

## Induced Suppressiveness in Solarized Soils

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This research was supported by Grant No. I-481-82C from BARD, the U.S.-Israel Binational Agricultural Research and Development Fund.

We thank A. Grinstein and H. Ashkenazi for planning the simulation system and for helpful suggestions and Sara Erez and Susan Lourie for their assistance.

Accepted for publication 27 July 1987 (submitted for electronic processing).

## ABSTRACT

Greenberger, A., Yogev, A., and Katan, J. 1987. Induced suppressiveness in solarized soils. *Phytopathology* 77:1663-1667.

The fate of inoculum added to untreated or previously disinfested soils and disease incidence in these soils were investigated. In most of the solarized soils tested, disease incidence was lower than in the comparable untreated soils, as shown with bean plants in soils infested with *Sclerotium rolfsii* and tomato seedlings inoculated with *Fusarium oxysporum* f. sp. *lycopersici*. The incidence of Fusarium wilt of tomato was also lower in artificially heated soil but higher in one out of 10 solarized soils and one out of two soils fumigated with methyl bromide. In solarized soils,

chlamydospore formation by *F. o. f. sp. lycopersici* was suppressed. In these soils, populations of lysing bacteria of *S. rolfsii* frequently increased, and fungistasis to this pathogen decreased, proportionally to the level of fungistasis in untreated soils. Establishment of *F. o. f. sp. lycopersici* was better in soils preheated to temperatures above 75 C. Solarized soils are frequently more suppressive and less conducive to certain soilborne pathogens than nonsolarized soils.

*Additional key words:* biological control, *Fusarium oxysporum* f. sp. *vasinfectum*, mulch, polyethylene tarping, solar heating.

Soil disinfestation by chemical or physical means is a drastic soil treatment that affects both the pathogen population and the microbial biological equilibrium in the soil (2,5). Hence, disinfestation may affect not only the primary natural inoculum existing in the soil but also pathogens introduced to the soil after the termination of disinfestation and, consequently, the rate of reinfestation (21,25). There are indications from field studies that in certain cases pathogen establishment in previously solarized (solar-heated) soils is more difficult than in untreated ones, apparently because of a shift in the microbial balance. Thus, levels of Verticillium wilt in eggplants and tomatoes and pink root disease in onions remained low for 160–195 days of plant growth, though soil tarping (in strips) allowed continuous reinfestation of the solarized soil from the surrounding infested nonsolarized soil, throughout the growing period (16,18). Similarly, solarization had a long-term effect (for 2–3 yr) in controlling several diseases, e.g., Fusarium wilt in cotton, even though recontamination of the soil cannot be completely avoided (14,15,17,32). There is also direct evidence that solarized soils become suppressive to certain pathogens, e.g., *Fusarium oxysporum* f. sp. *dianthi*, *Phytophthora cinnamomi*, and *Rosellinia necatrix* (10,13,26,31).

In the present work we studied suppressiveness, in various soils, induced by solarization and the possible mechanisms involved. A brief report of the results was published earlier (9).

## MATERIALS AND METHODS

Soils of various textures were collected from fields at 18 locations in Israel (Table 1). The soils were untreated, solarized, or fumigated with methyl bromide at 55 g/m<sup>2</sup>. Solarized and nonsolarized soils were collected from the upper 15-cm layer of experimental plots (8 × 15 m or larger) or commercial fields in which the soil was either manually or mechanically mulched. Solarization was carried out by mulching preirrigated soils with transparent polyethylene sheets (30–50 μm thick) in June or July, and the solarization lasted for 5–8 wk. Typical temperatures of the solarized soils were 44–48 C and 36–40 C at depths of 10 and 30 cm, respectively. The temperatures of the comparable nonsolarized

soils were 7–12 C lower. Fumigation with methyl bromide was carried out by the hot gas technique, with commercial equipment. Plants grown under greenhouse conditions at 24–30 C were maintained for 20–25 days after inoculation as described below. Artificial heating of the soil at 75–95 C was carried out in a water bath with a heating system (Fried Electric, Haifa, Israel) with an accuracy of ±0.1 C.

