Involvement of Fluorescent Pseudomonads and Other Microorganisms in Increased Growth Response of Plants in Solarized Soils

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ABSTRACT

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Enhancement of plant growth in the absence of known pathogens was studied in solarized soils and, to a limited extent, in methyl bromide- and in metham-sodium-treated soils. Increased growth response, expressed by increased dry weight of tomato plants in treated over untreated soils in the greenhouse, was evident in most of the 24 tested soils from various locations in Israel. Increased growth also was evident in field experiments and in an artificially heated soil. Regression analyses showed a significant, inverse relationship between soil pH and increased growth and between soil pH and population densities of fluorescent pseudomonads in the rhizosphere. Solarization reduced bacterial and fungal population densities to a depth of 90 cm, whereas actinomycetes were less affected. Thermotolerant bacteria and fungi also were reduced by solarization. Population densities of fluorescent pseudomonads were increased up to 130-fold in the rhizosphere of plants in solarized soils, although these bacteria are heat sensitive. Solarization drastically reduced population densities of total fungi in the rhizosphere and roots, especially *Penicillium pinophilum*, which causes plant stunting in greenhouse tests, and *Pythium* spp. Isolates of fluorescent pseudomonads, identified as *Pseudomonas putida*, *P. fluorescens*, and *P. alcaligenes*, which were recovered from solarized soil, stimulated growth of tomato plants. Solarization increased the frequency of recovery of bacteria showing antagonistic activity from the rhizosphere and roots of tomato plants.

Additional keywords: biological control, induced suppressiveness, minor pathogens, plant growth-promoting rhizobacteria.

Soil disinfestation is a preplanting treatment used for controlling harmful soilborne organisms. Disinfestation of pathogen-infested soils, by steaming, fumigation, or solarization usually results in the reduction of populations of these organisms and in improved plant growth and yield. However, increased growth response of plants in disinfested soils frequently was observed even in the absence of known pathogens (2,5,15,19,20,31–34). This phenomenon is one of the positive side effects of soil disinfestation and is attributed to chemical, physical, or biological changes that occur in soil during and after disinfestation. For example, increases in soluble mineral nutrients were found in fumigated (2,20,34) and solarized (5,33) soils.

Plant growth may be positively or adversely affected by soil organisms. Certain strains of fluorescent pseudomonads are beneficial organisms (17,18,27), whereas some harmful strains of fungi, e.g., *Penicillium* spp., and bacteria are referred to as minor pathogens (23,26,35). The latter invade roots, meristematic tissues, rootlets, and root hairs, reducing root activity and plant vigor. Soil disinfestation may alter populations or activity of soil organisms and, consequently, improve or suppress plant growth.

Soil solarization affects microbial activities in soil and may result in increased antagonistic activity and induced soil suppressiveness (9,32). Solarization increases populations of fluorescent pseudomonads in the rhizosphere of tomato plants grown in container media (8). In the present study, we investigated the effect of soil disinfestation, mainly solarization, on the growth response in several crops with a variety of soils; the effect of solarization on microbial populations in nonrhizosphere and rhizosphere soils and in plant roots under greenhouse and field conditions; and the possible relationship of microbial changes to increased growth response.

MATERIALS AND METHODS

Soils and disinfestation. Soils of various textures were collected from fields at 24 locations in Israel during 1984–1988. The pH of these soils ranged from 6.9 to 8.57, with 3–58% clay, 0–45% silt, 9.2–96% sand, and 0.1–3.4% organic matter. One soil (Machanayim) was exceptional in that it contained 25% organic matter. Soils were untreated or disinfested by solarization, fumigation with methyl bromide at 55 g/m^2, or treatment with metham-sodium at 600 L/ha. Soil samples were collected from the upper 20-cm layer (after removing the top 2–3 cm) from either experimental plots (8 × 15–20 m) or commercially disinfested fields, in which the whole field was disinfested; five plots were left untreated. In experimental plots, soil samples were taken from the four replicates of each treatment. In commercial fields, soil samples were taken randomly from five sites in the disinfested field and from the five plots that were left untreated. In some experiments, soil samples were also taken to a depth of 90 cm with a core auger (5-cm i.d.). Disinfestation was accomplished under field conditions according to standard procedures. Solarization was carried out either manually or mechanically by mulching preirrigated soil with transparent polyethylene sheets (30–50 μm thick) in July–August for 35–55 days. Typical temperatures of the solarized soils at depths of 10 and 30 cm were 44–48 and 36–40 C, respectively. The temperatures of the corresponding unsolarized soils were 7–12 C lower. Fumigation with methyl bromide was carried out by the hot-gas technique with commercial equipment. Metham-sodium was applied using a sprinkler irrigation according to the standard procedure.

Simulation of soil solarization. Artificial heating of soil was done in specially designed and modified Wisconsin soil-temperature tanks, as reported previously (9,36). The heating system in the simulation tank resulted in the gradual warming of the soil to a maximum temperature of 45 C for a period of

approximately 4 hr every day, after which the temperature dropped gradually to 30–34 C. The daily heating course of the soil was similar to that in the upper 10-cm layer of soil during solarization in Israel. Two-liter cylindrical glass jars (25 cm high, 12 cm diameter) were filled with soil moistened to field capacity. Jars were sealed with polyethylene sheets to prevent evaporation and maintained for 42 days in the tanks. Untreated soil was prepared similarly and kept in a shaded part of the greenhouse at temperatures of 22–28 C.

Plants. Tomato (*Lycopersicon esculentum* Mill. 'Rehovot 13'), cotton (*Gossypium barbadense* L. 'Pima S-5' and 'Pima F-27'), pepper (*Capsicum annuum* L. 'Maor'), eggplant (*Solanum melongena* L. 'Black Beauty'), corn (*Zea mays* L. 'Jubilee'), and sorghum (*Sorghum bicolor* L. '610') were used in these experiments.

Media. Selective media were used for enumeration of microbial populations in nonrhizosphere and rhizosphere soils and root tissues. Nutrient agar (N) (7) was used for total bacteria; King's B agar medium (KB) (7), modified by the addition of 100 mg/L of cycloheximide, 50 mg/L of ampicillin, and 12.5 mg/L of chloramphenicol (30), plus 5 mg/L of pentachloronitrobenzene (PCNB) to suppress *Rhizopus*, was used for fluorescent pseudomonads; Martin's agar (7) was used for total fungi; Martin's agar, supplemented with 5 mg/L of PCNB was used for enumeration of *Penicillium pinophilum*; colloidal chitin medium (11) was used for enumeration and isolation of actinomycetes; sucrose-asparagine agar (28) was used for isolating *Pythium* spp. from roots; peptone-PCNB medium (7), acidified with 1 ml/L of 90% lactic acid and supplemented with 250 mg/L of chloramphenicol instead of streptomycin, was used for *Fusarium* spp.; potato-dextrose agar (PDA) (7) was used for culturing fungi and inoculation tests.

