Increased Potato Yields by Treatment of Seedpieces with Specific Strains of Pseudomonas fluorescens and P. putida

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ABSTRACT

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Significant increases in growth and yield of potato plants were achieved by treating seedpieces with suspensions of two *Pseudomonas* spp. at $\sim 10^9$ colony-forming units (cfu)/ml prior to planting. The pseudomonads were selected from over 100 strains that were isolated from the surface of potato tubers and also exhibited antibiosis against *Erwinia carotovora* var. *carotovora* in vitro. The isolates were identified as strains of *Pseudomonas fluorescens* and *P. putida*. These strains survived for at least 1 mo on treated seedpieces planted in loamy sand field soil at populations of $\sim 10^9$ cfu/0.785 cm^2. Also, they colonized developing potato roots and were the predominant bacteria in the rhizospheres up to 2 mo after planting. Bacterization of seedpieces planted in field soils in the greenhouse resulted in up to 100% increase in fresh weight of shoot and root systems in a 4-wk period. Statistically significant increases in yield ranged from 14 to 33% in five of nine field plots in California and Idaho. The pseudomonads had no effect on plant growth or tuber yield when seedpieces were planted in peat soil, or in soil that was relatively dry. Both *Pseudomonas* spp. were compatible with fungicides that were commonly used to treat seedpieces, except for manganese ethylenebisdithiocarbamate zinc salt (mancozeb). The mechanism by which these bacteria enhance plant growth and tuber yield may be associated with changes in the composition of rhizosphere bacterial flora.

There are numerous instances in which bacteria inoculated onto plant seeds and roots (a process called bacterization) have been reported to enhance plant growth (4, 7, 13, 14, 17, 18, 19, 21, 25). Most of these have concerned bacteria in the genera *Azotobacter*, *Bacillus*, *Pseudomonas*, and *Clostridium*. Results from these studies have been highly variable, however, and the average yield data generally have not differed significantly from those of the nonbacterized controls. Brown et al. (5), for example, obtained significant increases in growth and yield of various crop plants inoculated with *A. chroococcum* in five of 19 greenhouse trials and two of 13 cases in the field. Increases in yield ranged from 3 to 11%, but replicate variance was great and differences usually were not significant even at $P = 0.10$. The results of Merriman et al. also were inconsistent for both greenhouse (18) and field experiments (19).

Most experimental and commercial bacterization efforts in Russia have been conducted with preparations of *A. chroococcum* (called "azotobacterin") and *Bacillus megaterium* (called "phosphobacterin"). Azotobacterin is considered to act as a nitrogen fertilizer by the fixation of atmospheric nitrogen, and phosphobacterin supposedly improves the phosphorus nutrition of the plant by mineralization of organic phosphorus and making it more available to the plant. However, researchers (6, 20) have concluded that the amounts of nitrogen fixed and phosphorus made available to the plants by the action of the bacteria could not be responsible for the yield increases that sometimes were obtained. Furthermore, they implied that these bacteria may not be rhizosphere organisms (9, 12, 16), but opinions vary on this aspect (11, 21).

We became interested in the phenomenon of bacterization upon noting increased root and foliar growth with several plants, such as potato, sugarbeet, and lettuce, when seeds or seedpieces were treated with specific bacterial strains prior to planting. This report presents the results of a study on the effect of specific rhizosphere pseudomonads on potato plant growth and tuber yield.

MATERIALS AND METHODS

Initial selection of antagonists.—Bacteria were isolated from the surface of freshly dug healthy potato tubers and arbitrarily selected for inhibition of *Erwinia carotovora* var. *carotovora* (Ecc) in vitro. Isolations were made from potato cultivars White Rose and Russet Burbank. Each tuber was washed in 100-ml sterile distilled water for ~10 min. Dilutions then were made from the wash water, plated on King's Medium B (KB), and incubated at 28 C for 24 hr. Then plates were sprayed with a 24-hr-old culture of Ecc and incubated an additional 24 hr at which time inhibition zones were apparent about antagonistic colonies. Colonies that exhibited antibiosis were restreaked, examined for purity, and stored. The strains were subsequently checked for antibiosis against Ecc, *E. carotovora* var. *atroseptica* (Eca), and the *Erwinia* sp.

