optimum daily temperature periods observed during solarization. Generally, as temperature within the regimes increased, the number of chlamydospores recovered in the soil dilution plates decreased (Tables 1–4). Propagule survival in the two temperature regimes simulating optimum solarization periods (47 °C for 3 h and 44 °C for 5 h daily) were significantly lower than those in the base temperature regime of 35 °C for 8 h daily, and generally lower than those treated at 41 °C for 5 h daily, regardless of the soil water matric potential ($P \leq 0.05$).

The use of a plant disease assay to confirm the pathogenicity of the surviving population of *P. nicotianae* indicated that, when the soil was maintained at 0 kPa and treated at 47 °C for 3 h daily, there was a reduction in infection of the seedlings in test 1 only (Table 2). In all other treatments under all three matric potentials, all of the seedlings were infected by *P. nicotianae* (Tables 2–4). A higher proportion of mortality of seedlings was observed in the second experiment than in the first experiment; however, little or no mortality occurred at any soil water matric potential when the soil was treated at 44 °C for 5 h daily or at 47 °C for 3 h daily.

Over all treatments, in both tests, soil water matric potential had a significant effect in reducing the populations of *P. nicotianae* in the soil ($P \leq 0.05$) (Tables 1 and 5). In both tests the lowest survival was observed in saturated soils (0 kPa) (Tables 1–4). No differences were observed in the survival of chlamydospores in soils maintained at either −10 or −30 kPa in test 1; however, in test 2 survival at −10 kPa was higher than at −30 kPa.

Table 1. Summary statistics for the effect of soil water matric potential, temperature regimes, and cabbage amendment on the survival of *P. nicotianae*

Factor	Propagules per gram of soil	
	Test 1	Test 2
Matric potential (−kPa)		
0	26.8 a	21.3 a
10	31.4 b	28.3 c
30	32.9 b	25.0 b
Temperature regime		
35-8	234.2 e	163.9 e
41-5	155.5 d	84.1 d
44-1.5	34.8 c	21.3 c
44-5	6.7 b	10.3 b
47-3	0.6 a	0.7 a
Cabbage amendment		
Non-amended	32.0 b	25.0 a
Amended (0.125%)	29.0 a	24.4 a
Time (days)		
1	37.8 c	33.5 c
2	13.0 a	15.3 a
3	22.6 b	17.1 b
6	79.6 d	43.6 d
Matric potential × temperature regime		
0 × 35-8	280.4 e	197.2 e
0 × 41-5	99.2 d	50.9 d
0 × 44-1.5	28.9 c	18.5 c
0 × 44-5	6.8 b	9.8 b
0 × 47-3	0.2 a	0.2 a
10 × 35-8	202.3 e	161.0 e
10 × 41-5	201.3 d	104.7 d
10 × 44-1.5	36.8 c	24.3 c
10 × 44-5	6.2 b	13.1 b
10 × 47-3	0.7 a	1.0 a
30 × 35-8	226.4 e	138.7 e
30 × 41-5	188.4 d	111.6 d
30 × 44-1.5	39.6 c	21.5 c
30 × 44-5	7.0 b	8.3 b
30 × 47-3	0.9 a	1.0 a
Matric potential × amendment		
0 × 0%	32.6 b	29.4 b
0 × 0.125%	22.0 a	15.4 a
10 × 0%	32.6 a	25.0 a
10 × 0.125%	30.4 a	32.1 b
30 × 0%	31.0 a	21.3 a
30 × 0.125%	36.3 b	29.2 b
Matric potential × time		
0 × 1	27.7 c	26.6 c
0 × 2	12.3 a	14.0 a
0 × 3	22.2 b	14.8 b
0 × 6	73.3 d	40.2 d
10 × 1	43.3 c	42.4 c
10 × 2	12.8 a	17.1 a
10 × 3	21.7 b	18.6 b
10 × 6	81.0 d	47.4 d
30 × 1	45.0 c	33.3 c
30 × 2	13.8 a	14.9 a
30 × 3	23.9 b	18.1 b
30 × 6	85.0 d	43.5 d
Temperature regime × amendment		
35-8 × 0%	251.9 b	205.0 b
35-8 × 0.125%	217.7 a	131.1 a
41-5 × 0%	222.4 b	130.2 b
41-5 × 0.125%	108.8 a	54.3 a
44-1.5 × 0%	23.8 a	11.8 a
44-1.5 × 0.125%	50.7 b	38.0 b
44-5 × 0%	8.9 b	10.8 a
44-5 × 0.125%	4.9 a	9.7 a
47-3 × 0%	0.4 a	0.5 a
47-3 × 0.125%	0.7 b	1.0 b
Temperature regime × time		
35-8 × 1	250.2 b	158.3 b
35-8 × 2	280.9 b	306.5 c
35-8 × 3	216.3 a	154.3 b
35-8 × 6	197.7 a	96.3 a
41-5 × 1	212.3 c	147.9 b
41-5 × 3	154.4 b	71.1 a
41-5 × 6	111.1 a	56.5 a
44-1.5 × 1	56.0 c	38.6 b
44-1.5 × 3	33.2 b	16.7 a
44-1.5 × 6	22.5 a	14.8 a
44-5 × 1	10.6 c	15.0 c
44-5 × 2	6.7 b	10.0 b
44-5 × 3	4.0 a	7.1 a
47-3 × 1	1.5 b	2.3 b
47-3 × 2	0.3 a	0.3 a
47-3 × 3	0.2 a	0.2 a
Amendment × time		
0% × 1	37.5 c	33.3 c
0% × 2	13.6 a	15.4 a
0% × 3	23.4 b	17.5 b
0% × 6	94.6 d	45.1 d
0.125% × 1	38.1 c	33.7 c
0.125% × 2	12.4 a	15.1 a
0.125% × 3	21.8 b	16.7 b
0.125% × 6	67.0 d	42.1 d