Assays of plant growth. *Greenhouse experiments.* Plants were grown in 10-cm-diameter pots filled with the test soils. With the

TABLE 1. Effect of soil solarization, heating in a simulation system for 42 days, treatment with metham-sodium, or fumigation with methyl bromide on growth of plants[a]

Location	Plant tested	Soil treatment	IGR (%)[b]		Number of experiments	
			Average	Range	Total[c]	Significant[d]
Barqay	Tomato	Solarization	50	3–90	3	2
	Sorghum	Solarization	41	38–45	2	2
Besor	Tomato	Solarization	24	...	1	1
Bet Dagan	Tomato	Solarization	57	23–96	5	4
	Tomato	Simulation	33	...	1	1
	Sorghum	Solarization	22	15–30	2	1
Bet Hananya	Tomato	Solarization	23	55–90	2	2
Bet HaShitta	Tomato	Solarization	68	59–77	2	2
Gamla	Tomato	Solarization	52	15–89	2	1
	Tomato	Methyl bromide	20	12–28	2	1
Eden	Tomato	Solarization	52	...	1	1
	Cotton	Solarization	74	25–128	3	3
	Cotton	Simulation	43	30–56	2	2
En Zurim	Sorghum	Solarization	131	...	1	1
Gaza	Tomato	Solarization	64	50–78	2	2
	Tomato	Methyl bromide	20	...	1	0
Gilgal	Tomato	Solarization	45	34–57	2	2
	Tomato	Methyl bromide	51	25–77	2	1
Kefar Warburg	Tomato	Solarization	30	...	1	1
Kefar Yedideya	Tomato	Solarization	29	...	1	1
	Sorghum	Solarization	134	...	1	1
Lakhish	Tomato	Solarization	9	...	1	1
Maale Gilboa	Tomato	Solarization	15	2–28	2	1
Machanayim	Tomato	Solarization	110	97–123	2	2
Magen	Tomato	Solarization	67	53–81	2	2
Qidron	Tomato	Solarization	34	...	1	1
	Tomato	Methyl bromide	42	...	1	1
Rehovot	Tomato	Solarization	53	23–191	5	5
	Tomato	Simulation	40	27–54	2	2
	Sorghum	Solarization	32	25–39	2	2
	Pepper	Solarization	108	...	1	1
	Eggplant	Solarization	131	...	1	1
	Cotton	Solarization	52	...	1	1
	Corn	Solarization	28	...	1	1
Revivim	Tomato	Solarization	17	...	1	1
	Tomato	Methyl bromide	−27	...	1	1
	Sorghum	Solarization	122	...	1	1
	Sorghum	Methyl bromide	40	...	1	1
Sede Eliyyahu	Tomato	Solarization	15	101–130	3	1
Tirat Zevi	Tomato	Solarization	18	16–120	2	1
Yad Mordekhay	Tomato	Solarization	113	...	1	1
	Tomato	Metham-sodium	82	...	1	1
Yahel	Tomato	Solarization	152	137–187	2	2
Zippori	Tomato	Solarization	51	32–170	2	2

[a] Solarization, metham-sodium, and methyl bromide treatments were carried out in the field at the indicated locations. After, soil was collected and used to plant the bioassayed plants in the greenhouse in six replicates. After 28 days of growth, dry weights were determined.

[b] IGR = Increased growth response, calculated as the percentage of increase in shoot dry weight over the untreated control. Midline dots indicate that only one experiment has been carried out.

[c] Total number of experiments at each location between 1984 and 1988. Each experiment represents a different year and is a mean of two repeated greenhouse tests.

[d] Number of experiments (out of total) in which the difference between untreated and disinfested soil was significant according to Student's t tests, ($P \leq 0.05$).

exception of sorghum and corn, which were seeded directly and thinned after emergence to five plants per pot, test plants initially were sown in the test soils and transplanted 1 day after emergence to new pots (five plants per pot) filled with the same soil. Plants were grown in the greenhouse (22–28 C) for 28 days without fertilization. They were then uprooted, and roots and the adhering rhizosphere soil were separated from the plant and used for rhizosphere and root-microbial analyses. Shoots were cut, and dry weight (70 C for 48 hr) was determined. Growth response was calculated as increased dry weight over the untreated control (Table 1). Experiments were carried out in a completely randomized design with six replicates for each treatment.

Field experiments. Field plots (8 × 16 m) in randomized complete block designs with four replicates were either solarized or left untreated. Tomato or cotton plants were grown in these plots according to standard agricultural recommendations. Five plant samples were collected from each plot at various periods after planting, and dry weight of the shoots was determined. Roots and adhering soil were used for rhizosphere and root-microbial analyses.

Root-development assay. Modular narrow glass boxes (20 cm long, 20 cm high, 1.5 cm wide) were filled with Rehovot or Bet HaShitta soils, either untreated or solarized, and moistened to field capacity (Fig. 1). The walls of the boxes could be separated, enabling easy separation of the root system from the soil. Seeds of tomato plants were sown on the surface of the soil and covered with 1 cm of the same soil. Boxes were placed in a completely randomized design in a growth chamber (25 C with 14 hr of daily artificial illumination) with five replicates for each treatment. Root length and microbial populations were assessed during seedling growth, as indicated.

Microbial assays. *Microbial counts by soil dilution.* Three 5-g soil subsamples of each replicate were added individually to 45 ml of sterile water agar (0.1%) supplemented with $MgSO_4 \cdot 7H_2O$ (0.1%), shaken for 15 min on a reciprocal shaker, and then serially diluted with the same solution. Samples of 0.1 ml (for bacterial and actinomycete counts) or 0.2 ml (for fungal counts) were spread on five petri dishes that contained the appropriate selective agar medium. Dishes were incubated in the dark at 28 or 40 C for the determination of thermotolerant microorganisms. Colonies were counted after 4–10 days. Results are expressed as colony-forming units (cfu) per gram of soil (dried at 105 C for 48 hr).

Microbial assay of rhizosphere. Plants from greenhouse pots, root-development glass boxes, or experimental field plots were removed from the soil, along with their roots and adhering soil. Soil adhering to the roots was collected by shaking the roots in sterile tubes. Remaining soil, which tightly adhered to the roots (less than 5% of the total amount of rhizosphere soil), was collected by shaking in sterile 0.1% water agar supplemented with 0.1% $MgSO_4 \cdot 7H_2O$. Both soil fractions were combined, constituting the rhizosphere soil sample. Rhizosphere soil suspensions were serially diluted, spread on the appropriate medium, and incubated as described.

