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Exposure Time to Lethal Temperatures for *Meloidogyne incognita* Suppression and Its Implication for Soil Solarization

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Abstract: Meloidogyne incognita eggs or J2 were incubated in test tubes containing sand:peat mix and immersed in a water bath heated to 38, 39, 40, 41, 42, 43, 44 and 45°C for a series of time intervals. Controls were maintained at 22°C. Nematodes surviving or hatching were collected from Baermann trays after three weeks of incubation. Regression analyses between percent survival or egg hatch and hours of heat treatment were performed for each temperature. Complete suppression of egg hatch required 389.8, 164.5, 32.9, 19.7 and 13.1 hours at 38, 39, 40, 41 and 42°C, respectively. Complete killing of J2 required 47.9, 46.2, 17.5 and 13.8 hours at 39, 40, 41 and 42°C, respectively. J2 were not completely killed at 38°C within 40 hours of treatment, but were killed within one hour at 44 and 45°C. Effect of temperature on nematode killing is not determined by heat units. Oscillating temperature between cool and warm did not interfere with the nematode suppressive effect by the heat treatment. Six-week solarization in the field during the summers of 2003 and 2004 in Florida accumulated heat exposure times in the top 15 cm of soil that surpassed levels required to kill *M. incognita* as determined in the water bath experiments. Although near zero *M. incognita* were detected right after solarization, the nematode population densities increased after a cycle of a susceptible pepper crop. Therefore, future research should address failure of solarization to kill nematodes in the deeper soil layers.

Key words: Capsicum annuum, bell pepper, soil temperature, heat units, *Meloidogyne incognita,* solarization, root-knot nematodes.

Soil solarization is the heating of soil beneath transparent polyethylene mulch by solar energy to temperatures detrimental to soil-borne pests and pathogens (Katan et al., 1976). Most recommendations in the literature suggest that solarization be conducted for at least four weeks to achieve sufficient pest or pathogen management (Katan, 1981; Stapleton and Devay, 1983; McGovern et al., 2002). The upper soil layers under the plastic increase in temperature, causing mortality of a variety of plant pathogens (Katan et al., 1976). The method has been used successfully against nematode pests in various regions in the world, including areas with relatively cloudless conditions and hot weather (Katan, 1981; Stapleton and Devay, 1983; Heald and Robinson, 1987), humid climates such as that in Florida (McSorley and Parrado, 1986; Chellemi et al., 1993) and even during summer in temperate regions such as Oregon (Pinkerton et al., 2000). However, the efficacy of solarization varies with climate and weather conditions. For example, a prolonged period of cool rainy weather during fall in Florida resulted in poor performance of solarization for nematode management in one study (Wang et al., 2004). Many factors might affect the performance of solarization, including soil structure and moisture, temperature, day-length and intensity of sunlight (Souza, 1994; Coelho et al., 2001). This research focuses on temperatures commonly achieved by solarization in Florida that can be lethal to the root-knot nematode, *Meloidogyne incognita* (Kofoid and White, 1912) Chitwood, 1949, one of the key plant-parasitic nematodes worldwide.

While extensive studies have shown that heating soil in water tanks to 50°C for 15 minutes will kill most of the important plant-parasitic nematodes (McSorley et al., 1984; Tsang et al., 2003), little information is available on exposure times required to kill plant-parasitic nematodes at temperatures below 45°C, temperatures commonly achieved through solarization. For convenience, temperatures below 45°C that kill nematodes after prolonged exposure are hereby referred to as sub-acute lethal temperature. Although solarization was considered one of the most effective non-chemical management strategies against plant-parasitic nematodes (Rosskopf et al., 2005), some farmers are reluctant to practice solarization due to the length of treatment required. Limited studies are available regarding the potential of a shorter solarization period if solarization were to be conducted during a hotter summer. The current study may lead to guidelines for minimizing the duration of the solarization period needed to manage *M. incognita*.