Main effect means followed by the same letter in each test do not differ according to Tukey's Honestly Significant Difference procedure ($P \leq 0.05$); data were transformed to ln(ppg + 1) for analysis and presented as weighted means ([exp{mean}] − 1).

As temperature increased, survival of *P. nicotianae* decreased (Tables 1 and 5), and survival at each temperature regime was significantly different from that in all others ($P \leq 0.05$). Survival was lowest in soil maintained at 47 °C for 3 h daily (Table 1).

Generally, the longer the soil infested with chlamydospores of *P. nicotianae* was exposed to the heat

Table 2. The effect of temperature regimes that simulate daily solarization periods and cabbage amendment, at a soil water matric potential of 0 kPa, on the survival of chlamydospores of *P. nicotianae*, and on the percentages of infection and mortality of tomato seedlings after 30 days of exposure in the previously treated soil

Temperature regime[1]	Cabbage (%)	Days[2]	Test 1			Test 2		
			PPG[3]	I[4] (%)	M[5] (%)	PPG	I (%)	M (%)
35-8	0	1	223.08 e[6]	100	0	308.82 e	100	33
35-8	0	2	433.85 f	100	0	540.86 e	100	33
35-8	0	3	413.47 f	100	0	409.76 e	100	33
35-8	0	6	672.84 f	100	0	213.86 de	100	100
35-8	0.125	1	236.46 e	100	0	91.48 cde	100	33
35-8	0.125	2	226.47 ef	100	0	226.47 de	100	0
35-8	0.125	3	169.72 e	100	0	110.16 cde	100	17
35-8	0.125	6	153.47 e	100	0	67.58 cde	100	100
41-5	0	1	150.41 e	100	0	214.51 de	100	33
41-5	0	3	248.39 ef	100	0	104.64 cde	100	33
41-5	0	6	126.74 e	100	0	62.37 bcd	100	67
41-5	0.125	1	90.84 de	100	0	37.78 bcd	100	0
41-5	0.125	3	62.43 de	100	0	11.06 b	100	100
41-5	0.125	6	34.52 c	100	0	27.73 bc	100	33
44-1.5	0	1	34.16 cd	100	0	29.14 bc	100	33
44-1.5	0	3	19.29 bcd	100	0	15.61 b	100	67
44-1.5	0	6	14.80 bcd	100	0	10.32 b	100	67
44-1.5	0.125	1	49.91 de	100	0	42.90 bcd	100	33
44-1.5	0.125	3	54.15 de	100	0	12.46 b	100	67
44-1.5	0.125	6	20.98 cd	100	33	15.01 b	100	67
44-5	0	1	14.80 bcd	100	0	18.39 bc	100	0
44-5	0	2	7.76 bcd	100	0	11.26 b	100	0
44-5	0	3	6.54 bcd	100	0	9.32 b	100	0
44-5	0.125	1	6.17 bc	100	0	10.94 b	100	0
44-5	0.125	2	5.42 bc	100	0	6.61 b	100	0
44-5	0.125	3	3.62 bc	100	0	6.24 b	100	0
47-3	0	1	0.62 a	100	0	0.78 a	100	0
47-3	0	2	0.00 a	67	0	0.00 a	100	0
47-3	0	3	0.00 a	67	0	0.00 a	100	0
47-3	0.125	1	0.52 a	100	0	0.92 a	100	0
47-3	0.125	2	0.00 a	33	0	0.00 a	100	0
47-3	0.125	3	0.00 a	50	0	0.00 a	100	0

[1]Temperature regimes that simulated daily solarization periods consisted of temperatures increased daily to 35, 41, 44, 44 or 47 °C for 8, 5, 1.5, 5 or 3 h, respectively; the temperature for the remainder of each day was maintained at 25 °C.
[2]Days = duration of temperature regime.
[3]PPG = propagules per gram of soil; initial population was 500 chlamydospores per gram of soil.
[4]I = seedling infection.
[5]M = seedling mortality.
[6]Main effect means followed by the same letter in each test do not differ according to Tukey's Honestly Significant Difference procedure ($P \leq 0.05$); data were transformed to ln(ppg + 1) for analysis and presented as weighted means ([exp{mean}] − 1).