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that causes soft rot of sugarbeet (24). They also were examined for their potential to rot potatoes by inoculating slices of Russet Burbank tubers with suspensions that contained $\sim 10^7$ colony-forming units (cfu)/ml of each isolate and incubating them at 28 C for 48 hr. *Erwinia carotovora* var. *carotovora* strain SR-55 and Eca strain SR-150 were obtained from Arthur Kelman (University of Wisconsin, Madison), and sugarbeet *Erwinia* strain Sh-1 was isolated from a rotted beet from Shandon, California.

Greenhouse screening of antagonists.—Ninety-seven strains of selected antagonistic bacteria were grown on KB for 48 hr, scraped from plates, and diluted to give suspensions of $\sim 10^9$ cfu/ml. Five uniformly cut potato seedpieces (cultivar White Rose) were dipped for 5 min in each suspension and planted in pots containing loamy sand field soil obtained from Shafter, California. Only single-eye pieces were planted. Fresh weights of roots and shoots were taken from 4-wk-old plants, or generally 1 wk after emergence of shoots. These experiments were repeated at least three times with strains that stimulated plant growth. Treated seedpieces were planted in the loamy sand soil from Shafter, UC mixture (2), or a peat soil from Tulelake, California.

Establishment of antagonists on seedpiece surfaces and in the rhizospheres of treated plants.—The bacteria selected for this study were *Pseudomonas* strains TL-3 and BK-1 which were isolated from freshly dug tubers (cultivar Russet Burbank) from Tulelake, and (cultivar White Rose) from Bakersfield, California, respectively. Seedpieces of potato cultivar White Rose, were dipped for 5 min in suspensions containing $\sim 10^9$ cfu/ml of TL-3 or BK-1, placed on paper towels in the laboratory, and sampled at various intervals to determine the effect of air-drying on the survival of inoculum. Laboratory temperature and relative humidity averaged 24 C and 20%, respectively, during air-drying period. Population determinations were made by removing tissue with a No. 5 cork borer (0.785 cm^2 surface area) contiguous to eyes from treated seedpieces and washing each sample in 100-ml of sterile distilled water. Serial water dilutions subsequently were made and plated on KB. One plug from each of three seedpieces was sampled at each time interval and three dilution plates were made from each plut. Plates were incubated for 24 hr at 28 C.

The ability of the pseudomonads to survive on seedpieces and roots in field soil was determined by the methods described above. This and the following work was performed with seedpieces planted in loamy sand soil in the greenhouse. The sampling of roots for the presence of pseudomonads was made by excising 1-cm root sections from the tips and midsections of three roots per plant and then washing each one along with clinging soil particles with 1-ml of sterile distilled water. One-tenth ml of this suspension then was plated on each of three KB plates. The populations of pseudomonads on roots of treated and nontreated seedpieces were followed up to 8 wk. No attempt was made to determine the precise location of the bacteria.

The pseudomonads were identified on KB by their characteristic colony morphologies and fluorescence. In most cases, the populations of the introduced pseudomonads were much greater than other rhizosphere bacteria and were detected by plating water dilutions of 10^{-6} to 10^{-7} on KB. Few, if any, other rhizosphere bacteria could be detected at those dilutions. The isolates were further examined for antibiosis toward *Erwinia* spp. An immunofluorescent staining technique (1) was utilized for final identification of one isolate (TL-3). Several fluorescent *Pseudomonas* spp. isolated from the surface of nontreated seedpieces were tested to determine the specificity of the prepared antibody.