Microbial assay of roots. Roots were washed under running tap water, cut into 2- to 3-mm segments, blotted on sterile filter paper, placed on the appropriate agar medium, and incubated as described. Results are expressed as percentage of segments colonized with the indicated microorganism. A direct assay of the total microbial populations of the whole root tissue was carried out by macerating washed roots in 0.1% water agar (supplemented with 0.1% $MgSO_4 \cdot 7H_2O$) with a high speed homogenizer (Ultra Turrax, Janke & Kunkel, Germany) for 1 min. The suspension was diluted further, and 0.1- to 0.2-ml samples from the proper dilution were spread on the solidified media. Microbial populations in the interior root tissues were assayed similarly to the whole root, except washed roots were surface-disinfested with 1% NaOCl for 30 sec before maceration.

Isolation and inoculation of microorganisms. Colonies of randomly selected microorganisms isolated from rhizosphere or root tissues were transferred to growth media: N for bacteria and actinomycetes, KB for fluorescent pseudomonads, and PDA for fungi. Cultures were incubated for 48 hr for bacteria and actinomycetes and 8 days for fungi. Bacteria were suspended in distilled water containing 0.5 mM $CaCl_2$ (13). Fungal conidia and mycelial fragments were suspended in tap water. Final inoculum density of fungi was 10^6 cfu/ml, as determined with the aid of hemacytometer; bacterial concentrations were 10^8–10^9 cfu/ml, as determined by optical density. Roots of tomato, 1–2 days after seedling emergence, were dipped for 10 min in the suspension of each bacterial or fungal isolate tested, and then the seedlings were replanted in natural Rehovot soil, which was uninfested with known pathogens. In some experiments, tomato seeds were immersed in suspensions of isolates of fluorescent pseudomonads for 20 min and then sown in untreated Rehovot soil. Isolates of *P. pinophilum* also were tested by mixing washed conidia with soil to a concentration of 10^6 cfu/g before planting tomato seedlings. Plants were uprooted 28 days after inoculation, and dry weight of the shoots was determined. Reisolation of microorganisms from interior root tissues of inoculated plants was done by placing 2- to 3-mm surface-disinfested segments of washed roots (1% NaOCl for 30 sec) on the appropriate medium.

Identification of fluorescent pseudomonads. Fluorescent pseudomonads were identified by fatty acid and methyl ester compositions with gas chromatographic analysis (24). Identifications were performed in the laboratory of B. C. Hemming, Monsanto Co., St. Louis, MO.

Test for antagonism on agar. Nonfluorescent and fluorescent pseudomonad bacteria were cultured on N or KB medium, respectively, for 48 hr. Then, bacteria from each isolate were spotted at three equidistant points 1 cm from the edge of petri dishes (85 cm diameter) containing PDA. After 48 hr of growth in the dark at 30 C, mycelial disks of a test fungus were placed in the center of each dish. After further incubation in the dark at 30 C for 2–3 days, bacterial isolates that induced a fungal inhibition zone were recorded. Test fungi were *Sclerotium rolfsii* Sacc. and *Macrophomina phaseolina* (Tassi) Goidanich.

Statistical analyses. Greenhouse experiments, root-development assays, and microbial analyses were conducted at least twice, unless otherwise indicated. Variances between experimental trials were homogeneous, and, thus, data from repeated experiments were pooled. Statistical analyses of the results included analysis of variance, correlation, linear regression, Student's *t* test, or calculations of standard error as indicated. Percentages were transformed to arcsine-square roots before analyses. Hierarchic analyses were done for the inoculation tests to determine whether the origin of the inoculants had a significant effect on plant growth. All analyses were performed with the SAS program (SAS Institute Inc., Cary, NC) at $P \leq 0.05$.

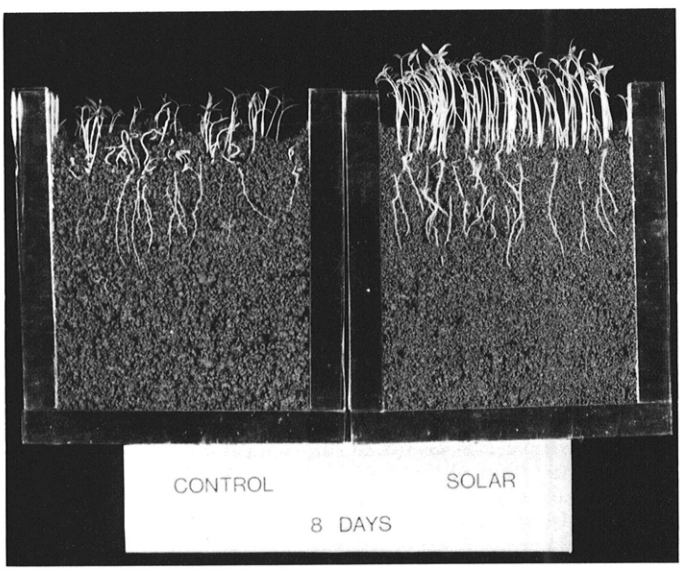

Fig. 1. Effect of soil solarization (solar) on emergence and growth of tomato seedlings in a glass box for root-development assay with Bet HaShitta soil.

RESULTS

Assay of plant growth. *Greenhouse experiments.* Growth response was determined in soils from 24 locations, with tomato as the major test plant. Compared with untreated controls, a significant increase in plant growth was recorded for most of the tested soils and plants after soil disinfestation (Table 1, Fig. 1). In solarized soils, the average percentages of increase in dry weight of tomato ranged from 9 to 152%. In six soils treated with methyl bromide, the average percentages ranged from 20 to 51%, plus one case of decreased growth. Significant increased growth response was recorded in cotton and tomato plants when treated with the simulated heating system. An increase in growth of tomato was evident in at least one experiment at each location. Of 46 experiments in solarized soils and seven in soils treated with methyl bromide, 39 and four, respectively, resulted in a significant growth increase in tomato plants. In one experiment (at Yad Mordekhay), increased growth in tomato also was evident in soil treated with metham-sodium. No visible symptoms of diseases were observed in any of the greenhouse experiments.

Regression analysis showed a significant, inverse relationship between increased growth of tomato in solarized soils and soil pH (Fig. 2), but not with organic matter, clay, silt, or sand content of the soil ($r^2 \leq 0.25$). For example, high increased growth values of 68 and 119% were recorded in two soils that differed greatly in texture (Bet HaShitta [75% clay] and Rehovot [3.8% clay], respectively).

Emergence of eggplant and pepper seedlings in one solarized Rehovot soil occurred 1–2 days earlier than in the comparable untreated soil. Increased growth of tomato plants was observed in soil from Sede Eliyyahu, although an initial growth retardation of carrot plants in solarized soil occurred in a previous field study carried out in this soil (12).

The duration of the increased growth phenomenon was determined. Untreated and solarized soil samples were collected from the field in Rehovot in October 1987, 1 mo after solarization was terminated. The dry weight of tomato shoots grown in pots filled with the solarized soil was significantly higher (146%) than that of plants grown in untreated soil. The field plots were left undisturbed, except for weeding. Six months later, soil samples again were collected and the plant-growth assay was repeated. A significant increase (114%) in shoot dry weight after soil solarization still was evident.