treatments, the lower the survival of the pathogen (Tables 2–5). However, the effect of time has to be analyzed with care because of the different durations of exposure to the temperature regimes. Because the time required to kill chlamydospores is inversely proportional to temperature, shorter sampling times (1, 2, and 3 days) were used at the higher temperature regimes (47 °C for 3 h daily and 44 °C for 5 h daily) and longer sampling times (1, 3, and 6 days) were used at the average temperature regimes (44 °C for 1.5 h daily and 41 °C for 5 h daily); the base temperature (35 °C for 8 h daily) was sampled at all time intervals (1, 2, 3, and 6 days). Therefore, the analysis of the effect of time across all other factors is biased in the following manner: the data for 2 days of exposure was obtained only from the temperature regimes that simulate optimum

Table 3. The effect of temperature regimes that simulate daily solarization periods and cabbage amendment, at a soil water matric potential of −10 kPa, on the survival of chlamydospores of *P. nicotianae*, and on the percentages of infection and mortality of tomato seedlings after 30 days of exposure in the previously treated soils

Temperature regime[1]	Cabbage (%)	Days[2]	Test 1			Test 2		
			PPG[3]	I[4] (%)	M[5] (%)	PPG	I (%)	M (%)
35-8	0	1	181.18 e[6]	100	17	202.16 cd	100	0
35-8	0	2	247.14 E	100	0	287.59 d	100	0
35-8	0	3	168.02 E	100	0	147.41 cd	100	17
35-8	0	6	191.48 E	100	0	115.63 cd	100	67
35-8	0.125	1	325.69 E	100	0	218.42 d	100	50
35-8	0.125	2	274.06 E	100	67	274.06 d	100	0
35-8	0.125	3	200.34 e	100	0	115.51 cd	100	17
35-8	0.125	6	107.85 de	100	0	65.02 cd	100	33
41-5	0	1	449.34 e	100	0	258.82 d	100	33
41-5	0	3	261.43 e	100	0	109.50 cd	100	100
41-5	0	6	209.61 e	100	0	73.22 cd	100	67
41-5	0.125	1	215.16 e	100	0	146.67 cd	100	33
41-5	0.125	3	127.77 e	100	0	77.89 cd	100	67
41-5	0.125	6	97.20 de	100	0	55.15 cd	100	67
44-1.5	0	1	44.15 cd	100	0	14.26 b	100	33
44-1.5	0	3	19.70 cd	100	0	6.24 b	100	33
44-1.5	0	6	14.03 c	100	0	8.73 b	100	33
44-1.5	0.125	1	70.95 de	100	0	74.19 cd	100	0
44-1.5	0.125	3	59.95 d	100	0	78.44 cd	100	33
44-1.5	0.125	6	45.34 cd	100	33	39.77 cd	100	33
44-5	0	1	16.10 c	100	33	23.83 b	100	0
44-5	0	2	10.10 bc	100	0	16.99 b	100	0
44-5	0	3	4.64 b	100	0	6.92 b	100	0
44-5	0.125	1	8.38 bc	100	0	16.37 b	100	0
44-5	0.125	2	3.65 b	100	0	12.38 b	100	0
44-5	0.125	3	1.80 ab	100	0	8.48 b	100	0
47-3	0	1	2.24 b	100	0	3.13 ab	100	0
47-3	0	2	0.30 a	100	0	0.25 a	100	0
47-3	0	3	0.09 a	100	0	0.00 a	100	0
47-3	0.125	1	1.70 ab	100	0	5.75 b	100	0
47-3	0.125	2	0.52 a	100	33	0.45 a	100	0
47-3	0.125	3	0.45 a	100	0	0.28 a	100	0

[1–6]See Table 2.

solarization periods and the base temperature regime; after 3 days of heat treatment, a final sample was collected from the optimum temperature regimes, and intermediate samples were collected from the average temperature regimes; after 6 days only the average temperature regimes and the base temperature regime were evaluated. Consequently, artificially higher survival rates were generated at 6 days as compared to 2 or 3 days because the lowest survival rates under the optimum temperature regimes had not been determined (Table 1).

Within each of the soil water matric potentials evaluated, each of the temperature regimes significantly reduced the populations of *P. nicotianae* in relation to the base temperature (35 °C for 8 h daily) ($P \leq 0.05$) (Tables 1–5). Survival of *P. nicotianae* at each temperature regime was significantly lower than that at all other preceding temperature regimes.