Exposure time for sub-acute lethal temperatures to suppress four soil-borne fungal pathogens has been studied by Pullman et al. (1981). A similar study in nematology is limited only to reniform nematode, *Rotylenchulus reniformis* (Heald and Robinson, 1987). Information, however, on the lethal temperature for the commonly occurring root-knot nematodes (*Meloidogyne* spp.) is still lacking. Thus, the goal of this study was to determine exposure times at sub-acute lethal temperatures necessary to kill the root-knot nematode species *M. incognita*. Specific objectives were: (i) to determine the lethal temperature and its exposure time to kill *M. incognita* under laboratory conditions, (ii) to examine if survival rate (or percent killed) of *M. incognita* is determined by heat units, (iii) to test if the exposure time to lethal temperature is cumulative, and (iv) to relate the laboratory-determined lethal temperature for *M. incognita* to the effect of soil solarization in the field during a hot summer in Florida.

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Materials and Methods

Experiment 1 (sub-acute lethal temperature and exposure time): A water bath experiment was conducted to determine the lethal temperature and duration of sub-lethal temperatures necessary to kill *M. incognita* under laboratory conditions. Eggs or second-stage juveniles (J2) of *M. incognita* race 2 (500 per tube) were added to 15 g of a sand:peat mix (4:1 v/v) with 6% moisture in test tubes. The test tubes were immersed in a water bath and heated for 10, 20, 30 and 40 hr at 38, 39 and 40°C, for 5, 10 and 15 hr at 41, 42 and 43°C, or 1 and 2 hr at 44 and 45°C. For each time × heat temperature combination, a room temperature treatment (average of 22°C) served as the control. Each treatment was replicated three times. At the end of the temperature treatment, eggs or J2 in the sand:peat mix were incubated at room temperature on Kimwipes (Kimberly-Clark Corporation, Roswell, GA) tissue paper in Baermann trays (Rodriguez-Kabana and Pope, 1981) for 3 wk, and surviving or hatching J2 were collected at weekly intervals. The experiment was conducted twice.

Experiment 2 (accumulation of exposure time): A separate water bath experiment was conducted to examine if the temperature needed to kill *M. incognita* J2 is cumulative. Aliquots of *M. incognita* J2 (100/tube) were added to test tubes containing a sand:peat mix described earlier. Test tubes were: 1) immersed in a water bath heated to 42°C continuously, 2) immersed in water bath heated to 42°C and cooled down at room temperature (22°C) at 3-hr intervals, or 3) kept at room temperature. The first two treatments were conducted for 6, 9, 15, 21, 27 or 33 hr. Tubes that were removed from the 42°C water bath were kept at 22°C until the 33-hr experimental period was complete. The third treatment (control) was left at room temperature for the entire 33 hr. Each temperature × exposure time combination was replicated three times, giving a total of 33 experimental units for these combinations.

Experiment 3 (Field Solarization): A 2-yr field study was conducted in 2003 and 2004 in Citra, Alachua County, FL, to examine the nematode suppressive effect of solarization. The soil was a Candler sand (hyperthermic, uncoated, Entisol) (95.2% sand, 1.5% silt, 3.3% clay; 1.64% organic matter). The most dominant plant-parasitic nematode found at this site was *M. incognita*. Solarization started at the end of July to the middle of August and lasted for 6 wk in both years. Solarization was conducted on a raised bed (0.9 m wide × 18.24 m long × 20 cm high), covered with a transparent, 25-µm-thick, UV-stabilized, low-density polyethylene mulch (ISO Poly Films, Inc., Gray Court, SC). Soil moisture content prior to solarization averaged 6%. A fallow with weed treatment was included as a control. Plots were arranged in a randomized complete block design with six replications. The exact same plot arrangement was used in 2003 and 2004. Soil temperatures were recorded at 5- and 15-cm depths throughout the solarization period using Watch Dog Model 425 data loggers (Spectrum Technologies, Inc., Plainfield, IL). Two weeks after solarization, 'Wizard X3R' bell pepper (*Capsicum annuum* L., a good host for *M. incognita*) seedlings were transplanted in each bed. Experiments lasted for 3 mon after pepper transplanting. Soil samples were collected from each plot after solarization and at the end of the pepper crop. Six soil cores (2.5-cm diam. × 20-cm deep) were taken from each plot and combined into one composite sample. Nematodes were extracted from a 100-cm^3 sub-sample by a modified sieving and centrifugal flotation method (Jenkins, 1964). Additional details of these experiments including crop yields are reported elsewhere (Wang et al., 2006; Saha et al., 2007).