**Introduction of sclerotia of *Sclerotium rolfsii* to soil.** Sclerotia of *Sclerotium rolfsii* Sacc. were produced by growing the pathogen (isolated from diseased bean seedlings) on Joham agar (22) for 50 days at 30 C. The dried sclerotia were removed from the plates and separated, using 0.50- to 0.84-mm sieves. Only sclerotia stocks with a 90–100% rate of eruptive germination were used. Soil was mixed with these sclerotia (30 mg/g of soil), initially moistened to 70% of field capacity, and incubated for 24 days under greenhouse conditions, in six 19 × 9 × 10-cm open plastic boxes, each containing 1,000 g of soil at 70–100% of field capacity. Each box

TABLE 1. Properties of soils used

Location	pH	Organic matter (%)	Clay (%)	Silt (%)	Sand (%)
Bet Alfa	7.6	1.3	57.5	27.5	15.0
Bet Dagan	7.5	1.4	52.5	25.0	22.5
Bet HaShitta	7.2	1.3	75.0	10.0	15.0
Bsor	8.1	0.4	5.0	0	95.0
Deganya	7.9	2.0	43.0	43.0	14.0
Dorot	7.7	1.2	30.0	7.5	62.5
Eden	7.9	2.2	21.2	23.8	55.0
En Dor	7.6	1.7	42.5	32.5	25.0
Gaash	7.3	0.7	5.0	1.3	93.7
Gilat	7.8	0.8	20.0	15.0	65.0
Gilgal	8.1	1.6	30.0	32.5	37.5
Mahanayim	7.5	25.0	17.5	20.0	62.5
Newe Ur	7.8	1.8	53.1	31.5	15.4
Rehovot	7.6	0.4	3.8	0	96.2
Sede Eliyyahu	7.7	3.4	37.5	37.5	25.0
Shoval	8.0	0.8	34.1	14.2	51.7
Tira	7.2	0.7	31.4	8.4	60.2
Tirat Zevi	8.3	2.1	55.8	35.0	9.2

was then planted with 12 bean seeds (*Phaseolus vulgaris* L. 'Brittle Wax'). No fertilizers were added. The number of plants showing postemergence damping-off was recorded throughout the growth period. Preemergence damping-off was calculated by comparison with the emergence percentage in control boxes with uninfested soil. Isolations showed the presence of the pathogen in diseased seedlings and rotted unemerged seeds and seedlings. Uninoculated plants maintained under the same conditions remained healthy.

**Inoculation of tomato seedlings with *Fusarium*.** Tomato seedlings (*Lycopersicon esculentum* Mill. 'Rehovot 13'), inoculated by dipping roots 2 min in a conidial suspension (300,000 conidia per ml) of *F. o. f. sp. lycopersici* (Sacc.) Snyder & Hans., race 2, were transplanted into untreated or disinfested soils in six replicates of 15 plants each. In one experiment (referred to in Fig. 2), the soil was artificially heated in a specially designed simulation heating system, in which the daily heating course of the soil was similar to that obtained during solarization in the upper 10-cm layer of soil. Two-liter plastic boxes (21 cm high) were filled with moistened soil at 100% of field capacity, covered with polyethylene to prevent evaporation, and maintained in water-filled modified Wisconsin temperature tanks for 35 days. The heating system in these tanks resulted in heating of the soil to 45 C for about 4 hr every day, after which the temperature dropped gradually to 30–33 C. This simulated the pattern obtained in the upper soil layer during natural solarization in hot-climate countries (14). The inoculated seedlings were maintained in the greenhouse for 25 days, and diseased seedlings showing typical wilt were counted daily. Uninoculated seedlings maintained under the same conditions remained healthy.