Although there was a significant interaction of soil water matric potential and cabbage amendment, the effect of the amendment on survival of *P. nicotianae* was not consistent throughout the range of soil water matric potentials evaluated ($P \leq 0.05$) (Tables 1–5). Cabbage amendment reduced the survival of propagules in soil maintained at 0 kPa (Table 1). However, when the soil was maintained at −30 kPa, higher survival of the pathogen was observed in soil amended with cabbage than in non-amended soil. At −10 kPa,

Table 4. The effect of temperature regimes that simulate daily solarization periods and cabbage amendment, at a soil water matric potential of −30 kPa, on the survival of chlamydospores of *P. nicotianae*, and on the percentages of infection and mortality of tomato seedlings after 30 days of exposure in the previously treated soils

Temperature regime[1]	Cabbage (%)	Days[2]	Test 1			Test 2		
			PPG[3]	I[4] (%)	M[5] (%)	PPG	I (%)	M (%)
35-8	0	1	225.11 e[6]	100	50	90.81 d	100	33
35-8	0	2	190.71 e	100	0	221.96 d	100	0
35-8	0	3	185.98 e	100	17	161.71 d	100	33
35-8	0	6	207.30 e	100	33	114.93 d	100	0
35-8	0.125	1	349.37 e	100	0	137.80 d	100	17
35-8	0.125	2	385.45 e	100	0	385.45 d	100	0
35-8	0.125	3	230.60 e	100	17	107.96 d	100	50
35-8	0.125	6	133.29 de	100	0	63.07 cd	100	100
41-5	0	1	183.93 e	100	0	288.17 d	100	33
41-5	0	3	253.68 e	100	0	153.93 d	100	33
41-5	0	6	240.29 e	100	0	82.18 cd	100	33
41-5	0.125	1	371.78 e	100	0	116.20 d	100	67
41-5	0.125	3	124.21 de	100	0	80.29 cd	100	67
41-5	0.125	6	85.57 de	100	0	56.34 cd	100	33
44-1.5	0	1	65.75 d	100	0	25.21 c	100	33
44-1.5	0	3	19.41 c	100	0	6.43 b	100	0
44-1.5	0	6	14.77 bc	100	0	6.55 b	100	33
44-1.5	0.125	1	86.01 de	100	0	95.06 d	100	0
44-1.5	0.125	3	53.27 cd	100	0	30.88 c	100	67
44-1.5	0.125	6	42.73 cd	100	33	28.11 c	100	100
44-5	0	1	10.67 bc	100	0	9.86 bc	100	0
44-5	0	2	9.52 bc	100	0	7.35 bc	100	0
44-5	0	3	5.83 b	100	33	4.80 b	100	0
44-5	0.125	1	9.31 bc	100	0	14.25 bc	100	0
44-5	0.125	2	6.01 b	100	0	8.55 bc	100	0
44-5	0.125	3	3.23 b	100	0	7.66 bc	100	0
47-3	0	1	1.90 ab	100	0	1.44 ab	100	0
47-3	0	2	0.09 a	100	0	0.10 a	100	0
47-3	0	3	0.09 a	100	0	0.28 a	100	0
47-3	0.125	1	2.79 b	100	0	4.07 b	100	0
47-3	0.125	2	0.79 a	100	0	1.15 ab	100	0
47-3	0.125	3	0.91 a	100	0	0.86 ab	100	0

[1–6]See Table 2.

the addition of cabbage to the soil had no impact on the survival of *P. nicotianae* in test 1, while in test 2 survival was greater in soil amended with cabbage than in non-amended soil.

The effect of cabbage amendment on survival of *P. nicotianae* within each temperature regime was significant, but not consistent ($P \leq 0.05$) (Tables 1 and 5). At the two lower temperature regimes (35 °C for 8 h and 41 °C for 5 h daily) the addition of cabbage to the soil reduced the number of propagules of *P. nicotianae* recovered on the selective medium (Tables 2–4). At 44 °C for 1.5 h, and 47 °C for 3 h daily, a higher proportion of the population of *P. nicotianae* survived in soil that was amended with cabbage than in non-amended soil. In test 1, at 44 °C for 5 h daily the number of propagules of the pathogen recovered was lower in the soil amended with cabbage than in non-amended soil; in contrast, in test 2 there were no differences in the survival of *P. nicotianae* in soils amended or non-amended with cabbage.

Generally, longer exposure of the infested soil to each temperature resulted in lower recovery of propagules (Tables 1–5). At the base temperature regime of 35 °C for 8 h daily, the lowest survival was observed after 3 or 6 days. In test 1 no differences in survival were observed between 3 and 6 days or between 1 and 2 days of exposure to the heat treatment. In contrast, in test 2, the highest survival was observed after 2 days of exposure, followed by 1 and 3 days of exposure to the heat treatment. When average temperature

Table 5. Analysis of variance of the effect of temperature regimes that simulate solarization periods, cabbage amendment, and soil water matric potential on the survival of chlamydospores of *P. nicotianae*

Source of variation	df	Test 1			Test 2		
		MS	*F*	*P*	MS	*F*	*P*
Soil water matric potential (Ψ_m)[1]	2	1.355	15.93	0.0001	1.967	16.68	0.0001
Temperature[2]	4	264.897	3114.24	0.0001	210.227	1782.67	0.0001
Cabbage[3]	1	0.924	10.87	0.0001	0.001	0.01	0.9149
Time[4]	3	6.740	79.24	0.0001	11.725	99.43	0.0001
Ψ_m × temperature	8	1.096	12.89	0.0001	1.366	11.59	0.0001
Ψ_m × cabbage	2	1.827	21.48	0.0001	6.789	57.57	0.0001
Ψ_m × time	6	0.375	4.41	0.0003	0.133	1.13	0.3442
Temperature × cabbage	4	4.658	54.77	0.0001	8.255	70.01	0.0001
Temperature × time	8	0.873	10.26	0.0001	2.024	17.16	0.0001
Cabbage × time	3	0.643	7.57	0.0001	0.036	0.30	0.8230
Temperature × Ψ_m × cabbage × time	54	0.225	2.65	0.0001	0.265	2.25	0.0001
Residual	228	0.085			0.118		