The effect of soil moisture on survival of bacteria on seedpieces was tested by planting seedpieces in a loamy sand soil from Shafter, California, adjusted to soil matric water potentials of −16.1, −2.8, and −1.7 bars, or air-dried. Moisture determinations were made with a C-51 sample chamber psychrometer (Wescor, Inc., Logan, UT 84321). Soil moistures were maintained constant by planting seedpieces in styrofoam cups and covering each cup with a plastic wrap. Survival capability of the bacteria was determined with the same population sampling methods described above.

Effectiveness of Pseudomonas spp. in increasing potato yields in the field.—Nine replicated field experiments were made to test the effectiveness of various bacterial species on potato yields. Strains TL-3, TL-10, and TL-12 were nonpectolytic, fluorescent *Pseudomonas* spp. and were isolated from Russet Burbank potatoes grown at Tulelake, California. Strain BK-1 (a fluorescent *Pseudomonas* sp.) and strain S-1-B (a *Bacillus* sp.) were isolated from White Rose potatoes grown at Shafter, California. *Bacillus subtilis* A-13 and *E. quercina* AC-1 were obtained from K. F. Baker and M. N. Schroth, respectively. All of the above strains inhibited *Erwinia* soft-rot spp. in vitro except AC-1 which was tested because of the growth-promoting characteristic it exhibited when inoculated onto carrot slices (10). Inocula for field trials were obtained from 48-hr cultures on KB in large plastic petri dishes, whereas *Bacillus* spp. were cultured on potato dextrose agar. Seedpieces were dipped for 5 min in suspensions that contained $\sim 10^9$ cfu/ml. Seedpieces then were placed in large polyethylene bags and immediately taken to the field for planting. Commercial planting procedures were followed in all plots and tubers were harvested mechanically unless otherwise specified. In early experiments, tubers were graded and yield increases were based on the increases of US No. 1 tubers. In later tests, total weight was used since grading did not reveal any differences in the size and quality of tubers among the various trials.

Identification of Pseudomonas strains TL-3 and BK-1.—*Pseudomonas* strains TL-3 and BK-1 were identified according to Stanier et al. (23) as modified by Sands et al. (22). Several nitrogen and carbon sources were used in addition to those listed by these authors.

RESULTS

Selection of antagonistic bacteria and their effect on plant development.—One hundred eight bacteria which inhibited Ecc in vitro were isolated from the surfaces of potato tubers. Antagonists were readily isolated from both potato cultivars. Eighty-six were fluorescent *Pseudomonas* spp., 12 were *Bacillus* spp., and 10 were not readily identifiable. All isolates which inhibited growth of Ecc also inhibited Eca and the sugarbeet soft-rot *Erwinia*. Eight *Pseudomonas* spp. and three *Bacillus* spp. rotted

potato slices and, therefore, were unsuitable for seedpiece inoculation.

Two *Pseudomonas* strains, TL-3 and BK-1, usually stimulated plant growth in the greenhouse (Fig. 1). Percent increase in fresh weight of shoot and root systems ranged from 0 to 367% (Table 1). Growth responses were observed with soils from different locations in Kern County and with UC mix (2), but were not observed in peat soil obtained from the Stockton delta area.

Establishment of pseudomonads on potato seedpieces and in the rhizospheres of potato plants.—Populations of strain TL-3 on the surfaces of potato seedpieces consistently averaged 10^7 cfu/0.785 cm^2 immediately after seedpieces were dipped in suspensions of $\sim 10^9$ cfu/ml. Populations declined rapidly if allowed to air-dry and were about 5×10^3 cfu/0.785 cm^2 after 4 wk (Fig. 2).

Planting of potato seedpieces in soils of low soil water potential adversely affected the survival of TL-3 (Fig. 3). Populations on seedpieces differed nearly 1,000-fold 96 hr after they were planted in soils with water potentials of -16.1 to -1.7 bars.

Strains TL-3 and BK-1 apparently spread from the inoculated seedpieces to the roots, because they were detected in the rhizospheres of potato plants in field soil harvested 1 mo after planting (Fig. 4). The bacteria were present at high but variable populations along all sections of roots, and were the predominant rhizosphere bacteria present on treated plants after 2 mo (Table 2).

