

Thermal Components of Soil Solarization as Related to Changes in Soil and Root Microflora and Increased Plant Growth Response

J. J. Stapleton and J. E. DeVay

Department of Plant Pathology, University of California, Davis 95616.

Research was supported by United States-Israel Binational Agricultural Research and Development Grant 1-68-79.

The authors thank Tri-Cal Inc., Morgan Hill, CA 95037 for providing polyethylene film.

Accepted for publication 27 July 1983.

ABSTRACT

Stapleton, J. J., and DeVay, J. E. 1984. Thermal components of soil solarization as related to changes in soil and root microflora and increased plant growth response. *Phytopathology* 74:255-259.

Solarized and "shaded" (moist soil covered by transparent polyethylene film but protected from solar heating by sheets of gypsum wallboard) soils were compared for population densities of selected soil microorganisms. Solarized soils usually contained the fewest microorganisms, untreated control soils contained the most, and shaded soils had intermediate population densities ($P < 0.05$). Greater plant growth occurred in solarized soils, and sometimes in shaded soils, than in untreated control soils. Plant growth increases in the field often were correlated inversely ($P < 0.01$ or 0.05) with decreases in soil population densities of several groups of bacteria and fungi. The percentage of colonies of Gram-positive bacteria exhibiting *in vitro* antibiosis against *Geotrichum candidum* increased nearly 20-fold in

solarized soil but not at all in shaded soil, as compared to untreated control soil. Six strains of fluorescent pseudomonad plant growth-promoting rhizobacteria colonized sugar beet and radish roots ~2 to 6× more effectively in solarized soils of four textures than in the same soils that were not solarized ($P < 0.05$). Soil and root population densities of *Pythium* spp. were each reduced by 38% after postplant soil solarization of a 2-yr-old almond orchard, but no reductions were seen after treatment of a 6-yr-old peach orchard. No visible differences in the extent of root infections by vesicular-arbuscular mycorrhizae (*Glomus* spp.) were apparent between roots from solarized and untreated trees at one orchard site.

Additional key words: polyethylene mulching, soil heating.

Increased plant growth responses (IGR) following soil solarization are usually indicators of the successful application of the treatment (10,16,19,21). Pathogen control and nematode population density reductions have been found in soils following solarization (1,5,9,10,16,21,22). However, IGR have been observed even when no major pathogens or nematode parasites have been detected in experimental soils (5,10,19,21). Other bases for IGR, such as increased levels of some soluble mineral nutrients (5,19,22), have been reported. Along with effects of solarization on major soilborne plant pathogens, changes in population dynamics of a wide spectrum of soil bacteria and fungi have been shown (19).

This study was made to further examine the relationship between qualitative and quantitative alterations in microbial ecology induced by soil solarization, and subsequent increases in plant growth. In addition to changes in population densities of native soil organisms, the ability of introduced beneficial bacteria (plant growth-promoting rhizobacteria [PGPR]) to colonize roots of plants grown in solarized soil (compared to untreated soil) was examined. Also, it has been shown that IGR have resulted from soils mulched with black polyethylene film where slight elevations in soil temperatures from solar heating occur (6,25), and that moist soil covered with transparent polyethylene film (0.025 mm = 1 mil thickness) for 4–6 wk but protected from solar heating (hereafter referred to as "shaded" soil) has resulted in reduced population densities of various soil microorganisms and nematodes, and subsequent IGR (20,21). This treatment and soil solarization were compared for effects on population densities of soilborne microorganisms. Part of these data have been reported (20).

MATERIALS AND METHODS

Isolation of soil microorganisms. Solarization of field soils was done for 4–6 wk, as described previously (21), in sand (Atwater and Winton, CA), loamy sand (Davis, CA), fine sandy loam (Davis, CA), loam (Davis, CA), silty clay loam (Esparto, CA), and silty

clay (Davis, CA). Soil samples were taken to desired depths either with a 2.5-cm-diameter soil tube or with a shovel. Existing fruit tree orchards were present at the Atwater and Winton sites. All other sites were fallowed for at least 2 mo prior to soil solarization. The procedure for assay of soil microorganisms and the selective media used to enumerate and compare Gram-positive bacteria, fungi recoverable on PDA, actinomycetes, fluorescent pseudomonads, and *Agrobacterium* spp. have been described previously (19). Also in this study, the crystal violet-pectate medium (CVP) developed by Cuppels and Kelman (7) was used to assay population densities of pectolytic bacteria, and the assay procedure of DeVay et al (8) with the agar developed by Mircetich and Kraft (13) was used for detecting *Pythium* spp.