[1]Soil water matric potential adjusted to 0, −10, or −30 kPa.
[2]Temperature regimes that simulated daily solarization periods consisted of temperatures increased daily to 35, 41, 44, 44 or 47 °C for 8, 5, 1.5, 5, or 3 h, respectively; the temperature for the remainder of each day was maintained at 25 °C.
[3]Soil amended or not amended with dry, ground cabbage at a rate of 0.125% (w/w).
[4]Time = number of days of exposure to heat treatment at a given temperature regime.

regimes were employed, the reduction in survival was not as consistent as with the optimum temperature regimes. At 41 °C for 5 h daily, and 44 °C for 1.5 h, survival decreased with increasing length of exposure in test 1; however, in test 2 no differences were observed between 3 and 6 days of exposure, in which survival was lower than after exposing the soil to 1 day of heat treatment. As time progressed, lower recovery was observed at 44 °C for 5 h daily. Exposing the chlamydospore-infested soil to either 2 or 3 days at 47 °C for 3 h daily resulted in lower survival as compared with a 1 day exposure.

Discussion

The findings of this study are in general agreement with related work on the thermal inactivation of spores of *Phytophthora* spp. (Barbercheck and Von Broembsen, 1986; Benson, 1978; Bollen, 1985; Juarez-Palacios et al., 1991). Bollen (1985) reported that a soil culture of *P. cryptogea* required 30 min at 45 °C to be completely inactivated, and a soil culture of *P. capsici* had to be heated to 50 °C for 30 min before oospores were killed. Benson (1978) found that culture disks of *P. cinnamomi* containing chlamydospores were killed after 90 min at 39 °C or 4.5 min at 44 °C; in contrast, Barbercheck and Von Broembsen (1986) noted that a suspension of chlamydospores of *P. cinnamomi* in water was inactivated after 10 min at 44 °C. The differential heat sensitivity of isolates of the same species was demonstrated by Juarez-Palacios et al. (1991). These authors found that chlamydospores of *P. cinnamomi* or oospores of a low-temperature isolate of *P. megasperma* added to soil did not survive 20 min at 45 °C; in contrast, a high-temperature isolate of *P. megasperma* survived more than 30 min at the same temperature. The discrepancies among the values reported in the literature could be related to the different types of substratum used to produce the spores and to the different media used for the heat treatment in each study. It is expected that spore suspensions in water would be inactivated faster than soil cultures saturated with water, which in turn would die faster than spores added to soil at a lower soil water matric potential. These assumptions are based on the differential transmission of heat throughout the substrata, the formation of air pockets, or simply due to the nature of the spores formed in each substratum, as noted by Myers et al. (1983) and Katan (1981).

One major benefit of the use of intermittent heat in thermal inactivation studies is the provision of estimations of the effectiveness of soil solarization to control plant pathogens. However, cycling temperatures have not been employed routinely, possibly due to the compounded difficulties of establishing appropriate temperature regimes, the daily requirement of adjusting each temperature, and the longer time required to

reach desirable control of the organism under study. Examples of the use of pulsing temperatures are provided by Gamliel and Stapleton (1993a), Porter and Merriman (1983), Tjamos and Fravel (1995) and Wicks (1988).

Wicks (1988) analyzed the effect of intermittent heat on the survival of mycelium of *P. cambivora*. None of the isolates tested survived after 1 day at a regime of 45 °C for 6 h and 20 °C for 18 h daily. The response of the isolates was variable and inconclusive at either 40 or 35 °C for 6 h daily during 4 days. However, mycelium is not the most likely survival structure of *P. cambivora* in the soil.

Tjamos and Fravel (1995) evaluated intermittent heat on the survival of a suspension of microsclerotia of *Verticillium dahliae* over 4 days. The following daily temperature regimes were used: base temperature of 31 °C for 10 h and high temperature at 35 °C for 14 h, base temperature of 33 °C for 10 h and high temperature at 36 °C for 14 h, and base temperature of 35 °C for 10 h and high temperature at 38 °C for 14 h. After 4 days at the highest temperature regime, less than 1% of the sclerotia germinated. In their study the use of sclerotium suspensions in water negated the insulating effect of air pockets in the soil, and the duration of the high temperature in each regime was longer than that which would normally occur under field conditions.

A more comprehensive study was done by Porter and Merriman (1983) with several soil-borne plant pathogens. These authors used infested soil held at field capacity, and over 15 days evaluated cycles of low temperature at 25 °C for 18 h, followed by 6 h daily at a supplemental temperature of 25, 30, 35, 40, 45 or 50 °C. Survival of each pathogen depended on the heat sensitivity of the type of propagule being evaluated. For example, *V. dahliae* did not survive for 15 days when the high temperature was above 40 °C; in contrast, *Pythium irregulare* was recovered at 5×10^4 propagules per gram of soil at 50 °C, even at the end of the experiment.