Identification of the pseudomonads in rhizospheres of treated plants was relatively simple because of their predominance and their characteristic colony morphologies and fluorescence on KB. The immunofluorescent staining procedure also was effective for identifying isolate TL-3. Of 15 rhizosphere *Pseudomonas* spp. isolates obtained from control plants, none reacted positively to the prepared fluorescent antibody.

Effect of Pseudomonas spp. on potato yields in field experiments.—Potato yields were increased up to 33% by inoculation of seedpieces with *Pseudomonas* spp. (Table 3). Strain TL-3 was responsible for the greatest increases in all plots except one. Strain BK-1 caused significant increases in yield in two plots. Yield increases of 20 to 24% or greater usually were necessary before significance could be demonstrated at $P = 0.05$ because of variation within plots. In the Idaho plot, however, a 13% increase in yield was significant at $P = 0.05$. This plot and the plot at Stockton, California were hand-harvested, and all other plots were machine-harvested.

Increases in yield were not obtained in plots located on peat soils at Tulelake and Stockton, California. This paralleled greenhouse studies in that no effect was obtained when seedpieces were planted in pots containing peat soils.

Effect of various fungicides on antagonistic bacteria.—Since potato seedpieces are treated with

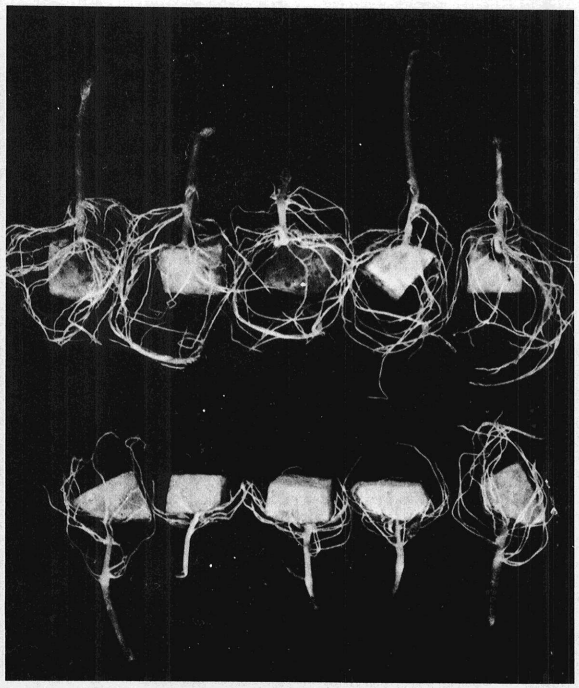

Fig. 1. Root and shoot increases of potato caused by seedpiece inoculation with *Pseudomonas* strain TL-3 (bottom row was control). Prior to being planted in a loamy sand field soil seedpieces were dipped in a suspension of TL-3 that contained $\sim 10^9$ colony-forming units/ml.