Effect of soil solarization on root microorganisms. Peach roots were obtained from the top 0.5 m of soil at the Winton and Atwater orchards 7 mo after solarization and populations of *Pythium* spp. in these roots were compared to soil populations. Soil was sampled as described previously (21). Root populations of *Pythium* spp. were assayed by embedding feeder roots, which were surface-sterilized with 0.05% NaOCl, in culture plates containing the selective medium. Also, roots from the Winton site were assayed for the presence or absence of vesicular-arbuscular mycorrhizae by using the staining method of Bird et al (4).

Effect of soil solarization on subsequent colonization of roots by rhizobacteria applied to seed. Sugar beet (*Beta vulgaris* L. 'USH-11') and radish (*Raphanus sativus* L. 'White Icicle') seed were pelleted with a 3% methyl cellulose and talcum powder mixture of PGPR strains, obtained from M. N. Schroth (University of California, Berkeley 94720), to determine the extent of colonization of roots in solarized soil, compared to roots grown in nontreated soil. Seeds were coated with $\sim 10^6$ bacteria per seed according to the method of Suslow and Schroth (24). In 1981, a combination of three strains of fluorescent pseudomonads (RV3, SH5, and B4), all marked for resistance to 100 μ g of rifampicin per milliliter of medium and 50 μ g nalidixic acid per milliliter of medium, were used. These strains have been beneficial to sugar beet growth (24). Treated seeds were planted in 15-cm-diameter pots (six pots per treatment) containing solarized and nontreated silty clay loam soil previously planted to sugar beets. After seedling

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

emergence, those in each pot were thinned to the single most vigorous seedling. Plants were harvested after 12 wk of growth in the greenhouse and their biomass (dry weight) was measured. PGPR were assayed by collecting several sections of feeder roots from root balls of experimental plants and grinding them with sterile mortars and pestles containing 10 ml of sterile phosphate-peptone buffer at pH 7.0. The resulting suspensions were diluted on King's B agar (11) amended with 250 μ g of cycloheximide per milliliter of medium to inhibit fungal growth, and the appropriate concentration of rifampicin and nalidixic acid to determine population densities of the antibiotic-resistant rhizobacteria.

In 1982, a combination of three strains of fluorescent pseudomonads (E2, E6, and E8), all marked for resistance to 100 μ g of rifampicin per milliliter of medium were used to coat radish seed as described above. These strains were reported to be beneficial to radish growth (12). The seeds were planted into solarized or nontreated soil of three textures (loamy sand, fine sandy loam, and silty clay) in 15-cm-diameter pots. Plants were thinned after emergence to three vigorous seedlings per pot, which were then grown for 8 wk in the greenhouse. The plants were harvested, biomass (dry weight) was measured, and the roots were assayed for population densities of the antibiotic-resistant bacteria as described above.

Effect of heating component of soil solarization on microbial population densities and plant growth increases under field conditions. Three treatments were used: solarized, shaded, and untreated control. In 1981, a field of Reiff fine sandy loam soil with a history of *Verticillium* wilt was used. Shaded soil was covered by transparent polyethylene film (0.025 mm thickness), and the soil beneath the film was then flooded with irrigation water. Sheets of gypsum wallboard (1.25 cm thickness) were then laid over the film to prevent solar heating. The treatments were left in place for 6 wk, during which time soil temperatures in the shaded plots were less than those in the control (nontreated plots). Following removal of the coverings, soil samples were taken to a 23-cm depth for assay of soil microorganisms and nematodes. Assays of *Agrobacterium* spp., fluorescent pseudomonads, Gram-positive bacteria, actinomycetes, fungi recoverable on potato-dextrose agar (PDA), and *Pythium* spp. were done by dilution-plating on selective media (sensitivity no greater than 100 colony-forming units [CFU] per gram of soil) as previously described (19). Nematode assay procedures and results from this site are described elsewhere (21). All plots were then bedded and planted with rooted cuttings of strawberry (*Fragaria chiloensis* L. 'Tufts'). The plot was furrow-irrigated, and normal cultural practices were followed. Runner growth and fruit yields were monitored throughout the following growing season.