Gamliel and Stapleton (1993a) selected two temperature regimes similar to those found in the San Joaquin Valley in California to evaluate the effectiveness of the regimes and cabbage amendment on the control of *P. ultimum* and *S. rolfsii*. Both pathogens were eliminated after 4 days in the cabbage amended soil at either temperature regime of 38 or 45 °C for 4 h daily plus 20 h at 30 °C; however, propagules of these pathogens could be recovered from the non-amended soil after 4 days at the same temperature regimes.

Comparisons between studies are further complicated due to the differences in length of the experiments, amplitude between low and high temperatures in each regime, and the duration of the high temperature. If a given *in vitro* experiment is to be compared with soil solarization in the field, then the duration of the *in vitro* study should be similar to the solarization trial, and the temperature regimes should simulate those observed during solarization.

In the present study populations of *P. nicotianae* decreased to residual levels after 15 days only when temperature regimes simulating optimum solarization conditions (47 °C for 3 h daily) were used; under these circumstances no infection of tomato seedlings was observed after as little as 3 days of heat treatment. The use of 44 °C for 5 h daily also reduced populations to levels below 1 propagule per gram of soil; however, infection of tomato seedlings was observed throughout the experiment. The use of temperature regimes simulating average field temperature regimes reduced the populations to at least 40% of the initial infestation level, but all seedlings were colonized at these regimes.

Although the effect of soil moisture on reproduction and dispersal of *Phytophthora* spp. has been researched extensively (Browne and Mircetich, 1988; Ferrin and Mitchell, 1986b; Lutz and Menge, 1991; McIntosh, 1972; Neher and Duniway, 1992; Ristaino et al., 1992; Sidebottom and Shew, 1985a,b), the effect of soil moisture and heat on the inactivation of spores of this genus had not been addressed before. Survival of chlamydospores of *P. nicotianae* was lower in saturated soil (0 kPa) than at the two other soil water matric potentials evaluated (−10 and −30 kPa). The two lower soil water matric potentials (−10 and −30 kPa) used for this study are close to what is normally considered field capacity of a soil and they represent an optimum for thermal inactivation studies. However, in field studies, these conditions are very difficult to maintain for the time required for soil solarization without supplemental irrigation.

Porter et al. (1991) evaluated the effect of two moisture contents (field capacity and 10% of field capacity) and constant temperature on survival of *Plasmodiophora brassicae* in two soils. Only 15 days were required to kill all spores of *P. brassicae* in either soil at 40 °C or above when the soil moisture was at field capacity. In dry soil, however, inactivation was observed only at 50 or 55 °C.

The effect of soil water matric potential on the thermal inactivation process is twofold. First, temperature maxima of the soil increase with increasing soil

moisture content (Mahrer et al., 1984). This principle is important in field experiments, but is not operative in an *in vitro* system as used in the present study. The second effect of moisture is the increase in heat transfer or conduction in the soil, with a subsequent reduction of air pockets that could provide an insulation for the spores (DeVay, 1991; Stapleton and DeVay, 1986).

Summary and conclusions

One of the few factors that can be controlled during soil solarization is the soil water matric potential through the use of irrigation. The analysis of the effect of soil water matric potential and temperature regimes on the inactivation of chlamydospores of *P. nicotianae* in cabbage amended soils indicated that survival was lowest in saturated soil; and as temperature increased, survival of the pathogen decreased at all soil water matric potentials evaluated (0, −10, and −30 kPa). The soil water matric potentials evaluated represent optimum levels for the study of thermal inactivation; however, under field conditions lower potentials may be found, as in the third trial in Site 3 (Coelho, 1997). Extending the range of soil water matric potentials to −50 or −100 kPa and the treatment time to 15–20 days would allow better comparisons with the field data.

Acknowledgements

The first author was supported by CNPq (Conselho Nacional de Pesquisa e Desenvolvimento, Brazil). This research was supported, in part, by the Gadsden County Tomato Growers Association and the United States Department of Agriculture, Specific Cooperative Agreement 58-6617-4-019. We thank N.T. Gargiulo for the use of soil from their tomato production fields.