Mineral nutrient content was recorded in 13 soils. In most cases, solarization resulted in an increase in mineral levels, i.e., NO_3^-, K^+, Ca^{+2}, and Mg^{+2}, and in electrical conductivity (data not shown) similar to a previous study (5). In all cases, solarization reduced the soil pH by 0.1–0.4 units.

Increased growth under field conditions. Growth response of tomato or cotton plants was determined periodically at three field locations (Table 2). Increased growth was recorded for both species (19–100%), but was more pronounced with tomato than with cotton plants. Growth still was evident 70 days after planting.

Root development in growth-chamber assays. Enhanced root development of tomato seedlings was recorded in two solarized soils during the first 11 days after sowing in a glass-growth apparatus (Figs. 1 and 3), and was observed even before seedling emergence. Similar results in root-length measurements were obtained in Bet HaShitta soil (results not shown).

Effect of solarization on microbial populations. *Nonrhizosphere soil.* A significant reduction in populations of bacteria and fungi was recorded in most of the soils tested (Tables 3 and 4). Popu-

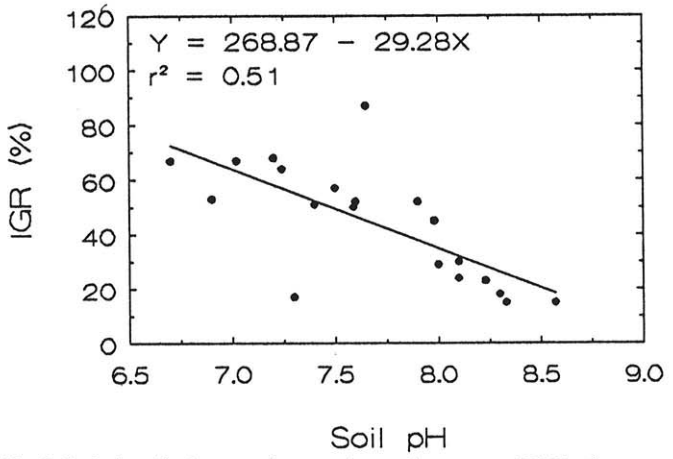

Fig. 2. Relationship between increased growth response (IGR) of tomato plants and pH of various soils. Variation due to regression was significant ($P = 0.05$).

TABLE 2. Effect of solarization on increased growth response (IGR) of plants tested under field conditions

Location	Crop	Planting date	Days after planting	IGR[a] (%)	Significance[b]
Bet HaShitta	Tomato	4/89	21	79	S
			42	45	S
Rehovot	Tomato	5/88	14	80	S
			28	100	S
			70	67	S
	Cotton	4/88	14	14	NS
			28	19	S
			70	17	NS
Eden	Cotton	4/87	14	22	S

[a] Calculated as percentage of increase in shoot dry weight over the untreated control.

[b] S and NS represent significant or nonsignificant differences ($P \leq 0.05$) between solarized and unsolarized soil, according to Student's *t* tests.

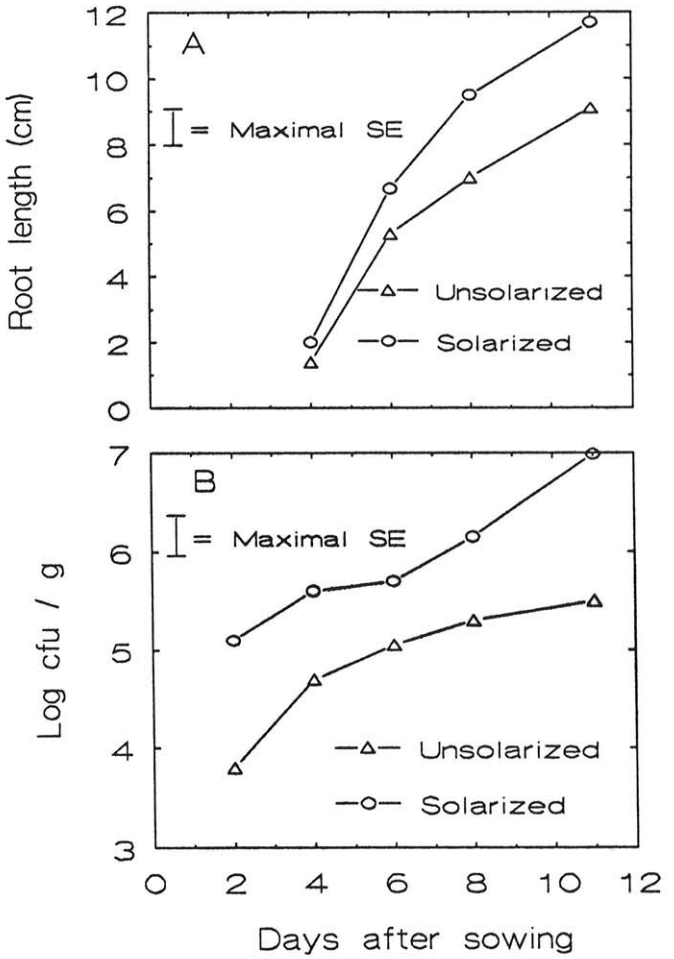

Fig. 3. Effect of solarization (Rehovot soil) on **A,** length of tomato roots and **B,** on population densities of fluorescent pseudomonads in the rhizosphere. Test carried out in a glass box for root-development assay. cfu = Colony-forming units per gram of soil.

lations of bacteria and of fungi were reduced 0–93% and 41–97%, respectively, by solarization. Populations of *P. pinophilum*, which was found in seven of 11 tested soils and adversely affected plant growth in preliminary experiments, were considerably reduced (94–99%). In most soils, populations of fluorescent pseudomonads were very low or at undetectable levels in both solarized and unsolarized soils. Changes in microbial populations were recorded at different depths in Rehovot soil (Fig. 4). A general trend of a decrease in populations with increasing soil depth in both solarized and unsolarized soils was observed. Smaller populations of all microorganisms tested were recorded in solarized soil at all depths, compared with unsolarized soil, thus, indicating an effect of solarization even in deep layers (Fig. 4). At all depths, fluorescent pseudomonads were detectable in the unsolarized soil, but not in the solarized soil. Actinomycetes were the group least affected by solarization to a depth of 60 cm. Populations of thermotolerant bacteria and fungi, i.e., those able to grow at 40 C, also were reduced after solarization, whereas thermotolerant actinomycetes were less affected (Table 4).