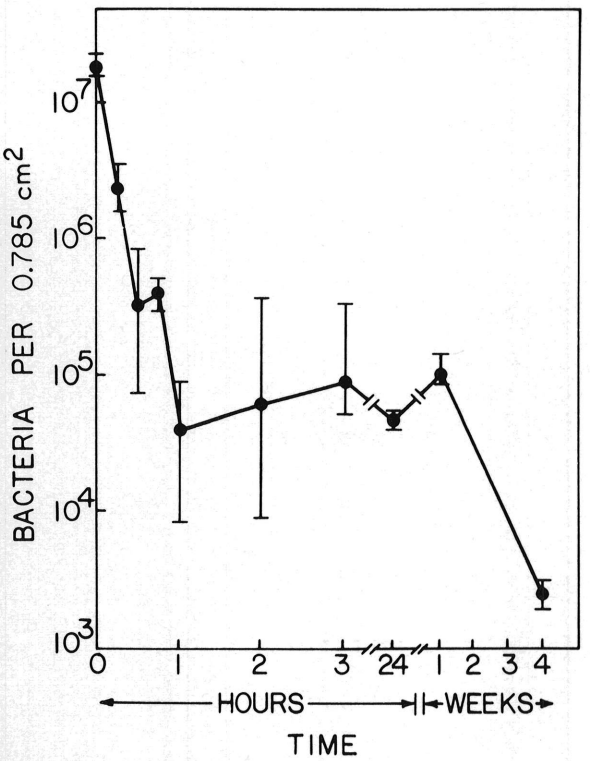

Fig. 2. Effect of air-drying (RH $\cong$ 20%) of *Pseudomonas* strain TL-3 on the surface of potato tubers. Potato seedpieces were dipped in a suspension of TL-3 that contained $\sim 10^9$ colony-forming units/ml. After various time intervals, a No. 5 cork borer plug (0.785 cm^2) was removed from three seedpieces; serial water dilutions were made of the bacterium and plated on King's Medium B. Each point is the mean population of TL-3 on three seedpieces.

fungicides in many potato-growing regions, their effect on survival of TL-3 and BK-1 was tested in vitro. One percent solutions of the wettable powder form of each fungicide were made. Analytical filter paper assay disks were dipped in each solution and placed on KB medium. Media were subsequently sprayed with suspensions of TL-3 or BK-1 that contained $\sim 10^7$ cfu/ml, incubated at 28 C for 24 hr, and then examined for the presence of inhibition zones.

None of the fungicides commonly used on potatoes, except mancozeb, inhibited growth on the pseudomonads on agar.

Identification of Pseudomonas strain TL-3 and Bacillus sp. strain BK-1.—*Pseudomonas* strains TL-3 and BK-1 fit the general descriptions of *P. fluorescens* and *P. putida*, respectively, based on 140 different tests. However, neither TL-3 nor BK-1 resemble the descriptions of the known biotypes for either species and presumably are representatives of undescribed biotypes.

DISCUSSION

Our studies have shown that bacterization of potato seedpieces with specific strains of *P. fluorescens* strain TL-3 and *P. putida* strain BK-1 can cause substantial increases in yields in certain soils. Although other

TABLE 1. Effects of bacterization of potato seedpieces with strains of *Pseudomonas* spp., a *Bacillus* sp., and *Erwinia quercina* on the growth of potato plants in greenhouse trials

Trial	Cultivar	Soil type[a]	Reps./ treat.	Strains[b] tested	Avg. fresh wt. of root and shoot (g)	Increase over checks (%)
1	White Rose	UC mix	20	Check	0.3	
				BK-1	1.4	367*[c]
				TL-3	1.1	267*
				Ac-1	1.2	300*
				S-1-B	0.6	100
2	White Rose	UC mix	10	Check	11.4	
				BK-1	13.8	21*
				TL-3	14.4	26*
				Ac-1	12.2	7
				TL-10	8.4	−26*
				Mixture	12.8	12
3	White Rose	Loamy sand	10	Check	3.78	
				BK-1	5.64	49**
				TL-3	4.46	18
				Ac-1	4.38	16
				TL-10	2.73	−38
4	White Rose	Loamy sand	12	Check	2.86	
				TL-3	5.25	84*
5	White Rose	Loamy sand		Check	0.8	
				TL-3	2.5	213**
6	White Rose	Loamy sand	12	Check	0.93	
				TL-3	1.8	94**
7	White Rose	Peat[d]	12	Check	0.95	
				TL-3	1.09	15[c]
8	Kennebec	UC mix	20	Check	4.22	
				BK-1	5.93	41**
				TL-3	7.13	69**
				Ac-1	5.48	30
				TL-10	5.54	31
				Mixture	6.12	45**

[a]Loamy sand soil was obtained from a potato field near Shafter, California. Peat soil was obtained from a potato field near Stockton, California. Each listing of loamy sand represents soil taken from a different location in Kern County.

[b]Strains (TL-3, TL-10) and BK-1 are fluorescent *Pseudomonas* spp. which were isolated from tubers grown at Tulelake and Bakersfield, California, respectively. Strain S-1-B is a *Bacillus* sp. isolated from a tuber grown at Bakersfield, California. Isolate Ac-1 is an *Erwinia quercina* strain obtained from M. N. Schroth.