References

Alfieri Jr. SA, Langdon KR, Kimbrough KR, El-Gholl NE and Wehlburg C (1994) Diseases and Disorders of Plants in Florida. Bull. 14, Division of Plant Industry, Florida Department of Agriculture and Consumer Services

Barbercheck ME and Von Broembsen SL (1986) Effects of soil solarization on plant-parasitic nematodes and *Phytophthora cinnamomi* in South Africa. Plant Disease 70: 945–950

Benson DM (1978) Thermal inactivation of *Phytophthora cinnamomi* for control of Fraser Fir root rot. Phytopathology 68: 1373–1376

Bernhardt EA and Grogan RG (1982) Effect of soil matric potential on the formation and indirect germination of sporangia of *Phytophthora parasitica, P. capsici* and *P. cryptogea*. Phytopathology 72: 507–511

Bollen GJ (1985) Lethal temperatures of soil fungi. In: Parker CA, Rovira AD, Moore KJ, Wong PTW and Kollmorgen JF (eds) Ecology and Management of Soil-borne Plant Pathogens (pp 191–193) APS Press, St. Paul

Browne GT and Mircetich SM (1988) Effects of flood duration on the development of Phytophthora root and crown rots of apple. Phytopathology 78: 846–851

Chellemi DO, Olson SM and Mitchell DJ (1994) Effects of soil solarization and fumigation on survival of soilborne pathogens of tomato in northern Florida. Plant Disease 78: 1167–1172

Coelho L (1997) Reduction of populations of *Phytophthora* spp. with soil solarization under field conditions and thermal inactivation of *Phytophthora nicotianae*. PhD Dissertation, University of Florida, 136 pp

Coelho L, Chellemi DO and Mitchell DJ (1999) Efficacy of solarization and cabbage amendment for the control of *Phytophthora* spp. in North Florida. Plant Disease 83: 293–299

Coelho L, Mitchell DJ and Chellemi DO (2000) Thermal inactivation of *Phytophthora nicotianae*. Phytopathology 90: 1089–1097

DeVay JE (1991) Use of soil solarization for control of fungal and bacterial plant pathogens including biocontrol. In: DeVay JE, Stapleton JJ and Elmore CL (eds) Soil Solarization (pp 79–93) FAO, Rome

Ferrin DM and Mitchell DJ (1986a) Influence of initial density and distribution of inoculum on the epidemiology of tobacco black shank. Phytopathology 76: 1153–1158

Ferrin DM and Mitchell DJ (1986b) Influence of soil water status on the epidemiology of tobacco black shank. Phytopathology 76: 1213–1217

Gamliel A, Hadar E and Katan J (1993) Improvement of growth and yield of *Gypsophila paniculata* by solarization or fumigation of soil or container medium in continuous cropping systems. Plant Disease 77: 933–938

Gamliel A and Stapleton JJ (1993a) Characterization of antifungal volatile compounds evolved from solarized soil amended with cabbage residues. Phytopathology 83: 899–905

Gamliel A and Stapleton JJ (1993b) Effect of chicken compost or ammonium phosphate and solarization on pathogen control, rhizosphere microorganisms, and lettuce growth. Plant Disease 77: 886–891

Ghini R, Bettiol W, Spadotto CA, Moraes GJ, Paraiba LC and Mineiro JLC (1993) Soil solarization for the control of tomato and eggplant Verticillium wilt and its effect on weed and micro-arthropod communities. Summa Phytopathologica 19: 183–189

Grinstein A, Katan J, Razik AA, Zeydan O and Elad Y (1979a) Control of *Sclerotium rolfsii* and weeds in peanuts by solar heating of the soil. Plant Disease Reporter 63: 1056–1059

Grinstein A, Orion D, Greenberger A and Katan J (1979b) Solar heating of the soil for the control of *Verticillium dahliae* and *Pratylenchus thornei* in potatoes. In: Schippers B and Gams W (eds) Soil-borne Plant Pathogens (pp 431–438) Academic Press, New York

Grooshevoy SE, Khudyna IP and Popova AA (1941) Methods for disinfecting seed-bed soil by natural sources of heat. Review of Applied Mycology 20: 87–88

Hartz TK, DeVay JE and Elmore CL (1993) Solarization is an effective soil disinfestation technique for strawberry production. HortScience 28: 104–106

Jacobsen BJ, Greenberger A, Katan J, Levi M and Alon H (1980) Control of Egyptian broomrape (*Orobanche aegyptiaca*) and other weeds by means of solar heating of the soil by polyethylene mulching. Weed Science 28: 312–316

Juarez-Palacios C, Felix-Gastelum R, Wakeman RJ, Paplomatas EJ and DeVay JE (1991) Thermal sensitivity of three species of *Phytophthora* and the effect of soil solarization on their survival. Plant Disease 75: 1160–1164

Kannwischer ME and Mitchell DJ (1981) Relationships of numbers of spores of *Phytophthora parasitica* var. *nicotianae* to infection and mortality of tobacco. Phytopathology 71: 69–73

Katan J (1980) Solar pasteurization of soils for disease control: status and prospects. Plant Disease 64: 450–454

Katan J (1981) Solar heating (solarization) of soil for control of Soil-borne pests. Annual Review of Phytopathology 19: 211–236

Katan J (1985) Solar disinfestation of soils. In: Parker CA, Rovira AD, Moore KJ, Wong PTW and Kollmorgen JF (eds) Ecology and Management of Soil-borne Plant Pathogens (pp 274–278) APS Press, St. Paul

Keinath AP (1996) Soil amendment with cabbage residue and crop rotation to reduce gummy stem blight and increase growth and yield of watermelon. Plant Disease 80: 564–570

Kulkarni RN, Kalra A and Ravindra NS (1992) Integration of soil solarization with host resistance in the control of dieback and collar and root rot diseases of periwinkle. Tropical Agriculture 69: 217–222