**Chlamydospore formation in the soil.** Disks (5 mm in diameter) cut from dialysis tubing were laid on potato-dextrose agar plates. Aliquots (0.2 ml) of *Fusarium* conidial suspension in sterile water were spread on the medium in each plate. After 48 hr of incubation at 27 C, disks covered with mycelium and conidia were incubated 4 hr in plates containing distilled water agar, to remove adhering nutrients by diffusion. The disks were then placed between two 2 × 2-cm pieces of dialysis tubing, buried in the test soil, which was moistened to 65% of field capacity, and incubated at 27 C. During the following 7 days, disks were periodically removed from the soil, gently cleaned with a small paintbrush to remove adhering soil, separated from the two dialysis tubing pieces, stained with 0.1% aniline blue in lactic acid, and then examined microscopically.

**Lytic capacity of bacterial soil population.** *S. rolfisii* was grown for 6 days in Joham broth medium. The mycelial mats were then thoroughly washed with water and cut into 2-cm-diameter disks. Each disk was transferred to a flask with 25 ml of liquid medium, containing Czapek salts but no carbon source for lytic soil bacteria except for the mycelial mat, and 500 mg of the test soil was added to each of the flasks, which were incubated in a shaker bath at 30 C. In this system only bacteria developed. Samples of the liquid were withdrawn from the flasks after 2–3 days to assess bacterial population density by dilution plating on nutrient agar medium (Difco) and incubation at 30 C.

Lytic capacity against *F. o. f. sp. lycopersici* was assessed similarly, except that the mycelial mats were produced on a broth medium containing 5 g of yeast extract, 5 g of peptone, and 20 g of glucose per liter. Then 7-cm-diameter disks of mycelium were incubated with the test soil for 5 days. In certain experiments, bacterial colonies were transferred at random to plates containing potato-dextrose agar. *S. rolfisii* was introduced, and colonies that lysed the pathogen counted.

**Fungistasis.** Sclerotia of *S. rolfisii* were incubated at 30 C in soils moistened to field capacity, in 9-cm-diameter culture plates containing about 100 g of soil. During the following 6 days, all germinating sclerotia, which were visibly distinct, were recorded.

The greenhouse and laboratory tests were repeated once or twice, with similar results. The experiment mentioned in Table 3 was repeated with five of the tested soils, with similar results. Greenhouse experiments were carried out in six replicates, and other experiments in three replicates. Unless otherwise stated, statistical analysis was done according to Duncan's multiple range test ( $P = 0.05$ ).

## RESULTS

### Disease incidence in disinfested and subsequently infested soils.

The incidence of post- and preemergence damping-off in bean seedlings, planted in two solarized soils subsequently infested with sclerotia of *S. rolfisii*, was significantly lower in one soil than in the nonsolarized infested control (Table 2). A similar trend was obtained in an additional experiment. Similarly, the percentages of wilted tomato seedlings infected with *F. o. f. sp. lycopersici* were lower in solarized soil (Fig. 1) and in soil heated in a simulation system (Fig. 2) than in untreated soils. This test was carried out in various soils, previously subjected to either solarization or fumigation with methyl bromide. Progress in disease development was delayed in eight out of 10 solarized soils tested and accelerated in one (Table 3). In one out of two soils fumigated with methyl bromide, disease development was accelerated.

**Effect on chlamydospore formation in the soil.** Three days after incubation of disks of *F. o. f. sp. lycopersici* containing mycelia and conidia, in Rehovot soil, typical chlamydospores were formed in the nonsolarized but not in the solarized soil. Partial lysis of the mycelium was observed in the solarized soil. On the fifth and seventh days both conidia and chlamydospores increased in number in the nonsolarized soil. They were absent or rare in samples from solarized soils, where the disks became heavily colonized by various fungi. Chlamydospore formation by both *F. o. f. sp. lycopersici* and *F. o. f. sp. vasinfectum*, followed for 7 days in Gaash soil, was suppressed in the solarized soil and enhanced in