[c]Asterisks * and ** denote statistical significance $P = 0.05$ and $P = 0.01$, respectively.

[d]Statistically nonsignificant results were obtained in three other experiments.

[e]This experiment was repeated three times with similar results.

pseudomonads have been tested as seed treatments to improve crop yields (7, 13, 14), statistically significant data on yield improvement have not been obtained in field plot work conducted over a period of years.

Because of the high degree of variability universally encountered in bacterization experiments, many field trials in different locations are necessary to verify positive results. In this study, in greenhouse tests conducted over a period of 3 yr, strain TL-3 consistently increased plant growth at statistically significant levels. Yield increases in

TABLE 2. Survival of *Pseudomonas* sp. strain TL-3 on potato roots in field soil in the greenhouse[a]

Age of plant (wk)	Soil type[b]	Plants sampled (no.)	Root piece length (cm)	Avg. TL-3 population[c] on roots	
				root tips ($\times 10^{-2}$)	mid root ($\times 10^{-2}$)
2	loamy sand	9	4	1,602 ± 1,675[d]	...
4	loamy sand	6	1	128 ± 107	90 ± 97
8	loamy sand	5	1	...	24 ± 28
4	peat	11	1	...	146 ± 218

[a]Plants originated from seedpieces dipped in a suspension of strain TL-3 containing approximately 10^9 colony-forming units/ml.
[b]Loamy sand soil was obtained from a potato field near Bakersfield, California. Peat soil was obtained from a potato field near Stockton, California.
[c]Root sections of 1 or 4 cm in length were placed in 1-ml of water, agitated, and 0.1 ml was plated on King's Medium B.
[d]Average bacteria from 10 root pieces from the designated number of plants.

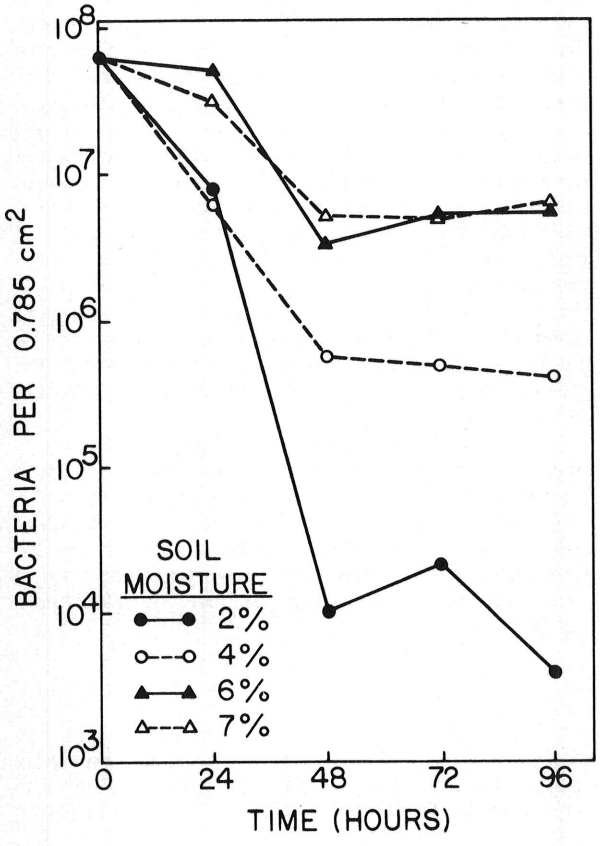

Fig. 3. Effect of soil moisture on the survival of *Pseudomonas* strain TL-3 on potato seedpieces planted in field soil in the greenhouse. Potato seedpieces were dipped in a suspension of TL-3 containing ~ 10^9 colony-forming units/ml and planted in a loamy sand field soil of various moisture levels of 2%, 4%, 6%, and 7% (air-dried, −16.1, −2.8, and −1.7 bars, respectively). A no. 5 cork borer plug (0.785 cm^2) was removed from three seedpieces at each sampling time, serial water dilutions were made of the bacteria and planted on King's Medium B.