In 1982, the experiment was repeated in Yolo loam soil. After 6 wk of treatment of field soil, soil samples to a 23-cm depth were taken and assayed for population densities of the microorganisms described above, and also for pectolytic bacteria recoverable on selective agar. Pepper seedlings (grown from seeds of *Capsicum annuum* L. 'Early Jalapeno,' 'Pimiento L,' and 'Resistant Giant' obtained from Petoseed Co., Woodland, CA) were transplanted into the field plot 1 wk later as previously described (21).

Assay of in vitro antibiosis of recovered soil microorganisms. Colonies of soil fungi, Gram-positive bacteria, and fluorescent pseudomonads recovered on selective agar plates described above were killed by exposure to chloroform and overlaid with a layer of 5% water agar. After 48 hr of incubation to allow diffusion of antibiotic substances, plates were sprayed with an arthrospore suspension of *Geotrichum candidum* Link ex. Pers., as described by Baigent et al (2). Forty-eight hours later, antibiotic production on plates from solarized, shaded, and nontreated soil was assessed by the presence of distinct inhibition zones of *G. candidum* surrounding the killed colonies on the dilution plates. Percentages of colonies demonstrating antibiotic activity were compared among plates from the solarized, shaded, and control soil dilutions to estimate possible shifts in relative antibiotic production in soil following solarization.

Soil temperature data. Maximum soil temperatures in solarized soil at each site were 7–12 C higher than in untreated control soil (Table 1). Temperatures in shaded soil were not higher than those in untreated control soil.

Effect of soil solarization on root microorganisms. Peach roots from solarized plots at the Winton site (2-yr-old trees) had significantly ($P < 0.05$) fewer CFU of *Pythium* spp. (38%) than roots from untreated trees 7 mo after soil solarization (Table 2). These results are consistent with those obtained from soil assays of *Pythium* spp., which showed significant reductions in propagules in solarized plots of 33, 54, and 38% at depth ranges of 0–23, 23–46, and 0–46 cm (average of both ranges), respectively, compared to untreated control plots immediately after soil solarization at the Winton site. Although not quantitatively assayed, no visible differences in the extent of root infections by vesicular-arbuscular mycorrhizae (*Glomus* spp.) were apparent between roots from solarized or untreated trees at the Winton site.

At the Atwater site, the canopy of the larger 6-yr-old trees shaded the solarization treatments to a much greater extent than at the Winton site. Assays of *Pythium* spp. from root samples showed no significant differences between the solarized and untreated control treatments (Table 2), and soil assays from the two treatments were not significantly different at any of the sampling depth ranges.

Effect of soil solarization on subsequent colonization of roots by rhizobacteria applied to seeds. Sugar beet tap root dry weights (1981 experiment) were significantly increased by ~3.5 times following growth in solarized silty clay loam soil, as compared to untreated control soil (Table 3). After 12 wk of growth, PGPR on sugar beet roots in solarized soil colonized sugar beet roots in population densities 4.7 times greater ($P < 0.05$) than on roots grown in untreated control soil. In the 1982 experiment on radish roots, whole plant radish dry weights were increased by 0.6 to 5 times ($P < 0.05$) in each of the three experimental soil types, compared to those grown in untreated control soils. The PGPR colonized roots grown in solarized soil significantly better (3.7 times) than those grown in untreated soil in loamy sand (3.7 times), fine sandy loam (6.3 times), and silty clay (1.8 times). No increase in plant growth was observed from seed coated with PGPR as compared to noncoated seed, in either experiment.