Rhizosphere. Four weeks after transplanting, bacterial populations in the rhizosphere of tomato plants were much larger in most soils, as compared with the corresponding nonrhizosphere

TABLE 3. Microbial population densities (colony-forming units per gram) in nonrhizosphere and rhizosphere soils, and root colonization of tomato plants as affected by soil solarization

		Nonrhizosphere soil[a]			Rhizosphere soil				Root colonization (%)[b]		
Location	Treatment	Bacteria ($\times 10^6$)	Fungi ($\times 10^3$)	*Penicillium pinophilum* ($\times 10^2$)	Bacteria ($\times 10^6$)	FP[c] ($\times 10^4$)	Fungi ($\times 10^3$)	*P. pinophilum* ($\times 10^2$)	FP	*Pythium*	*P. pinophilum*
Barqay	Control	100*[d]	31*	0[e]	3,200	1*	93*	0	7*	0	0
	Solarization	50	5	9	2,000	20	6	0	30	0	0
Bet Dagan	Control	9*	110*	80*	16	1*	77*	30*	3*	32*	0
	Solarization	2	41	3	16	25	6	0	30	0	0
Bet Hananya	Control	150*	66*	26*	186*	1	61	10*	46*	66*	0
	Solarization	11	10	0	82	1	58	1	78	0	0
Bet HaShitta	Control	70*	27*	23*	150*	11*	44*	63*	56	0	21*
	Solarization	9	4	0	85	106	21	0	68	0	0
Bsor	Control	22*	44*	0	270	6*	45*	0	12*	60*	16*
	Solarization	9	8	0	280	80	7	0	51	0	4
Gilgal	Control	61*	32*	0	170*	2*	20*	15*	4*	0	0
	Solarization	12	4	0	16	30	3	1	51	0	0
Maale Gilboa	Control	13	51*	16*	110	1*	63	0	17*	40*	3
	Solarization	13	30	0	93	13	61	0	52	0	1
Sede Eliyyahu	Control	120*	46*	40*	840*	1*	50*	0	22	24*	11*
	Solarization	17	5	0	280	130	25	0	34	0	0
Yahel	Control	79*	31*	30*	140	1*	33*	0	8*	20*	20*
	Solarization	7	8	0	130	46	15	0	88	0	0
Zippori	Control	22*	53*	0	240*	1*	48*	10*	25*	76*	23*
	Solarization	2	6	0	24	60	7	0	67	0	0

[a] Composite sample of a soil collected after termination of solarization.
[b] Percentage of root segments colonized by the indicated microorganism.
[c] FP = Fluorescent pseudomonads.
[d] Asterisk denotes a significant difference ($P \leq 0.05$) from the corresponding solar treatment, according to Student's *t* tests.
[e] Zero denotes below detectable level.

TABLE 4. Microbial population densities (colony-forming units per gram) in Rehovot soil and in different parts of tomato roots as affected by solarization or by heating in a simulation system after incubation at the indicated temperatures

	Temperature[a]	Nonrhizosophere soil[b]			Rhizosphere soil			Whole root tissue[c]		Interior root tissue[d]		Root colonization (%)[e]	
Organism	(C)	Unsolar.	Solar.	Simul.	Unsolar.	Solar.	Simul.	Unsolar.	Solar.	Unsolar.	Solar.	Unsolar.	Solar.
Bacteria	30	137	18*[f]	15*	3,000	1,200	1,100*	600	450	...[g]	...	...	...
($\times 10^5$)	40	60	12*	...	80	100	...	...	...	...	...	...	...
Fluorescent pseudomonads	30	0[h]	0	0	15	800*	200*	1.3	200*	0.14	2.8*	18	93*
($\times 10^4$)	40	0	0	...	0	0	...	...	...	...	...	...	...
Actinomycetes	30	12.2	11.3	...	13	11	...	0.36	11*	...	...	...	...
($\times 10^5$)	40	9.8	8	...	10	9.8	...	...	...	...	...	...	...
Fungi	30	36	1.3*	2.4*	340	43*	40*	470	51*	...	...	...	...
($\times 10^2$)	40	11	0.54*	...	48	30	...	...	...	...	...	...	...
Penicillium pinophilum	30	60	0*	0*	2,500	0*	0*	500	0*	...	...	38	1*
Fusarium spp.	30	720	0*	0*	3,500	500*	350*	500	200*	...	...	66	67
Pythium spp.	30	...	...	...	...	...	...	...	...	...	...	65	0*

[a] Temperature of incubation of the indicated organisms.
[b] A composite sample of a soil collected after the termination of solarization. Unsolar. = unsolarized soil; Solar. = solarized soil; Simul. = soil heated in a simulation system.
[c] Macerated and washed root tissue.
[d] Disinfested and macerated root tissue.
[e] Percentage of root segments colonized by indicated microorganism.
[f] Asterisk denotes a significant difference ($P \leq 0.05$) from the corresponding unsolarized treatment according to Student's *t* tests.
[g] Midline dots indicate that this parameter was not tested.
[h] Zero denotes below detectable level.

soils (Tables 3 and 4). This trend was less pronounced with fungi. An increase in populations of fluorescent pseudomonads in the rhizosphere of plants in the solarized soils of up to 130-fold higher than in the comparable unsolarized soils was recorded. This rapid establishment of fluorescent pseudomonads was evident at early stages of seed germination, reached its highest level at seedling emergence, and remained high throughout the growth period (Figs. 3 and 5). Similarly, solarization increased populations of fluorescent pseudomonads in the rhizosphere of emerging tomato seedlings grown in soils collected from Magen, Eden, and Sede Eliyyahu soils (data not shown). Regression analysis showed significant, inverse relationships between soil pH levels and the population densities of fluorescent pseudomonads in unsolarized soil ($r^2 = 0.36$; equation of regression line: log bacteria number = 51.3–6.17 pH) or in solarized soil ($r^2 = 0.38$; equation of regression line: log bacteria number = 214.2–29.7 pH). No significant regression was found between pH level and populations of fungi ($r^2 < 0.36$) (data not shown). Recovery of *P. pinophilum* remained low in the rhizosphere of plants in solarized soil. Populations of actinomycetes were not greatly affected by solarization (Table 4).