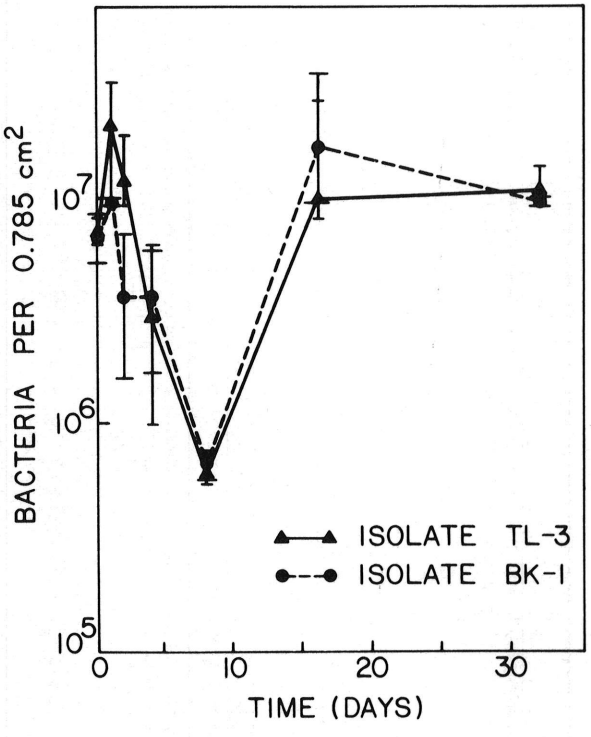

Fig. 4. Populations of *Pseudomonas* strain TL-3 and *Bacillus* sp. strain BK-1 on potato seedpieces. Potato seedpieces were dipped in a suspension of TL-3 containing ~ 10^9 colony-forming units/ml and planted in a loamy sand field soil in the greenhouse. At various time intervals, a No. 5 cork borer plug (0.785 cm^2) was taken from three seedpieces and washed in 100 ml of sterile distilled water. Serial dilutions of the wash water were made and plated on King's Medium B from which the bacteria were isolated.

TABLE 3. Effect of bacterial treatments on potato yields in field plot experiments

State, location,[a] and cultivar name	Season and year	Bacterial strain[b]	Yield[c] (avg.)	Increase (%)
California	Spring '75	Check	29.6	
Shafter		TL-3	36.8	24**[d]
White Rose		TL-10	32.9	11
		Ac-1	34.4	16**
		A-13	33.2	12
	Fall '75	Check	4.5	
		TL-3	4.2	−7
		TL-10	6.0	33**
		Ac-1	3.5	−22
		S-1-B	3.8	−16
	Spring '76	Check	76.7	
		TL-3	78.4	2
		TL-10	75.6	−1
		Ac-1	76.1	−1
		BK-1	81.0	6
		Mixture	74.3	−3
Tulelake	Fall '75	Check	82.8	
Russet Burbank		TL-3	77.0	−7
		TL-10	95.6	15
		Ac-1	83.4	−1
		A-13	76.0	−9
		TL-10	70.0	−14
	Fall '76	Check	71.2	
		TL-3	74.8	5
		TL-10	69.4	−3
		Ac-1	69.0	−4
		BK-1	72.6	2
		Mixture	74.0	4
Arvin	Spring '76	Check	48.7	
Kennebec		TL-3	57.5	18*
		TL-10	49.5	0
		Ac-1	47.9	−2
		BK-1	50.3	3
		Mixture	53.0	9
Stockton	Winter '76	Check	72.3	
White Rose		TL-3	82.4	14
		TL-10	79.0	9
		BK-1	78.4	8
		TL-3 (powder)	77.9	8
Bakersfield	Spring '76	Check	56.0	
White Rose		TL-3	67.4	20*
		TL-10	63.7	14
		Ac-1	66.1	18
		BK-1	63.3	13
		Mixture	54.1	−3
Idaho				
Minidoka	Fall '76	Check	84.0	
Russet Burbank		TL-3	95.4	14**
		TL-10	89.7	7
		BK-1	93.0	11**
		Fungicide (Maneb)	86.8	3