Effect of the heating component of solarization on microbial population densities and plant growth increases under field conditions. In the 1981 study, population densities of *Agrobacterium* spp., fluorescent pseudomonads, Gram-positive bacteria, actinomycetes, and *Pythium* spp. in the shaded soil differed significantly from those found in both the solarized and untreated control soils; they were reduced (19–56%) compared to the untreated soil, but the reductions were only approximately half those attained in solarized soil (Table 4). Reductions of *Verticillium dahliae* Kleb. in shaded (54%) versus solarized (98%) soil were proportionally similar to those found with the above microorganisms (G. S. Pullman and J. E. DeVay, unpublished). Population densities of all except *Agrobacterium* spp. and *Pythium* spp. in shaded soil were reduced less than in solarized soil, and no differences in population densities of fungi recoverable on PDA were observed among any of the treatments in 1981.

Strawberry runner fresh weights from the experimental plot were increased in solarized (61%) and shaded (14%) plots at a significance level of ($P < 0.06$), compared to those from untreated control soil. Fruit-plus-runner fresh weights were increased in solarized (44%) and shaded (14%) plots at a significance level of $P < 0.10$ compared to those from untreated control soil. No significant differences in fruit fresh weight yields were found (G. S. Pullman and J. E. DeVay, unpublished). These growth increases were inversely correlated ($P < 0.05$) to decreases in population densities of Gram-positive bacteria, fluorescent pseudomonads, and *Verticillium dahliae*, but not to fungi recoverable on PDA in the 0- to 23-cm soil depth range. This field site was solarized late in the summer, when soil temperature maxima were lower than those in mid-summer (Table 1).

Following the 1982 field experiment, population densities of

TABLE 1. Maximum soil temperatures (C) during soil solarization treatment periods (1980–1982)

Site	Dates	Soil type	Treatment	Soil depth (cm)		
				15	30	46
Atwater	14 July–13 August 1980	Atwater sand	Solarized (full sun)	45	38	...
			Solarized (under tree canopy)	38
			Control (full sun)	37	31	...
			Control (under tree canopy)	31
Esparto	18 July–1 Sept 1981	Marvin silty clay loam	Solarized	36
			Control	28
Davis	19 August–29 Sept 1981	Reiff fine sandy loam	Solarized	39	...	35
			Shaded	30	...	25
			Control	32	...	27
Davis	16 June–26 July 1982	Yolo loam	Solarized	44
			Shaded
			Control	34
Davis	17 June–3 August 1982	Capay silty clay	Solarized	46
			Control	34
		Yolo fine sandy loam	Solarized	44
			Control	34
		Loamy sand	Solarized	46
			Control	36

TABLE 2. Population density reductions of *Pythium* spp. in soil and in peach roots following postplant soil solarization at two orchard sites (1980–1981)

Site, crop, tree age	Soil treatment	Recovery of <i>Pythium</i> spp. from:			
		soil ^u			roots ^w
		0–23 cm ^v	23–46 cm	0–46 cm	
Winton	Solarized	21.8 ^{x,y}	4.2*	13.0*	0.11 ^{z*}
Almond on 'Lovell' peach third leaf	Untreated control	32.5	9.3	20.9	0.18
Atwater	Solarized	52.7	7.9	30.3	0.04
Peach on 'Nemaguard' peach sixth leaf	Untreated control	46.7	11.8	29.2	0.06

^u Atwater sand soil solarized 14 July–13 August 1980; sampled 13 August 1980.

^v Soil sampling depth ranges.

^w Feeder roots sampled 17 March 1981.

^x *Pythium* spp. propagules per gram of air-dried soil.

^y Asterisk (*) = value different from untreated control at $P < 0.05$ according to Student's *t*-test.

^z *Pythium* spp. infections per centimeter of root.

pectolytic pseudomonads and total pectolytic bacteria from CVP agar, actinomycetes, and *Pythium* spp. (depth ranges of 23–46 cm and mean 0–46 cm) in the shaded plots were significantly reduced by 20–55%, compared to the untreated control plots (Tables 4 and 5). The population densities of fluorescent pseudomonads, Gram-positive bacteria, and fungi recoverable on PDA were not reduced in the shaded treatment, compared to the control treatment. Treatment by solarization, conversely, significantly reduced population densities of all assayed microorganisms by 58–87%. Population density reductions of all microorganisms tested except *Pythium* spp. (23–46 cm depth range only) following solarization were significantly greater than those following the shaded treatment. Pectolytic enteric bacteria were recovered from shaded soil, but not in control or solarized soil.