Roots. The percentage of colonization of roots of tomato plants grown in the solarized soils by fluorescent pseudomonads was higher than in corresponding unsolarized soils (Tables 3 and 4). This was also true for populations of fluorescent pseudomonads in whole and interior root tissues, as differentiated by surface-disinfestation. In contrast, colonization of roots by *Pythium* spp. and *P. pinophilum* was reduced to very low or undetectable levels in the solarized soils. Plant roots in solarized soils were colonized intensively by actinomycetes (Table 4). Similar microbial trends were recorded when assessing colonization of root segments or

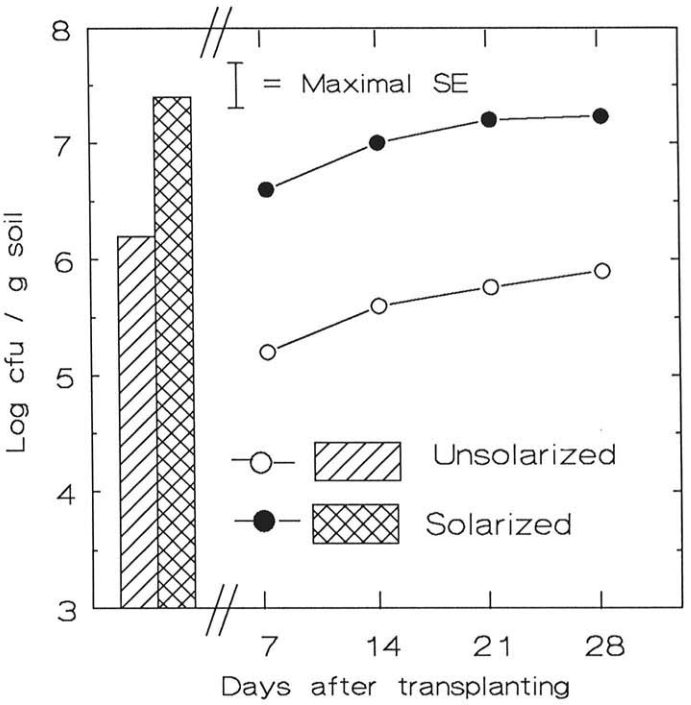

Fig. 5. Effect of solarization (Rehovot soil) on population densities of fluorescent pseudomonads (FP) in the rhizosphere of tomato plants over time. Columns represent FP population densities in the rhizosphere of emerging seedlings before transplanting (10 days after sowing); cfu = Colony-forming units per gram of soil.

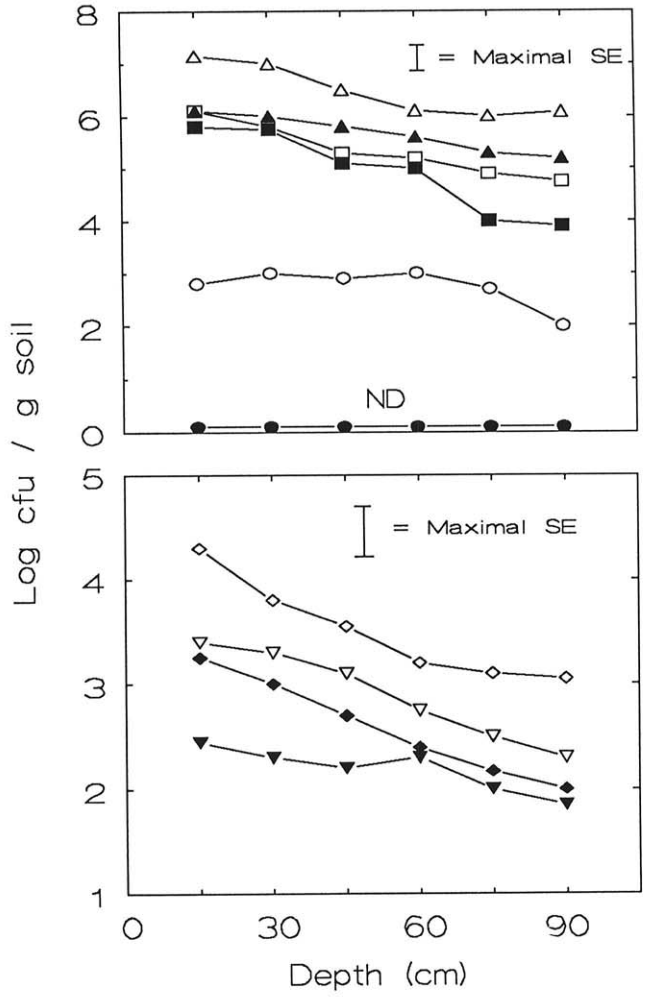

Fig. 4. Effect of soil solarization (Rehovot soil) on microbial population densities in the 15- to 90-cm depth. △, ▲ = bacteria; □, ■ = actinomycetes; ○, ● = fluorescent pseudomonads; ◇, ◆ = fungi; ▽, ▼ = *Fusarium* spp. Open symbols represent untreated soil; black symbols represent solarized soil. ND = below detectable level; cfu = Colony-forming units per gram of soil.

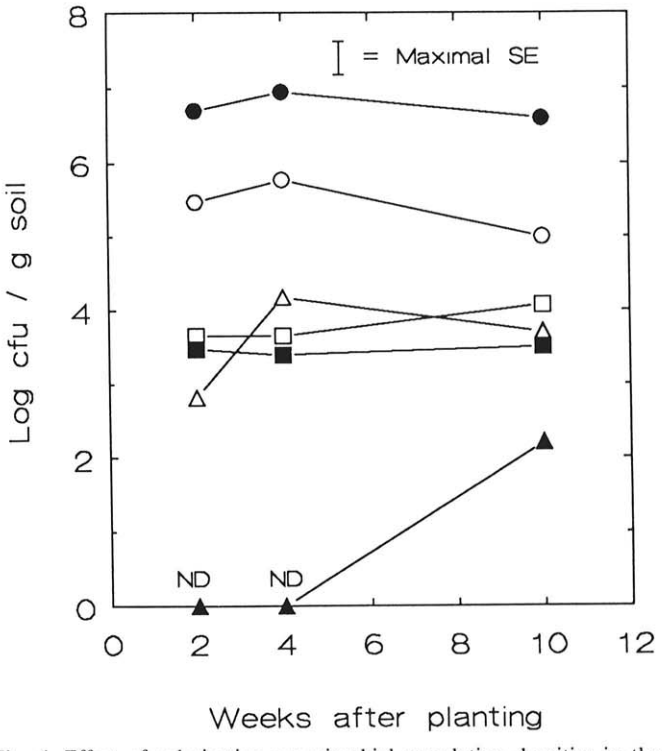

Fig. 6. Effect of solarization on microbial population densities in the rhizosphere of tomato plants grown in the field in Rehovot soil. ○, ● = fluorescent pseudomonads; △, ▲ = *Penicillium pinophilum*; □, ■ = *Fusarium* spp. Open symbols represent untreated soil; black symbols represent solarized soil. ND = below detectable level; cfu = Colony-forming units per gram of soil.

by directly assessing microbial populations in macerated roots (Table 4).

Simulated heating. Tomato plants were grown in untreated and artificially heated Rehovot soil. Changes in populations of total bacteria, fluorescent pseudomonads, total fungi, *P. pinophilum* and *Fusarium* spp. in nonrhizosphere and rhizosphere soils caused by artificial heating were similar to those caused by solarization (Table 4).