TABLE 2. Effect of soil solarization on incidence of preemergence and postemergence damping-off caused by *Sclerotium rolfisii* in beans planted in two soils

Soil and treatment <sup>x</sup>	PR disease <sup>y</sup>		PR + PO disease <sup>y</sup>	
	Incidence (%)	Incidence as percentage of incidence in NS soil	Incidence (%)	Incidence as percentage of incidence in NS soil
Rehovot, NS	52 a <sup>z</sup>	100	54 a	100
Rehovot, S	6 b	11	6 b	11
Bet Dagan, NS	31 A	100	37 A	100
Bet Dagan, S	19 A	61	27 A	73

<sup>x</sup> Nonsolarized (NS) and solarized (S) soils were infested with the pathogen at the rate of 30 mg of sclerotia per kilogram and incubated for 24 days before planting of bean seeds.

<sup>y</sup> The presence of the pathogen was verified by plating portions of plants with preemergence (PR) or postemergence (PO) damping-off on potato-dextrose agar medium.

<sup>z</sup> In each soil, figures with a common letter in each column are not significantly different ( $P = 0.05$ ). Rehovot and Bet Dagan soils are designated by lower- and upper-case letters, respectively.

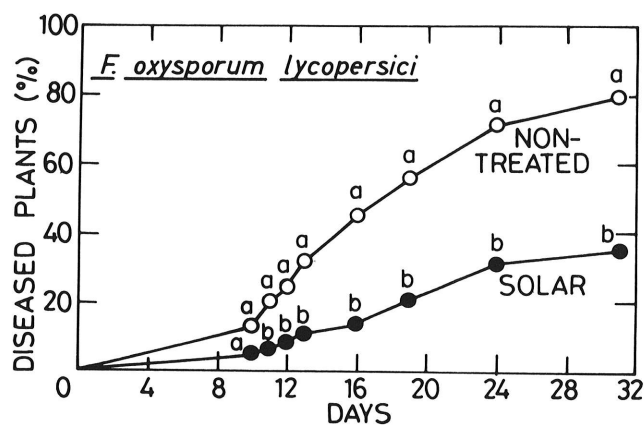


Fig. 1. Effect of soil solarization on disease percentage in tomato plants inoculated with *Fusarium oxysporum* f. sp. *lycopersici* and subsequently transplanted to nonsolarized or solarized Gaash soil. In each test period, figures with a common letter are not significantly different ( $P = 0.05$ ).

the soil treated with methyl bromide, as compared to nonsolarized soil. Abundant formation of conidia was also observed in soil treated with methyl bromide.

**Lytic capacity of the soils.** In two out of four soils tested, significantly more bacteria capable of lysing mycelium of *S. rolfesii* were isolated from the solarized soil than from the nonsolarized control treatment (Table 4). Mycelial mats added to solarized soils became partially or completely disintegrated after 3 days of incubation in Rehovot, Bet Dagan, and Tirat Zevi soils. This effect was considerably less obvious when nonsolarized soil was used. Solarization also increased percentages of lytic bacteria in one soil, assessed directly on agar plates. A similar trend of increased lytic capacity was obtained with *F. o. f. sp. lycopersici* in two soils, using mycelial mats as the sole carbon source. After 5 days of incubation with nonsolarized and solarized Bet Dagan soil,  $20 \times 10^6$  and  $58 \times$

$10^6$  cfu of bacteria, respectively, developed. Mycelial mats of this fungus incubated with solarized Gaash soil were disintegrated after 5 days of incubation. In comparison, mycelial mats incubated with nonsolarized soil became partially disintegrated, whereas those incubated with soils treated with methyl bromide remained almost intact.