Statistical analysis: Regression analyses between percent J2 survival, or egg hatch compared to the control, and hours of heat treatment were performed for each temperature. Regression equations were derived using SAS software (Statistical Analysis System, Cary, NC). Length of time to kill and lethal heat units for eggs and J2 were determined for each temperature based on these regression equations. Heat units (in degree hours) were calculated according to the following equation:

$$\text{Heat units} = (T_m - T_b) \times \text{hours of exposure} \quad (1)$$

where T_m = the measured experimental temperature and T_b = an experimentally determined base or threshold temperature for heat unit accumulation.

Results

Sub-acute lethal temperature and exposure time: Less than 1% of J2 were recovered when exposed to 44°C or 45°C for 1 hour. No J2 survived when exposed to 43°C for 3 hours (data not shown). No mortality occurred at 38°C. While no significant regression between percent J2 surviving and exposure time occurred for treatments at 43°C to 45°C as well as at 38°C, significant ($P < 0.01$) regressions were obtained at 39°C to 42°C, and these followed exponential decline curves (Fig. 1). Based on these results, we determined that 38°C is the minimum temperature to kill 100% of *M. incognita* race 2 J2, and this was used as the base temperature for heat unit calculation. Using each of the regression equations for 39 to 42°C, the hours to kill 100% of J2 were calculated (Table 1). Over the range from 39 to 42°C, hours needed to kill 100% of J2 decreased as the temperature increased. Only 13.8 hours were required to kill 100% of J2 at 42°C (Table 1).

No egg hatch occurred at 45°C when eggs were exposed for only 1 hour. Significant ($P < 0.01$) exponential regression curves occurred between percent egg hatched and hours of exposure for temperatures from 38 to 42°C (Fig. 2). However, among these tempera-

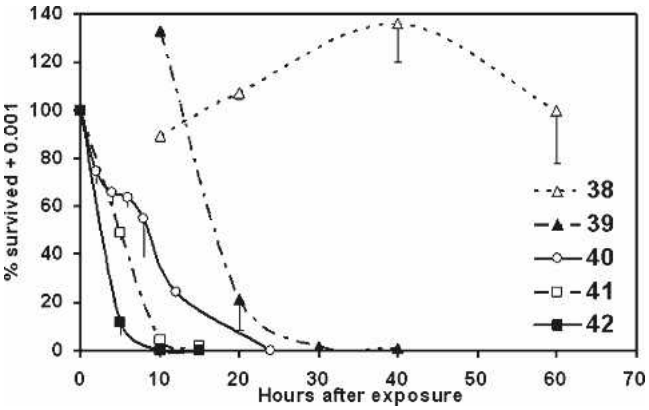

FIG. 1. Percentage of *Meloidogyne incognita* J2 surviving after exposure to 38–42°C for various time intervals. Each point represents percentage of recovery compared to that recovered at 22°C over a 3-week period. Data from 38°C did not fit in an exponential curve. Equations for exponential curves fitted to data are: for 39°C, y = Exp (2.02 – 0.19 x) (R^2 = 0.86, P < 0.0001, df = 11); for 40°C, y = Exp (0.23 – 0.15 x) (R^2 = 0.80, P < 0.0001, df = 11); for 41°C, y = Exp (1.18 – 0.46 x) (R^2 = 0.75, P < 0.002, df = 11); for 42°C, y = Exp (–0.63 – 0.45 x) (R^2 = 0.78, P < 0.002, df = 11), where y = log[(% of J2 surviving + 0.1)/100], and x is the hours of exposure. Vertical bars represent lower limit of standard error bars. No visible SE bar indicates that SE was very low.