replicated field experiments also were statistically significant during a 3-yr testing period, in five of nine trials in different locations and soil types. The nonsignificant data obtained in fields with peat soil were consistent with the greenhouse tests as were the results of the Shafter, 1976, spring and fall field plots in which seedpieces were planted in dry soil. These exceptions were not unexpected since bacterization apparently is greatly affected by soil type, soil moisture, and fertility; increases in crop production in Russia were reported to occur mostly in highly cultivated soils of high fertility where the principal crops were vegetables (6, 20). The failure of strain TL-3 to promote increased plant growth in the dry field soil was not surprising since greenhouse studies showed that survival of inocula was influenced greatly by soil moisture. Bacterial populations usually decline in dry soil. Accordingly, Russian workers showed that *Azotobacter* inoculants were most effective in soils in which the water content was greater than 40% of field capacity, but not saturated (20).

Researchers agree that there is little correlation between the capacity of microorganisms to exhibit antibiosis in agar plating methods and their capacity to biologically control pests in the field (3, 15, 17). The *Pseudomonas* isolates used in this study were isolated from the surface of healthy potato tubers, and were apparently well-adapted to the potato rhizosphere. Non-antagonists, with one exception, were not tested for beneficial effects and, therefore, it is not known whether the antibiosis that was exhibited in vitro is an important characteristic for the selection process, or even if antibiosis is related to the subsequent enhancement of plant growth. The dependability of greenhouse tests in assessing an isolate's potential in the field was essential to the selection process. It was possible to screen many isolates prior to field testing since the capacity of *Pseudomonas* isolates to stimulate plant growth in the greenhouse paralleled their ability to increase tuber yield in the field.

The mechanisms that account for the apparent periodic benefits from bacterization remain enigmatic. Both Brown (4) and Mishustin and Naumova (20) suggest the importance of microbially elaborated growth-regulating substances such as gibberellins, but also point out the importance of the antagonistic properties of bacteria in depressing the activities of the pathogenic organisms in the rhizosphere.

TABLE 3. (footnotes):

[a]A Latin square or randomized block design with four to six replications was used in each plot. All soils were sandy loam types except the Tulelake and Stockton locations which had peat soils.

[b]Isolates (TL-3, TL-10, TL-12, and BK-1) are nonpectolytic, fluorescent *Pseudomonas* spp. which were isolated from tubers grown at Tulelake and Bakersfield, California, respectively. Isolates S-1-B and A-13 are *Bacillus* spp. isolated from a tuber grown at Bakersfield, California and obtained from K. F. Baker, respectively. Isolate Ac-1 is an *Erwinia quercina* isolate obtained from M. N. Schroth.

[c]Plot rows ranged from 15.2 to 30.4 m in length.

[d]Asterisks * and ** denote statistical significance $P = 0.10$ and $P = 0.05$, respectively.

We speculate that the *Pseudomonas*-stimulated yield increase with potatoes is related to the suppression of populations of various parasitic and non-parasitic pathogens in the rhizosphere. The predominance of the introduced pseudomonads on roots and their ability to overcome the biological buffering capacity (8) in rhizosphere soils, should alter the composition of "normal" flora, at least during the early stages of plant growth. The mechanisms by which bacteria promote increased plant growth will be difficult to ascertain because of the many interactions that occur on root systems when inordinately high populations of bacteria are introduced, and the absence of sensitive methods to detect population changes.

The employment of beneficial bacteria to increase yields and reduce use of chemicals is an attractive development and the potential benefits may be considerable. The success of bacterization programs, however, will ultimately depend on such aspects as cost-benefit ratios, widespread applicability of specific strains, development of practical delivery systems, and consistently sustained positive results.

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