**Effect on fungistasis.** Various levels of fungistasis (17–96% reduction in germination) were observed in untreated soils (Table 5). Solarization reduced fungistasis in 10 out of 11 soils tested. The exception was a soil (Newe Ur) in which fungistasis was very low to begin with. In one soil (Mahanayim), which had an unusually high percentage of organic matter (25%) and was the most fungistatic (4% germination), solarization had the most pronounced effect. The effect of solarization in reducing the fungistatic capacity could not be correlated with soil texture or other parameters. However, there was a positive correlation between the fungistatic capacity of the soil and the extent of its reduction by solarization ( $r = 0.9$ ).

**Establishment of *Fusarium* in preheated soil.** Soil samples were moistened to 70% of field capacity, heated for 1 hr at various temperatures, cooled, and infested with conidia of *F. o. f. sp. lycopersici* at the rate of 10,000 conidia per gram of soil. *Fusarium* population levels after 35 days of incubation were 24, 24, 66, 126, and 1,200% of the initial level in soil that was, respectively, unheated and heated at 75, 85, 95, and 121 C (autoclaved). Hence,

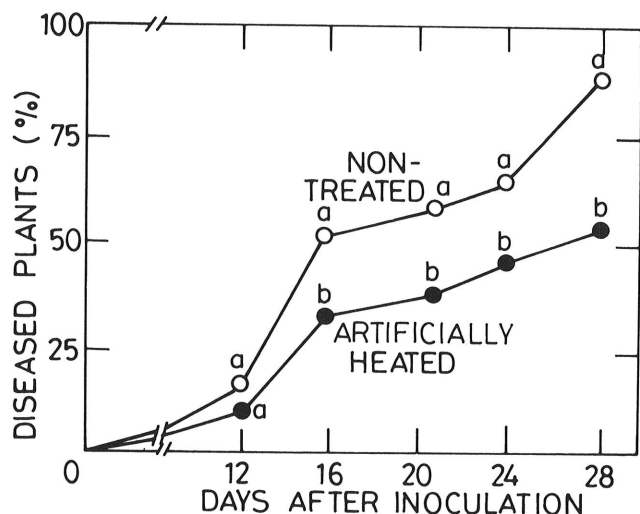


Fig. 2. Effect of heat treatment on disease percentage in tomato plants inoculated with *Fusarium oxysporum* f. sp. *lycopersici* and subsequently transplanted to the heat-treated Gaash soil in a simulation system. In each test period, figures with a common letter are not significantly different ( $P = 0.05$ ).

TABLE 3. Disease development in various soils and effect of soil solarization and fumigation with methyl bromide before inoculation<sup>y</sup>

Location	Disease development			Reduction from disease development in untreated soil <sup>z</sup> (%)
	Untreated soil (%)	Solarized soil (%)	Fumigated soil (%)	
Bet Alfa	46	9	—	80
Gaash-1	40	12	—	70
Gaash-1	40	—	53	-32
Bet Dagan	40	15	—	63
Sede Eliyyahu	42	20	—	52
Gilat	36	21	—	42
Rehovot	42	29	—	31
Bet HaShitta	34	24	—	29
Shoval	47	34	—	28
Dorot	38	37	—	3
Gaash-2	11	26	—	-136
Rehovot	28	—	29	-4

<sup>y</sup> Tomato seedlings were inoculated with *Fusarium oxysporum* f. sp. *lycopersici* before transplanting to the tested soil, and diseased plants were recorded daily throughout the test period. For each soil, disease development is defined as the percentage of diseased plants on the day when, in the respective untreated soil, the disease percentage reached 50% of its maximum obtained by the end of the experiment.

<sup>z</sup> Calculated as  $[1 - (A/B)] \times 100$ , where *A* is the disease percentage in the solarized or fumigated soil, and *B* is the disease percentage in the respective untreated soil.