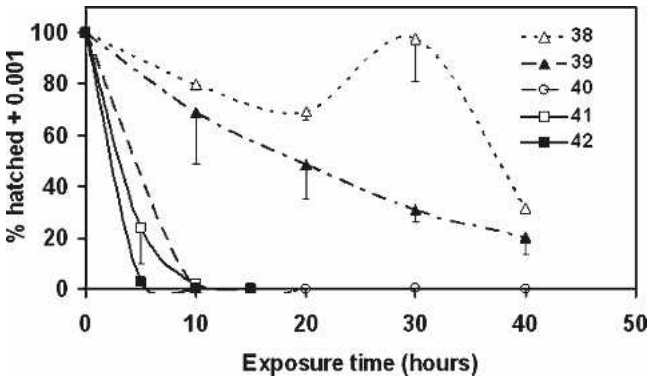

FIG. 2. Percentage of egg hatch of *Meloidogyne incognita* race 2 after exposure to 38–42°C for various time intervals. Each datum represents percentage of hatch as compared to that hatch at 22°C over a 4-week period. Equations for curves are: on 38°C, y = Exp (0.03 – 0.0178 x) (R^2 = 0.46, P < 0.01, df = 14); 39°C, y = Exp (0.0007 – 0.042 x) (R^2 = 0.72, P < 0.001, df = 14); 40°C, y = Exp (–2.68 – 0.13 x) (R^2 = 0.46, P < 0.01, df = 14); 41°C, y = Exp (0.04 – 0.35 x) (R^2 = 0.99, P < 0.0001, df = 12); and 42°C. y = Exp (–0.85 – 0.47x) (R^2 = 0.86, P < 0.0001, df = 12), where y = log[(% hatch + 0.1)/100], x is the hours of exposure. Vertical bars represent lower limit of standard error bars. No visible SE bar indicates that SE was very low.

tures, data at 38°C resulted in the poorest fit (R^2 < 0.5, P < 0.01) to the exponential curve, with an increased percent egg hatch when exposed for 30 hours (Fig. 2). Therefore, 38°C was also considered as the base temperature for heat unit calculation. Nearly 390 hours were required to kill 100% of *M. incognita* eggs at 38°C. The exposure time necessary to kill 100% of eggs dropped greatly when temperature was increased to 40°C, and only 13.1 hours were required at 42°C (Table 1).

Using 38°C as the base temperature, the heat units required to kill 100% of *M. incognita* eggs and J2 differed between temperatures (Table 1). While heat units required for killing eggs decreased quickly as temperature increased, total heat units needed for killing J2 were similar at 39 and 40°C (Table 1).

Accumulation of exposure time: No *M. incognita* J2 survived 15 hours or more of either continuous (42°C) or oscillating (42/22°C) heat treatment (Table 2). Higher numbers of nematodes survived when exposed to 42/22°C than when exposed to 42°C continuously for 9 hours (P < 0.05). Comparing J2 survival at fluctuating vs. continuous temperature regimes with a maximum of 42°C under the same heat exposure time, a greater (P < 0.05) number of J2 survived after 9 hours at 42/22°C (equivalent to 6 hours at 42°C) than after 6 hours of continuous 42°C (Table 3). However, survival was similar (P > 0.05; Table 2) after 15 hours at 42/22°C (equivalent to 9 hours of 42°C) and 9 hours at continuous 42°C.

Field Solarization: Detailed temperature data collected from the field solarization experiment was previously published (Wang et al., 2006), but hours accumulated above 40°C at 5- and 15-cm soil depths are calculated here for each temperature interval (Table 3). As expected, the majority of temperatures in solarized beds were between 40 to 45°C, especially at a 15-cm soil depth (Table 3). In both 2003 and 2004, the hours of exposure above the specific temperature, either at 5- or 15-cm soil depth, exceeded the minimum number of

TABLE 1. Hours and heat units required to kill 100% of *Meloidogyne incognita* eggs or juveniles (J2).

Temperature (°C)	Hours to kill 100%[a]		Heat units to kill 100%[c]	
	Eggs	J2	Eggs	J2
	(Hours)		(Degree hours)	
38	389.8	—[b]	14,812	—
39	164.5	47.9	6,415	1,868
40	32.9	46.2	1,316	1,848
41	19.7	17.5	808	718
42	13.1	13.8	550	580

[a] Hours to kill and heat units were estimated from regression equations in Fig. 1

[b] Not determined because no significant regression line fit for data at 38°C.

[c] Heat units = temperature × hours to kill 100% of eggs or J2; heat units accumulated above base temperature of 38°C, see text.

TABLE 2. Percentage of root-knot nematode juveniles (J2) surviving under continuous (42°C) and oscillating (42°C and 22°C at 3-hr intervals) heat at different heat exposure times.

Hours of treatment	Continuous heat	Oscillating heat
	J2 surviving (%)	
6	0 b	—
9	3.2 b	11 a
15	0 b	0 b

Means are average of three replications. Data from all hour-heat treatments were subjected to one-way analysis of variance. Means followed by same letter are not different (P > 0.05) according to Waller-Duncan k-ratio t test (k-ratio = 100).

