

## Effects of *Pseudomonas fluorescens* on Potato Plant Growth and Control of *Verticillium dahliae*

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### ABSTRACT

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*Pseudomonas fluorescens* strain M-4, an antagonist of *Verticillium dahliae* in vitro, was studied to determine its potential as an inhibitor of *V. dahliae* and growth promoter of potato plants. In pot experiments of soil fortified with *V. dahliae*, fresh weights of shoots and roots and plant height from potato seed pieces dusted with *P. fluorescens* were significantly greater for plants treated with *P. fluorescens*. In addition, the number of propagules of *V. dahliae* in stem tissue was significantly lower for treated potatoes. In pasteurized soil, potato growth was not enhanced by *P.*

*fluorescens*, even though the roots were colonized by the bacteria significantly more than in soil infested with *V. dahliae*. In 1982 and 1984 field trials, *P. fluorescens* applied to hand-planted seed pieces as a dust or liquid coating containing  $10^8$  cfu/ml resulted in root population densities of about  $10^4$  cfu/g of root, similar to populations on roots in greenhouse pot experiments. In the field, however, *P. fluorescens* had no effect on yield, percent U.S. No. 1 tubers, or incidence of *Verticillium* wilt.

*Additional key words:* biological control.

*Verticillium* wilt of potatoes is a major disease in most potato-growing regions in the western United States. In Washington state, yield, grade, and tuber quality have been reduced at least 20% by *Verticillium dahliae* Kleb. (2). The persistence of *V. dahliae* in soil for years makes this disease difficult to control (11). The use of long rotations with nonsusceptible crops to control wilt is uneconomical or ineffective (2). Soil fumigation provides control for 1 yr and is expensive (2). Alternative methods of disease control are needed.

In recent years, bacterization of potato seed pieces with fluorescent *Pseudomonas* species improved plant growth and tuber yield in several studies (1,4,5,8,14,15). These pseudomonads, referred to as "plant-growth-promoting rhizobacteria (PGPR)" (8), appear to displace or suppress deleterious microorganisms or inhibit pathogens that attack the roots.

In greenhouse tests, Burr et al (1) obtained up to 100% greater fresh weights of shoots and roots of 4-wk-old potato plants when they were grown from seed pieces treated with *Pseudomonas fluorescens* and *P. putida* originally isolated from tuber surfaces. When these isolates were applied to seed pieces in field tests in California and Idaho, yields were 14–33% greater for treated than for untreated seed pieces in five of nine field plots. Kloepper et al (8) reported that strains of fluorescent *Pseudomonas* species applied to potato seed pieces improved plant growth and increased yields up to 17% in field tests.

The PGPR used by Burr et al (1) and Kloepper et al (8) inhibited *Erwinia carotovora* pv. *carotovora* and other microorganisms in vitro. Howie and Echandi (5) found strains of *P. putida* and *P. fluorescens* initially selected for production of siderophores and inhibitory to *E. carotovora* that improved plant growth in greenhouse tests and increased yields in two of three field trials.

In Washington, Xu and Gross (14) tested fluorescent *Pseudomonas* strains that inhibited *E. carotovora* in vitro and reduced potato seed piece decay in the greenhouse. In field plots, strains were selected for their ability to colonize potato roots and increase yield (15).

Wadi and Easton (13) were the first to use bacterization in an effort to control *V. dahliae* on potato in Washington. They found more than 150 bacterial isolates from potato roots that were

antagonistic to *V. dahliae* in vitro. When applied to seed pieces as either a dust or liquid at planting, some strains of *Pseudomonas*, *Cellulomonas*, and *Streptomyces* species colonized potato roots and increased plant growth and tuber production in glasshouse tests.

The purpose of this study was to test the ability of *P. fluorescens* biovar III, strain M-4 (13), to suppress *Verticillium* wilt and improve growth of potato in both glasshouse and field tests. The influence of method and rate of application of *P. fluorescens* and inoculum density of *V. dahliae* on plant growth and incidence of disease was also studied.

### MATERIALS AND METHODS

**Glasshouse studies.** For greenhouse experiments, Quincy loamy sand, 85% sand, 2% clay, and less than 0.5% organic matter at 6.2 pH was collected from a commercial field near Paterson, WA. The field, under center-pivot irrigation, had been cropped previously to potatoes. Barrels of soil were stored at 4 C.

*P. fluorescens* biovar III, strain M-4, a mutant resistant to 100 µg/ml rifampicin and streptomycin sulfate, was used for these trials. This isolate was originally isolated from potato rhizosphere soil and identified by Wadi and Easton (13). It was transferred from a lyophilized culture onto King's medium B (KB) and allowed to grow for 48 hr at 23 C (13). Resultant single colonies were retested for inhibition of *V. dahliae* in vitro (13), and an antagonistic colony of M-4 was selected as primary inoculum. Inoculum to treat seed pieces was prepared by adding 5 ml of sterile distilled water to a 48-hr plate culture, and the suspension was transferred to a Chromist Spray Unit (Gelman Sciences, Inc., Ann Arbor, MI). Fifty milliliters of sterile distilled water was added, and the suspension of bacterial cells was sprayed onto 160 plates of KB and incubated for 48 hr.