Yield and growth data from two of the pepper cultivars (Early Jalapeno and Pimiento L) planted into solarized or shaded soil in the field plot included significant increases as compared to plants grown in untreated soil in percentages of surviving plants (34–42%), pod yields on a per plant basis (40–65%), projected pod yield on a kilograms per hectare basis (calculated by multiplying the number of surviving plants per hectare by pod yield per plant) (64–100%), and vegetative growth fresh weights (32–130%). No increased growth response was found in the pepper cultivar Resistant Giant for any of the measured growth parameters. Plant growth increases were not significantly correlated with any of the monitored soil microorganisms population densities. Pepper growth data were summarized in a previous report (21).

Assay of in vitro antibiosis. Assay of soil dilution plates with *Geotrichum candidum* revealed very little antibiotic activity from fungi on PDA plates, and no difference between solarized and untreated controls (Table 6). Fluorescent pseudomonads on the

TABLE 3. Root colonization of sugar beet (*Beta vulgaris* 'USH-11') and radish (*Raphanus sativus* 'White Icicle') by plant-growth-promoting rhizobacteria (PGPR) following soil solarization (1981–1982)

Soil texture, crop, year	Soil treatment	PGPR ^y root population density (cfu/g tissue)	Increase over control (%)
	Control	6.5×10^4	—
Loamy sand radish (1982)	Solarized	1.7×10^5	372*
	Control	3.6×10^4	—
Fine sandy loam radish (1982)	Solarized	4.9×10^4	631*
	Control	6.7×10^3	—
Silty clay radish (1982)	Solarized	5.1×10^4	183*
	Control	1.8×10^4	—

^y Sugarbeet PGPR-fluorescent pseudomonad strains B4, SH5, and RV3; radish PGPR-fluorescent pseudomonad strains E2, E6, and E8 (obtained from M. N. Schroth).

^z Asterisk (*) = values different at $P < 0.05$ according to Student's *t*-test.

selective agar (19) showed some antibiotic activity against *G. candidum*, as indicated by diffuse zones of inhibition surrounding bacterial colonies. The incidence of antibiotic activity directly followed the population densities of the fluorescent pseudomonads in the solarized and untreated soils, as nearly all of the fluorescent colonies demonstrated some activity. Since there were ~86% more fluorescent pseudomonad colonies recovered from untreated soil than from solarized soil, the antibiotic activity toward *G. candidum* was probably decreased by the same amount in soil following solarization.

When the activity of the antibiotics produced on the modified

TABLE 4. Population density reductions of soilborne microorganisms following soil solarization or soil shading (1981-1982)

Organism	Treatment	Decrease over control treatment (%) (0-23 cm depth)						
		1981 ^w			1982 ^x			
Fluorescent pseudomonads	Control	- a ^z			- a			
	Shaded	39 b			13 a			
	Solarized	78 c			86 b			
Gram-positive bacteria	Control	- a			- a			
	Shaded	33 b			32 a			
	Solarized	80 c			87 b			
Actinomycetes	Control	- a			- a			
	Shaded	19 b			20 b			
	Solarized	45 b			58 c			
<i>Agrobacterium</i> spp.	Control	- a			ND ^z			
	Shaded	47 b						
	Solarized	72 c						
Fungi recoverable on PDA	Control	- a			- a			
	Shaded	30 a			32 a			
	Solarized	44 a			82 b			
			cm depth			cm depth		
			0-23	23-46	0-46	0-23	23-46	0-46
<i>Pythium</i> spp.	Control	- a	- a	- a	- a	- a	- a	- a
	Shaded	22 a	56 b	31 b	14 a	55 b	21 b	
	Solarized	65 b	77 b	68 c	72 b	58 b	70 c	

^wReiff fine sandy loam soil was treated from 19 August-29 September 1981.