TABLE 3. Hours accumulated at different temperature above 40°C at 5- or 15-cm soil depths in 2003 and 2004 field experiments.

Temperature (°C)	Soil depth			
	2003		2004	
	5 cm	15 cm	5 cm	15 cm
40–40.9	31	28	21	33
41–41.9	18	26	31	25
42–42.9	15	14	22	23
43–43.9	26	9	21	8
44–44.9	51	9	26	2
45–45.9	11	0	18	0
46–46.9	4	0	11	0
47–47.9	13	0	22	0
48–48.9	8	0	17	0
49–49.9	3	0	2	0
50–50.9	4	0	1	0
51–51.9	4	0	2	0
52–52.9	0	0	0	0
53–53.9	0	0	2	0
54–54.9	0	0	1	0

hours required to kill 100% of *M. incognita* eggs or J2 as determined in the water bath experiment (Table 1). However, solarization did not suppress ($P > 0.05$) numbers of *M. incognita* J2 in soil at the beginning or end of the pepper crop as compared to a non-solarized control (Table 4).

DISCUSSION

The water bath experiment demonstrated that exposure time to kill all *M. incognita* J2 decreased as the temperature above 38°C increased. At 38°C, J2 that survived did not decrease exponentially as the hours of heat exposure increased. Therefore, 38°C is considered to be the base temperature to kill 100% of root-knot nematode J2 in the water bath, and thus heat units are calculated as:

$$\text{Heat units} = (T - 38°C) \times \text{hours of exposure} \quad (2)$$

Similar results were observed for the elimination of *M. incognita* eggs. Although percent egg hatch at 38°C fit an exponential equation, the trend of egg hatch fluctuated, with high survival rates even when exposed to this temperature for 30 hours. At 38°C, up to 390 hours were required to kill 100% of the eggs, which was more than twice the duration needed to kill eggs at 39°C. Therefore, 38°C is also a suitable base temperature for egg suppression.

Since less than 14 hours of exposure to 42°C is enough to suppress 100% *M. incognita* egg hatch or J2 development, this exposure time can generally be obtained with a six-week period of solarization during a hot summer in Florida (Table 2). In earlier research, Ploeg and Stapleton (2001) reported that heating the soil to 40°C for 10 days generally eliminated nematode infestation and root-galling. However, the current experiment showed that at 40°C, only 46 and 33 hours are required to kill 100% of the J2 and eggs, respectively. Differences between the current and previous research could be attributed to differences in soil edaphic factors and also the fact that a melon-plant bio-assay was used to detect nematode survival in the study by Ploeg and Stapleton (2001).

At temperatures of 43°C or higher, *M. incognita* J2 and eggs were killed rapidly. We can only conclude that less than one hour is needed to kill *M. incognita* at 44°C. However, it was not our objective to determine the duration of time needed to kill *M. incognita* at each lethal temperature, since many similar studies have demonstrated the duration of heat treatment required for sanitizing planting materials at relatively high temperatures. For example, treating bamboo palm in a pot at 50°C for 15 minutes eliminated *Radopholus similis* (Tsang et al., 2003), and treating garlic at 47.5°C for 15 minutes eliminated *M. incognita* (McSorley et al., 1984).

Based on Equation (1), heat killing of *M. incognita* is not heat-unit dependent. Heat units required to kill the nematodes varied from one temperature to another; at temperatures above 38°C, fewer heat units are required to kill the nematodes. It is surprising that the amount of heat units to kill eggs was not always higher than that required to kill J2. Since eggs are the survival stage for *M. incognita,* we anticipated that eggs would be harder to kill than J2, but the data did not support this theory. This could be due to the fact that eggs tested here were not clustered as egg masses, since the gelatinous matrix surrounding the *M. incognita* eggs used in laboratory experiments was removed when eggs were extracted from the roots in NaOCl.

Heald and Robinson (1987) demonstrated that repeated daily exposure of soil for 100 minutes to 44°C in a water bath for eight days killed more *R. reniformis* than a single day of 100 minutes exposure to 44°C. This indicated that a cumulative lethal effect occurred for exposure time to lethal temperatures. The current experiment supported this finding when minimum accumulated exposure time was achieved. At 42°C, 13 to 14 hours were required for total kill of *M. incognita* (Table 1). Oscillating cool and warm temperatures kill *M. in-*

TABLE 4. Numbers of *Meloidogyne incognita* per 100 cm^3 soil in solarized and control plots at the end of solarization and at end of pepper crop in 2003 and 2004.