TABLE 4. Lytic capacity against *Sclerotium rolfesii* and density of bacteria originating in nonsolarized and solarized soils

Soil and treatment <sup>y</sup>	Bacteria <sup>w</sup> ( $10^5$ cfu/ml)	Lysis <sup>x</sup> (%)
Rehovot, NS	16 a <sup>y</sup>	1.8 a
Rehovot, S	22 a	2.3 a
Bet Dagan, NS	93 a	0.8 b
Bet Dagan, S	560 a	3.3 a
Tirat Zevi, NS	155 b	NT <sup>z</sup>
Tirat Zevi, S	761 a	NT
Gilgal, NS	383 b	NT
Gilgal, S	829 a	NT

<sup>y</sup> Flasks containing mineral solution and mycelial mats of *S. rolfesii* as the sole carbon source were exposed to samples of nonsolarized (NS) and solarized (S) soils and incubated at 30 C.

<sup>w</sup> Evaluated in the suspension by diluting on nutrient medium; cfu = colony-forming units.

<sup>x</sup> Percentage of bacteria showing lytic activity against *S. rolfesii* in a plate on potato-dextrose agar.

<sup>z</sup> In each soil, figures with a common letter in each column are not significantly different ( $P = 0.05$ ).

<sup>z</sup> Not tested.

TABLE 5. Effect of soil solarization on germination of sclerotia of *Sclerotium rolfesii* in 11 soils

Location	Germination <sup>y</sup> (%)		Increase over germination in NS soil (%)
	NS soil	S soil	
Mahanayim	4	21	425
Eden	21	75	257
Bsor	29	61	110
Sede Eliyyahu	43	82	91
Rehovot	43	68	58
Deganya	61	79	30
En Dor	68	82	21
Bet Dagan	71	82	15
Dorot	71	79	11
Tira	79	89	13
Newe Ur	93	64	-31
Average	53	71.3 <sup>z</sup>	34

<sup>y</sup> Sclerotia were collected from a stock with 95% eruptive germination. NS = nonsolarized; S = solarized.

<sup>z</sup> Solarization significantly increased the germination of sclerotia over that in nonsolarized soil ( $P = 0.05$ , one-way analysis of variance test).

the establishment of *Fusarium* improved only in soils heated at temperatures above 75 C.

## DISCUSSION

The primary goal of soil disinfestation is to significantly reduce pathogen inoculum level in soil. However, under field conditions, recontamination cannot be avoided. Therefore, the behavior and fate of the reinfesting inoculum in the soil also determine the effectiveness of disinfestation, especially in the long run. Since disinfestation affects the biotic and abiotic components of the soil, it may consequently affect its conduciveness, or receptivity (1,23), to invading inoculum. Drastic soil disinfestation procedures, e.g., steaming and fumigation with methyl bromide, promote rapid development of subsequently introduced pathogens in certain cases (2,5,6,13,21,24,34). With other procedures, especially following mild disinfestation measures, the opposite or no change occurs. Baker (2,3) advocates the use of lower temperatures for soil heating and described cases in which mild soil heating preserves or even increases its suppressiveness, as found for *Fusarium* yellows of strawberries in Japan (20). Disinfestation creates a biological vacuum (2,21) and may induce either soil conduciveness and subsequent disease accentuation or soil suppressiveness, depending on the relative damage caused to soil antagonists or their competitors and the degree of alteration of the original ecosystem (21).

The present study shows that solarization frequently induced suppressiveness in a variety of soils, even with the severe root-dip infestation technique used for *Fusarium* here. Suppressiveness was also induced in artificially heated soil (Fig. 2). This is supported by previous findings on soil solarization, carried out under different conditions, for suppression of a number of pathogens, e.g., *P. cinnamomi*, *Pythium*, *Verticillium dahliae*, *R. necatrix*, and *F. o. f. sp. dianthi* (8,10,13,26,31). Hyphal growth and chlamyospore formation of *P. cinnamomi* are suppressed in solarized soils (26). In one solarized soil, suppressiveness against *R. necatrix*, as expressed by the inhibition of mycelial growth, may last for at least 9 mo (31). Solarization also induced suppressiveness to preemergence damping-off disease of *Eucalyptus*, where the invading propagules originated from contaminated dam irrigation water (13). Our assays for suppressiveness were carried out with untreated, intact inoculum. It might well be that exposure to sublethal heating weakens the inoculum (14,22), rendering it even more sensitive to suppressiveness.