Lutz AL and Menge JA (1991) Population fluctuations and the numbers and types of propagules of *Phytophthora parasitica* that occur in irrigated citrus groves. Plant Disease 75: 173–179

Mahrer Y, Naot O, Rawitz E and Katan J (1984) Temperature and moisture regimes in soils mulched with transparent polyethylene. Soil Science Society of America Journal 48: 362–367

Mayton HS, Olivier C, Vaughn SF and Loria R (1996) Correlation of fungicidal activity of *Brassica* species with allyl isothiocyanate production in macerated leaf tissue. Phytopathology 86: 267–271

McIntosh DL (1972) Effects of soil water suction, soil temperature, carbon and nitrogen amendments, and host rootlets on survival in soil of zoospores of *Phytophthora cactorum*. Canadian Journal of Botany 50: 269–272

Mitchell DJ (1978) Relationships of inoculum levels of several Soil-borne species of*Phytophthora* and *Pythium* to infection of several hosts. Phytopathology 68: 1754–1759

Mitchell DJ and Kannwischer-Mitchell ME (1992) *Phytophthora*. In: Singleton LL, Mihail JD and Rush CM (eds) Methods for Research on Soil-borne Phytopathogenic Fungi (pp 31–38) APS Press, St. Paul

Myers DF, Campell RN and Greathead AS (1983) Thermal inactivation of *Plasmodiophora brassicae* Woron. and its attempted control by solarization in the Salinas Valley of California. Crop Protection 2: 325–333.

Neher D and Duniway JM (1991) Relationship between amount of *Phytophthora parasitica* added to field soil and the development of root rot in processing tomatoes. Phytopathology 81: 1124–1129

Neher D and Duniway JM (1992) Dispersal of *Phytophthora parasitica* in tomato fields by furrow irrigation. Plant Disease 76: 582–586

Neher DA, McKeen CD and Duniway JM (1993) Relationships among Phytophthora root rot development, *P. parasitica* populations in soil, and yield of tomatoes under commercial field conditions. Plant Disease 77: 1106–1111

Porter IJ and Merriman PR (1983) Effects of solarization of soil on nematode and fungal pathogens at two sites in Victoria. Soil Biology and Biochemistry 15: 39–44

Porter IJ, Merriman PR and Keane PJ (1991) Soil solarization combined with low rates of soil fumigants controls clubrot of cauliflowers, caused by *Plasmodiophora brassicae* Woron. Australian Journal of Experimental Agriculture 31: 843–851

Pullman GS, DeVay JE and Garber RH (1981) Soil solarization and thermal death: a logarithmic relationship between time and temperature for four soilborne plant pathogens. Phytopathology 71: 959–964

Pullman GS, DeVay JE, Garber RH and Weinhold AR (1979) Control of soil-borne fungal pathogens by plastic tarping of soil. In: Schippers B and Gams W (eds) Soil-borne Plant Pathogens (pp 431–438) Academic Press, New York

Ramirez-Villapudua J and Munnecke DE (1987) Control of cabbage yellows (*Fusarium oxysporum* f. sp. *conglutinans*) by solar heating of field soils amended with dry cabbage residues. Plant Disease 71: 217–221

Ramirez-Villapudua J and Munnecke DE (1988) Effect of solar heating and soil amendments of cruciferous residues on *Fusarium oxysporum* f. sp. *conglutinans* and other organisms. Phytopathology 78: 289–295

Ristaino JB, Duniway JM and Marois JJ (1988) Influence of frequency and duration of furrow irrigation on the development of Phytophthora root rot and yield in processing tomatoes. Phytopathology 78: 1701–1706

Ristaino JB, Hord MJ and Gumpertz ML (1992) Population densities of *Phytophthora capsici* in field soils in relation to drip irrigation, rainfall, and disease incidence. Plant Disease 76: 1017–1024

Shew HD (1983) Effects of soil matric potential on infection of tobacco by *Phytophthora parasitica* var. *nicotianae*. Phytopathology 73: 1160–1163

Sidebottom JR and Shew HD (1985a) Effects of soil texture and matric potential on sporangium production by *Phytophthora parasitica* var. *nicotianae*. Phytopathology 75: 1435–1438

Sidebottom JR and Shew HD (1985b). Effect of soil type and matric potential on infection of tobacco by *Phytophthora parasitica* var. *nicotianae*. Phytopathology 75: 1439–1443

Souza NL (1994) Solarização do solo. Summa Phytopathologica 20: 3–15

Stapleton JJ and DeVay JE (1986) Soil solarization: a non-chemical approach for management of plant pathogens and pests. Crop Protection 5: 190–198

Tjamos EC and Fravel DR (1995) Detrimental effects of sublethal heating and *Talaromyces flavus* on microsclerotia of *Verticillium dahliae*. Phytopathology 85: 388–392

Wicks TJ (1988) Effect of solarisation on the control of *Phytophthora cambivora* in almond and cherry. Australian Journal of Experimental Agriculture 28: 539–545