Treatment	2003	2004
	End of solarization	
Solarization	0	1.2
Control	0	0.7
	End of pepper crop	
Solarization	56	32
Control	181	122

Means are average of six replications. Data in a column for each sampling date are not different according to analysis of variance based on log (x+1) transformation ($P > 0.05$).

cognita J2 after 15 hours of exposure, achieving the same complete kill as the continuous heat treatment. This effect was not observed if the exposure time was below 14 hours. This result also suggested that the interruption of heat treatment by cool temperatures did not interfere with nematode suppression at a particular temperature, provided that the minimum heat exposure time was achieved.

Soil solarization for six weeks in 2003 and 2004 accumulated many hours of exposure from 40°C to 45°C that easily surpassed the lethal exposure time for *M. incognita* at soil depths of 5 and 15 cm. Based on the data collected from the water bath experiment, *M. incognita* should be eliminated from the top 15-cm soil layer, which is reflected in the nematode sample collected at the end of solarization. Heald and Robinson (1987) conducted a similar study on *R. reniformis*, in the Lower Rio Grande Valley of Texas and found that soil solarization for four, six and eight weeks substantially reduced *R. reniformis* population density 0- to 15-cm deep when sampled after solarization as compared to the control and consistently surpassed soil fumigation with 1,3-dichloropropene in reducing nematode population density within the top 7.5 cm of soil. However, suppression of *R. reniformis* by solarization was not efficient at deeper soil layers (Heald and Robinson, 1987).

It is well known that fallow is a strategy to suppress plant-parasitic nematodes (Barker and Koenning, 1998). Therefore, it is not surprising to find no *M. incognita* in fallow control and solarization treatments at the end of the solarization period in 2003 and 2004. Following one cropping season of pepper in both the 2003 and 2004 experiments, *M. incognita* population densities increased to levels not statistically different from the control, indicating that solarization did not eliminate *M. incognita* from the soil in our field studies. This result is consistent with previous reports (McSorley and Parrado, 1986; McSorley et al., 1999) showing that plant-parasitic nematode levels recovered in solarized plots when a susceptible crop was introduced to the soil. However, residual suppression of *M. incognita* by solarization lasting until the end of a susceptible crop has been reported in one study (McGovern et al., 2002). Failure of solarization to eliminate *M. incognita* despite the sufficient exposure time to lethal temperature in the upper soil layers was most likely due to lower soil temperatures deeper in the soil. Temperature data from deeper soil layers were not collected in our research, however Chellemi et al. (1993) reported that soil temperatures at a 25-cm depth in a plot following eight weeks of solarization during the summer in south Florida only reached 26 to 35°C. Similar results were obtained by Heald and Robinson (1987) for *R. reniformis*. Hewlett and Dickson (1991) demonstrated that *Meloidogyne* spp. J2 and eggs can be present and survive at soil depths much greater than 15 cm. When crops are planted on solarized soil, host roots can attract nematodes from lower in the soil profile that may move up to the topsoil layer, eventually negating the beneficial effect of many nematode-management tactics. Heald and Robinson (1987) suggested that the length of the duration of the solarization period is not the limiting factor for failure of solarization for suppression of plant-parasitic nematodes at the end of a susceptible crop, but rather the temperature that is reached in the lower soil depths is more critical to sustaining reductions in nematode levels achieved by solarization. Future work to improve heating of the deeper soil layers may improve the longevity of solarization benefits.

In conclusion, heat-kill of nematodes is dependent on cumulative exposure time at a specific lethal temperature but not on accumulated heat units. Soil temperatures achieved during a six-week solarization period in two field experiments surpassed the accumulated exposure time required to kill *M. incognita*. Although near-zero numbers of *M. incognita* were detected after solarization and in the control plots, the nematode population densities began to recover after a cycle of a susceptible pepper crop. The length of current solarization period is not the limiting factor for the suppression of plant-parasitic nematodes; rather, the temperature reached at deeper soil depth is more critical. Alternatively, it is possible that one could solarize when the majority of the nematodes are in the higher soil profile.

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