^xYolo loam soil was treated from 16 June-26 July 1982.

^yValues followed by different letters are different at $P < 0.05$ according to Duncan's multiple range test.

^zND = No data.

TABLE 5. Effect of soil solarization and soil shading on population densities of pectolytic bacteria recoverable on CVP agar in loam soil

Soil treatment	Population density of pectolytic pseudomonads ^y	Decrease over control treatment (%)	Population density of:		Decrease over control treatment (%)
			pectolytic enteric bacteria ^y	total pectolytic bacteria ^y	
Solarized	6.0×10^2	80 a ^z	- a	6.0×10^2	80 a
Shaded	1.8×10^3	38 b	5.7×10^3 a	7.5×10^3	-250 b
Control	3.0×10^3	- c	- a	3.0×10^3	- b

^yColony-forming units per gram of oven-dry soil.

^zValues followed by different letters are different at $P < 0.05$ according to Duncan's multiple range test.

TABLE 6. Effect of soil solarization and soil shading on antibiotic activity of Gram-positive bacteria recovered from loam soil versus *Geotrichum candidum*

Soil treatment	CFU ^y causing inhibition zones (%)	Increase over control (%)
Solarized	20.8	1,980 a ^z
Shaded	1.2	20 b
Control	1.0	- b

^yCFU = colony forming units.

^zValues followed by different letters are different at $P < 0.05$ according to Duncan's multiple range test.

523 agar (mostly from *Bacillus* spp.) was assayed against *G. candidum*, sharp inhibition zones were usually observed. The percentage of bacterial colonies producing inhibition zones on plates from solarized soil was 1,980% ($P < 0.05$) higher than those from untreated soil. The percentage of antibiotic-producing colonies from the shaded treatment plates did not differ from those from untreated soil.

DISCUSSION

Plant growth, yield, and quality may be limited by major soilborne pathogens, as well as minor pathogens or deleterious soil microorganisms (16,22). Several soilborne fungal pathogens (1,9,10,16) and other soil microorganisms (9,10,19) have been reduced in population densities following soil solarization. The results reported here further indicate that soil solarization affects a

wide range of soil microflora, including many potential minor pathogens or deleterious organisms. Alterations in population densities of monitored soil microorganisms not known to be major plant pathogens following solarization sometimes have been correlated significantly with increases in plant growth.

The successful control of Verticillium wilt in established Pistachio nut groves using soil solarization has been reported (1). In the present study, infections of peach roots by *Pythium* spp. were significantly reduced in a 3-yr-old almond orchard, but not in a 6-yr-old peach orchard; this was probably due to increased canopy shading during solarization by the older trees. Continuous coverage of the entire orchard floor by the polyethylene film would probably increase the soil heating efficiency, and hence, reductions of root population densities of *Pythium* spp. Infections of peach roots by vesicular-arbuscular mycorrhizae were not visibly reduced by soil solarization. This agrees with previous reports of the survival of mycorrhizal fungi following soil solarization (16). Moreover, nematode population densities in solarized orchard soils were initially reduced, compared to those in untreated soil, but the nematodes rapidly recolonized the solarized soil (21).

Trichoderma spp. have been reported to recolonize solarized soil to a greater extent than untreated soil (10). We found similar results with several strains of fluorescent pseudomonads. Although these PGPR strains were not associated with increased sugar beet or radish growth in our greenhouse experiments, the consistent increases in root colonization in four soil textures suggest that PGPR could be of value on seed planted into solarized soil, both as a protectant of plant roots against surviving soil pathogens, and as

a means of selectively recolonizing solarized soil with beneficial soil microorganisms to prolong the favorable effect of the treatment. These findings should be further tested under field conditions.