Field conditions. Samples of rhizosphere soils and roots of tomato or cotton plants were collected periodically from two field experiments. In Rehovot soil, populations of fluorescent pseudomonads in the rhizosphere were increased after solarization during all sampling periods (Fig. 6). Similarly, colonization of tomato roots by fluorescent pseudomonads in the solarized soil to a depth of 60 cm was greater than in the unsolarized soil, whereas colonization by *P. pinophilum* and *Pythium* spp. was suppressed (Fig. 7). Populations of *Fusarium* spp. were not affected by solarization. These trends also were observed with cotton plants in Rehovot soil and with tomato plants in Bet HaShitta soil (results not shown). For example, solarization increased populations of fluorescent pseudomonads in the rhizosphere by 40- and 19-fold at Rehovot and Bet Hashitta, respectively. In both soils, solarization reduced root colonization by *P. pinophilum* and *Pythium* spp. by 80–100%.

Effect of soil microorganisms on plant growth. *Bacteria.* One hundred randomly selected isolates of bacteria from the rhizosphere of tomato plants from unsolarized or solarized Rehovot soil were used to inoculate tomato seedlings. None of these 200 isolates had a significant effect on tomato growth, as compared with uninoculated plants. Fifty isolates of fluorescent pseudomonads from the tomato rhizosphere and 100 isolates from the plant roots from either unsolarized or solarized soils were used to inoculate tomato seedlings. In contrast to the results with nonfluorescent bacteria isolates, three and seven isolates of fluorescent pseudomonads from the rhizosphere and 10 and 29 isolates from the roots of plants from unsolarized and solarized soils, respectively, significantly increased the dry weight of tomato shoots by 25–65% over the uninoculated plants. Plant growth increase also was evident when the seed inoculation method was used with 15 of these isolates. Twelve isolates of fluorescent pseudomonads, which significantly increased dry weight, were identified by fatty-acid composition with chromatographic analysis. Six isolates were identified as *P. putida*, three as *P. fluorescens*, and three as *P. alcaligenes*, with similarity indices of 0.55–0.72, 0.45–0.68, and 0.40–0.48, respectively.

Fungi. One hundred randomly selected fungal isolates from soil in the rhizosphere and 100 isolates from tomato roots, from either unsolarized or solarized Rehovot soil, were tested. Of the fungi from the rhizosphere, nine isolates from unsolarized and three from solarized soil significantly reduced plant growth by 19–40%. Of the fungi from roots, 23 isolates from unsolarized and nine from solarized soil significantly reduced plant growth by 18–42%. Most of the growth-suppressing fungi were identified as *P. pinophilum*. Of the 50 isolates of *P. pinophilum* randomly isolated from tomato roots from unsolarized Rehovot or Bet HaShitta soil, 12 and 9 isolates, respectively, significantly reduced growth of inoculated tomato seedlings by 32–41% and 42–57%. Twelve growth-suppressing isolates of *P. pinophilum* that originated from Bet HaShitta soil also were tested by soil infestation instead of root dipping. In all cases, significant plant growth suppression resulted. The growth-suppressing fungi could be reisolated (after surface-disinfestation) from the interior root tissues, indicating the invasion and establishment of these fungi in the roots. None of the fungi tested stimulated plant growth.

Inoculation tests were repeated with representative isolates of fluorescent pseudomonads and *P. pinophilum*. The results were similar to those mentioned.

Hierarchic statistical analyses were conducted to examine the effect of microbial populations on plant growth, with regard to the origin of the population. An analysis of all isolates of fluorescent pseudomonads showed that those originating from plants grown in solarized soil increased plant growth significantly more than those from plants in unsolarized soil. Similarly, fungi from unsolarized soil decreased plant growth significantly more than those from plants grown in solarized soil.

Actinomycetes. One hundred isolates of actinomycetes from the rhizosphere soil of tomato plants of each unsolarized and solarized Rehovot soil were used to inoculate tomato seedlings. None of these isolates significantly affected tomato growth.

Antagonism on agar. Isolates of bacteria from the soil, rhizosphere, and roots of tomato plants grown in either solarized or unsolarized soils were tested for antagonistic activity against *S. rolfsii* and *M. phaseolina* on agar. With each of the 10 tested combinations, the number of bacteria from solarized soil evincing antagonistic activity was higher than that of microorganisms from the respective unsolarized soil (Table 5).

DISCUSSION

Increased growth in heat-treated and fumigated soils (19,34) and in solarized soils (1,5,15,25,31–33) has been extensively reported. We also demonstrated increased growth of several crops in several solarized or fumigated soils in the greenhouse (Table 1). Increased growth and the respective microbial changes also were evident in three field experiments (Table 3; Figs. 6 and 7). Results in soils artificially heated to simulate solarization were similar to those obtained in solarized soil (Tables 1 and 4), thus, supporting the reliablity of this simulated system (9,36). Suppression of plant growth by solarization was not observed in this study, but has been reported (12). Reproducibility of increased growth response in solarized soils was evident when the soil was solarized in different years at the same location, e.g., at Barqay, Bet Dagan, and Rehovot (Table 1).

Increases in crop yield after solarization were obtained in field experiments without apparent infestation (8,10,25). However, the relationship between increased crop yield in the field and increased growth of young plants in greenhouse experiments has to be studied further because of important economic implications.

Previous investigators correlated increased growth response with chemical changes in the soil (2,5,20,33); the increase in

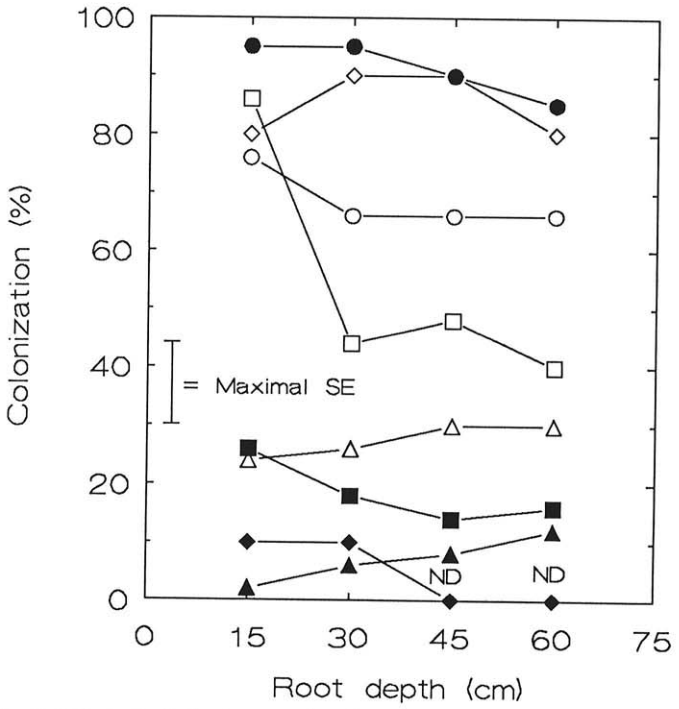

Fig. 7. Effect of solarization on microbial colonization at various depths of roots of tomato plants grown in the field in Rehovot soil. Colonization was calculated as percentage of segments colonized with the indicated organism. ○, ● = fluorescent pseudomonads; △, ▲ = *Penicillium pinophilum*; □, ■ = *Fusarium* spp.; ◇, ◆ = *Pythium* spp. Open symbols represent untreated soil; black symbols represent solarized soil.