Soil suppressiveness is a common phenomenon, with varying degrees of specificity to pathogens. It occurs naturally in certain soils, as has been shown for fusarial diseases and several other soilborne pathogens (1,4,5,19,23,24,27,33). It can be induced or intensified by means of agricultural practices, such as composting or monoculture (5,11,12). Suppressiveness induced by solarization is characterized by its broad spectrum of activity against different pathogens and its existence in diverse types of soils, as mentioned above. In the present study, suppressiveness was also induced in soils that had no known history of infestation with the test pathogen. It seems that solarization induces "horizontal suppressiveness" (1), which is analogous to genetic horizontal resistance. The long-term disease control of various pathogens in solarized soils apparently is related to this phenomenon. Suppressiveness in solarized soils resembles that which develops during the composting of certain plant materials (11,12), usually at temperatures comparable to those prevailing during solarization.

Various mechanisms involved in the suppressiveness of solarized soils described here are enhanced lytic activity, suppression of chlamyospore formation, and reduction in soil fungistasis, which was correlated positively with the fungistatic capacity of the soils. Similar phenomena have been observed for other soils exhibiting natural or induced suppressiveness. Thus, suppression of chlamyospore formation by *F. solani* f. sp. *phaseoli* was found in "resistant" (i.e., suppressive) soils (4). Aqueous extracts of suppressive soils were shown to suppress chlamyospore formation by *F. o. f. sp. melonis* (23). In a composted hardwood bark medium suppressive to *P. cinnamomi*, sporangium

production was inhibited (12). Reduced fungistasis was found in preheated soils (16). Finally, germination of *Fusarium* macroconidia and chlamyospores was stimulated in water extracts from suppressive forest soil (33), but germination of the chlamyospores was reduced in other suppressive soils (23,27). It is at present unknown whether suppressiveness in solarized soils and that observed in the other situations share a similar basic mechanism. Several studies support the concept that processes of biological control are frequently stimulated in solarized soils. Thus, in such soils, populations of the antagonistic fungi *Trichoderma* and *Talaromyces* increased (7,20,32), and saprophytic *Fusarium* isolates replaced pathogenic isolates (15); these findings are similar to those for *Fusarium* in suppressive soils (1,23). Furthermore, beneficial microorganisms, such as antibiotic-producing bacteria and fluorescent pseudomonad rhizobacteria, are stimulated (29). It was also shown that populations of *F. o. f. sp. lycopersici* decline more rapidly in soil preheated to 45–50 C than in unheated soil (16). However, the possibility that solarization induces conduciveness in certain cases should not be excluded. Populations of *Paratylenchus hamatus*, initially reduced by solarization, were increased later (28), and, as shown in this work, in one out of 10 solarized soils *Fusarium* wilt incidence was increased (Table 2). Induced conduciveness was found in one out of two soils treated with methyl bromide, yet more studies are needed to determine the effect of this fumigant on soil suppressiveness.

Suppressiveness in solarized soils is possibly not related to a single universal mechanism. In fact, its widespread occurrence indicates that the mild heating involved in solarization produces basically similar and general, nonspecific mechanisms, because many saprophytes survive this temperature treatment (2,3,25). Possible explanations for the increased sensitivity of the pathogens to this treatment over that of their antagonists have been discussed (2,14,30). It could also be that the surviving saprophytes are more successful than the pathogens in rapidly occupying available niches created by solarization in soil.

In certain cases, such as *Fusarium* wilt of muskmelon, certain biocidal treatments eliminate natural soil suppressiveness (24). It is necessary, therefore, to develop soil assays to determine the minimal dosage of the disinfestant needed to reasonably reduce inoculum density without disturbing suppressiveness. Finally, the addition of antagonists to disinfested soil is a potentially powerful tool to control reinfestation (6).

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