The covering of moist soil with polyethylene film, but without solar heating (shaded soil), significantly reduced population densities of several groups of soil microorganisms and sometimes resulted in significant IGR. The increase of enteric pectolytic bacteria found in shaded soil indicates that anaerobic conditions may be found in moist soils covered by polyethylene film. Previous suggestions as to the possible roles of biological control agents and/or volatile compounds in reducing population densities of microorganisms in these soils have been made (10,21). Possible problems could result, however, if solarization is attempted in areas where insufficient soil heating is attained, and where crops susceptible to enteric pectolytic bacteria are subsequently planted. The volume of water present in covered soils is likely to be the determining factor regarding the oxygen/carbon dioxide ratios and concentrations in solarized or shaded soil. Where soil heating is maximal, the importance of soil moisture content on microorganism survival may be diminished. Where soil heating is minimal, the importance of soil moisture content on the survival of soil microflora may be increased. Soil flooding has been shown to decrease population densities of soilborne plant pathogens and result in increased plant growth (14,15,18). Although no growth increases resulted from shaded soil in the 1981 field experiment, vegetative and fruit growth of pepper in shaded soil in the 1982 experiment was often as much as in the solarized soil. These data indicate that very moist soil covered by black polyethylene film commonly used as a mulch may sometimes result in similar plant growth increases as obtained following soil solarization. Other nonthermal factors of the treatment, such as light and water potentials, and accumulation of volatile compounds may also be involved.

Bacillus spp. were reported previously (19) to be the predominant Gram-positive bacteria surviving soil solarization. The assay of in vitro antibiosis done in this study confirms the possible importance of *Bacillus* spp. in the recolonization of soil following solarization. These bacteria have been shown to be beneficial to plant growth (3). In addition to the increased proportion of antibiotic-producing bacteria following solarization, there was also a numerical increase of these bacteria of 182% ($P < 0.05$), compared with untreated soil. The lack of increase of antibiotic production by Gram-positive bacteria colonies from shaded soil supports the theory that *Bacillus* spp., as well as many actinomycetes and thermotolerant/thermophilic fungi (19), and other high-temperature soil microorganisms, are able to flourish in solarized soils. These organisms, many of which produce antibiotic metabolites, are likely to be prominent among the primary microorganisms recolonizing solarized soil. Although the importance of microbial antibiotic production in solarized soil was not determined in this study, it has been reported that antibiotic production is increased in soils that have available organic substrates to colonize (3,26), such as those which have been subjected to heating.

In a previous study (19), increased walnut and peach seedling growth was found in soil with no detectable major plant pathogens. These growth increases were correlated ($P < 0.01$ and $P < 0.05$, respectively) with reductions in population density of Gram-positive bacteria, fluorescent pseudomonads, and fungi recoverable on PDA after solarization in the 0-46 cm soil depth range. Significant correlation of increased strawberry runner and fruit fresh weights with decreased bacteria and fungal population densities were also found in this study. However, in the field experiment described in this report with pepper crops, no correlations between plant growth and microbial population densities were found. This indicates that at some field sites, soil solarization reduces soilborne phytopathogenic microorganisms below the point at which they become the limiting factors to plant growth. At other sites, however, microorganisms responding to solarization in the same manner as these that were assayed are not the limiting plant growth factors. In these cases, other biological and physical aspects of soil and crop ecology must be examined in

order to determine the bases for increased plant growth responses following soil solarization.