TABLE 5. Antagonistic activity of fluorescent pseudomonads or nonfluorescent bacteria against *Sclerotium rolfsii* and *Macrophomina phaseolina* in culture

Source of soil	Bacteria origin	Soil treatment[a]	Micro-organism[b]	No. of isolates	*S. rolfsii*[c]	*M. phaseolina*[c]
Kfar Warburg	Rhizosphere	US	NFC	60	19	15
	Rhizosphere	S	NFC	60	20	21
Rehovot	Soil	US	NFC	60	6	5
	Soil	S	NFC	60	7	6
	Rhizosphere	US	NFC	60	3	7
	Rhizosphere	S	NFC	60	11*[d]	10
	Root	US	NFC	60	7	19
	Root	S	NFC	60	16*	23
	Root	US	FP	45	1	9
	Root	S	FP	45	4	12

[a] US = Unsolarized soil; S = solarized soil.
[b] NFC = Nonfluorescent bacteria; FP = fluorescent pseudomonads.
[c] Number of isolates that inhibited growth. The total numbers of isolates from unsolarized Rehovot soil that inhibited growth of *S. rolfsii* and *M. phaseolina* were 17 and 40, respectively and the total numbers of isolates from solarized Rehovot soil were 38 and 51, respectively. The total number of isolates used was 225 each from unsolarized and solarized Rehovot soil.
[d] Asterisk denotes a significant difference ($P = 0.05$) between isolates from solarized and unsolarized soil from Rehovot, according to Student's *t* tests.

mineral nutrients in solarized soils we obtained in our study apparently may have a role in the phenomenon. However, the long-lasting effects of the increased growth observed in this study and by others (1,16,25,31) may be due to shifts in the components of the soil microbial populations.

Significant regressions between soil pH and increased plant growth (Fig. 2) or populations of fluorescent pseudomonads were shown, yet it is not known how soil pH affects factors related to the increased growth, or what the relationship is between pH levels in the soil and in the rhizosphere. Correlations between soil properties (e.g., pH) and increased plant growth and microbial colonization of the rhizosphere might be useful for developing systems for predicting increased plant growth in soils.

Populations of bacteria and fungi (including thermotolerant fungi) were reduced by solarization. Actinomycetes were least affected, as also reported by others (14,21,31). Stapleton and DeVay (31) found a decrease in populations of various bacteria (including fluorescent pseudomonads) and fungi in the upper soil layer immediately after solarization; whereas, in other studies bacteria increased after solarization (14,21). Microbial changes in solarized soils were observed even at depths between 60 and 90 cm (Figs. 4 and 7), at which the temperature is not increased markedly (15). Thus, factors other than heat, such as volatiles, should also be considered.

Significant changes in microbial populations, especially fluorescent pseudomonads, occurred in the root zone. Populations of these bacteria were very low in nonrhizosphere soil and decreased further after solarization. However, they rapidly colonized the rhizosphere and plant roots in the solarized soil, and their populations increased up to 130-fold over numbers in unsolarized soil. This trend was evident in 11 different soils, including field experiments (Tables 3 and 4; Figs. 3, 5–7). Surprisingly, heat-sensitive fluorescent pseudomonads, rather than thermotolerant microorganisms, were the most successful in exploiting the rhizosphere. Apparently, heat sensitivity of these bacteria is counterbalanced by other beneficial characters, such as short generation time and probably rapid growth as compared with other colonizers. Being poor competitors (22), fluorescent pseudomonads eventually may benefit from the reduction in population densities of competing microorganisms by solarization. Root exudates are the dominant factors in the rhizosphere (6) and may be the trigger or signal for the massive proliferation of these bacteria in this region, as verified by us in another study (A. Gamliel and J. Katan, *unpublished data*). Of the bacteria tested in this study, only fluorescent pseudomonads significantly increased growth of inoculated plants. Fluorescent pseudomonads have been studied intensively as plant growth-promoting rhizobacteria (17,18,27). Hence, elucidating the mechanisms related to their successful establishment in solarized soils has broad implications. Isolates of *Bacillus* and *Trichoderma* spp. also improve plant growth (3,4). Because these organisms are stimulated by solarization in certain cases (16,32), their possible role in increased plant growth should be considered in future studies. Root colonization was assessed by using root-segment and root-maceration methods (Tables 3 and 4). The segment-colonization assay is less sensitive but is much less tedious and time-consuming than the direct assay.

With the increase in growth-promoting fluorescent pseudomonads, a decrease in population densities of *P. pinophilum*, which suppresses plant growth, was observed. The two microbial shifts may have contributed simultaneously to increased plant growth in solarized soil in our study. The harmful effect of *Penicillium* spp. was reviewed by Salt (23). *P. pinophilum* fulfills some of the requirements for a "minor pathogen" (23): it suppresses plant growth although distinctive disease symptoms are lacking; it parasitizes root tissues; it is widely distributed in soils (Tables 3 and 4); and it is not restricted to one host (*unpublished data*). The possibility that the root-surface microflora also include deleterious microorganisms, namely, those affecting the plant by metabolites without parasitizing its tissues (23,35), was not excluded. Relationships between control of *Pythium* spp., known to affect root growth adversely (29), and increased growth response has yet to be determined. A possible beneficial effect of fluorescent pseudomonads is the suppression of deleterious and other harmful microorganisms through aggressive colonization of roots and antibiotic production (17,18,26). A similar mechanism may operate in solarized soils. An increase in population densities of bacteria and fungi showing antagonistic activity in culture may indicate the potential of such microorganisms in biological control. The poor establishment of *P. pinophilum* and *Pythium* spp. in the solarized soils might be attributable to induced suppressiveness, as shown with certain pathogens (9). It is not yet known whether microbial shifts related to increased growth response in solarized soils are related to mechanisms of induced suppressiveness (9,15).

By using hierarchic analyses, we demonstrated qualitative changes in population densities of beneficial bacteria and of harmful fungi in the plant root zone in solarized soils. We suggest that increased plant growth can be attributed to a combination of biotic and abiotic mechanisms, which may vary in different soils. The involvement of other biotic and abiotic mechanisms related to plant growth, e.g., mycorrhizae, phytotoxic-decomposition products, and plant growth-promoting substances (3,4,16) should not be excluded. A fuller understanding of the mechanisms of the increased growth response may contribute to knowledge of the basic principles of plant health.

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