LITERATURE CITED

1. Ashworth, L. J., Jr., and Gaona, S. A. 1982. Evaluation of clear polyethylene mulch for controlling *Verticillium* wilt in established pistachio nut groves. *Phytopathology* 72:243-246.
2. Baigent, N. L., DeVay, J. E., and Starr, M. P. 1963. Bacteriophages of *Pseudomonas syringae*. *N.Z. J. Sci.* 6:75-100.
3. Baker, K. F., and Cook, R. J. 1974. Biological control of plant pathogens. W. H. Freeman and Company, San Francisco. 433 pp.
4. Bird, G. W., Rich, J. R., and Glover, S. U. 1974. Increased endomycorrhizae of cotton roots in soil treated with nematicides. *Phytopathology* 64:48-51.
5. Chen, Y., and Katan, J. 1980. Effect of solar heating of soils by transparent polyethylene mulching on their chemical properties. *Soil Sci.* 130:271-277.
6. Courter, J. W., and Oebker, N. F. 1964. Comparison of paper and polyethylene mulching on yields of certain vegetable crops. *Proc. Am. Soc. Hortic. Sci.* 85:526-531.
7. Cupples, D., and Kelman, A. 1974. Evaluation of selective media for isolation of soft-rot bacteria from soil and plant tissue. *Phytopathology* 64:468-475.
8. DeVay, J. E., Garber, R. H., and Matheron, D. 1982. Role of *Pythium* species in the seedling disease complex of cotton in California. *Plant Dis.* 66:151-154.
9. Katan, J. 1980. Solar pasteurization of soils for disease control; status and prospects. *Plant Dis.* 64:450-454.
10. Katan, J. 1981. Solar heating (solarization) of soil for control of soilborne pests. *Annu. Rev. Phytopathol.* 19:211-236.
11. King, E. O., Ward, M. K., and Raney, D. E. 1954. Two simple media for the demonstration of pyocyanin and fluorescein. *J. Lab. Clin. Med.* 44:301-307.
12. Kloepper, J. W., and Schroth, M. N. 1978. Plant growth promoting bacteria on radishes. Pages 879-882 in: *Proc. Fourth Int. Conf. Plant Pathol. Bacteria* (Angers, France) II.
13. Mircetich, S. M., and Kraft, J. M. 1973. Efficiency of various selective media in determining *Pythium* populations in soil. *Mycopathol. Mycol. Appl.* 50:151-161.
14. Newhall, A. G. 1955. Disinfestation of soil by heat, flooding, and fumigation. *Bot. Rev.* 21:189-250.
15. Pullman, G. S., and DeVay, J. E. 1981. Effect of soil flooding and paddy rice culture on the survival of *Verticillium dahliae* and incidence of *Verticillium* wilt in cotton. *Phytopathology* 71:1285-1289.
16. Pullman, G. S., DeVay, J. E., Garber, R. H., and Weinhold, A. R. 1981. Soil solarization: Effects on *Verticillium* wilt of cotton and soilborne populations of *Verticillium dahliae*, *Pythium* spp., *Rhizoctonia solani*, and *Thielaviopsis basicola*. *Phytopathology* 71:954-959.
17. Salt, G. A. 1979. The increasing interest in 'minor pathogens.' Pages 289-312 in: *Soil-borne Pathogens*. B. Schippers and W. Gams, eds. Academic Press, New York.
18. Sewell, G. W. F. 1965. The effect of altered physical condition of soil on biological control. Pages 479-494 in: *Ecology of Soil-borne Pathogens: Prelude to Biological Control*. K. F. Baker and W. C. Snyder, eds. University of California Press, Berkeley and Los Angeles.
19. Stapleton, J. J., and DeVay, J. E. 1982. Effect of soil solarization on populations of selected soilborne microorganisms and growth of deciduous fruit tree seedlings. *Phytopathology* 72:323-326.
20. Stapleton, J. J., and DeVay, J. E. 1982. Changes in microbial populations in solarized soils as related to increased plant growth. (Abstr.) *Phytopathology* 72:985.
21. Stapleton, J. J., and DeVay, J. E. 1983. Response of phytoparasitic and free-living nematodes to soil solarization and 1,3-dichloropropene in California. *Phytopathology* 73:1429-1436.
22. Stapleton, J. J., DeVay, J. E., Quick, J., Van Rijckevorsel, H., and DeBoer, G. J. 1983. Increased soluble mineral nutrients in soils as related to increased plant growth response following soil solarization. (Abstr.) *Phytopathology* 73:814.
23. Suslow, T. V., and Schroth, M. N. 1982. Role of deleterious rhizobacteria as minor pathogens in reducing crop growth. *Phytopathology* 72:111-115.
24. Suslow, T. V., and Schroth, M. N. 1982. Rhizobacteria of sugar beets: Effects of seed application and root colonization on yield. *Phytopathology* 72:199-206.
25. Waggoner, P., Miller, P. M., and DeRoo, H. C. 1960. Plastic mulching, principles and benefits. *Conn. Agric. Exp. Stn. Bull.* 634.
26. Weinhold, A. R., and Bowman, T. 1968. Selective inhibition of the potato scab pathogen by antagonistic bacteria and substrate influence on antibiotic production. *Plant Soil* 28:12-24.