Preliminary trials showed that cells of M-4 scraped from the surface of one plate and diluted in 40 ml of 3% methylcellulose provided a liquid inoculum containing  $10^4$  cfu/ml and that cells from 159 plates diluted in 40 ml of 3% methylcellulose provided  $10^8$  cfu/ml. Dry formulations containing 0,  $10^4$ , and  $10^8$  cfu/g were prepared from talc (C-400, 325-mesh, Van Waters and Rogers, Seattle, WA) mixed with 20% gum xanthan (Sigma Chemical Co., St. Louis, MO) as described by Kloepper and Schroth (6). After drying, the inoculum was ground in a Waring Blendor and

screened through a 0.25-mm screen. Populations of bacteria in the inoculum were determined by plating serial dilutions on plates of KB containing rifampicin and streptomycin sulfate each at 100 µg/ml. *P. fluorescens* at rates of 0, 10<sup>4</sup>, and 10<sup>8</sup> cfu/g were dusted on potato seed pieces and planted in greenhouse trials. The inoculum was stored at 4 C between trials.

**Preparation of soil in pots for planting.** Population densities of *V. dahliae* occurring in natural, nondried field soil collected near Paterson, WA, for greenhouse pot experiments were determined on ethanol-streptomycin medium (3). Percent soil moisture was obtained for each individual determination and used with plate counts in estimating the *V. dahliae* propagules per gram (p/g) of oven-dried soil. Individual 15-cm-diameter clay pots of unpasteurized soil were fortified with *V. dahliae* to produce either 10<sup>2</sup> or 10<sup>3</sup> p/g of oven-dried soil (13). To test bacterial treatments in the absence of *V. dahliae* or other soilborne pathogens, a portion of soil was steam-pasteurized 8 hr at 77 C. All test soils were fertilized with N:P:K:Zn at 283:94:471:9 kg/ha. Pots were placed on overturned pot saucers to prevent contamination from the bench. Soil samples were collected from each pot to assay for initial populations of *V. dahliae*.

**Treatment of tubers and planting.** Certified seed tubers of *Solanum tuberosum* 'Russet Burbank' were removed from storage (4 C) 6 days before planting and held at 24 C. Seed pieces with individual eyes were removed with a sterile 3-cm-diameter melon ball scoop. For each treatment, 24 seed pieces were shaken with 6 g of dust inoculum in a polyethylene bag, equivalent to 15 g of dust per kilogram of potato. Three seed pieces were planted per pot. New disposable polyethylene gloves were used for each treatment to prevent cross-contamination. Each treatment of eight pots was placed in a completely random arrangement. Glasshouse day/night temperatures were maintained near 26/21 C.

**Assessment of plant growth and monitoring populations of *P. fluorescens* and *V. dahliae*.** Plant heights were measured from the soil line 6 wk after planting. Plants were harvested and fresh weight determined 8 wk after planting. To determine populations of M-4 on root surfaces, roots were shaken to remove all but tightly adhering soil. Lateral roots (0.5 g) from each of three plants were agitated in 49.5 ml of sterile distilled water for 15 min. Serial dilutions were plated in triplicate on KB agar containing 100 µg/ml each of rifampicin and streptomycin sulfate, and cycloheximide and nystatin each at 100 and 20 µg/ml. Plates were incubated 48 hr at 23 C. Single colonies of M-4 isolated from each treatment were retested in vitro for inhibition as previously described.

Population densities of *V. dahliae* in the rhizosphere were obtained from 0.5-g soil samples diluted as before. A 0.3-ml aliquot of each dilution was spread on each of three plates of ethanol-streptomycin medium. Plates were incubated at 23 C, and propagules of *V. dahliae* were counted after 15 days.

Potato stems were dried in a forced-air dryer for 3 days at 31 C and then ground by a Wiley mill and passed through a 0.25-mm screen. Compressed air was used to clean the machine between samples. Propagule numbers of *V. dahliae* in dried stems were estimated from serial dilutions in sterile distilled water plated on ethanol-streptomycin medium.

Population densities of *P. fluorescens* and *V. dahliae* were transformed to log<sub>10</sub>(x + 1) before analysis.

The effects of the three rates of *P. fluorescens* on plant growth or population densities of *V. dahliae* were evaluated using orthogonal polynomials for treatments with equal intervals. A factorial, completely randomized design was used. The treatment mean squares for the three rates of *P. fluorescens* were partitioned into two single-degree-of-freedom orthogonal contrasts, one associated with the linear response and one for the quadratic response. Only the linear effect was found significant, and the *F* values for this response are reported.

**Field location and preparation.** Tests were conducted in 1982 and 1984 under sprinkler irrigation on a Warden silt loam soil near Prosser, WA. The field had been alternately cropped to wheat and potatoes. In April, the field was chisel-plowed 45 cm deep, two ways on the diagonal. Ammonium sulfate was applied at 336 kg of nitrogen per hectare, broadcast before plowing 30 cm deep.

**Treatment of potatoes with *P. fluorescens* and planting.** In both 1982 and 1984 tests, treatments were applied in plots 3.7 m wide (four rows) by 6.1 m long in a randomized complete block design with six replicates. Seed pieces of Russet Burbank were coated with liquid inoculum containing 0 or 10<sup>8</sup> cfu of *P. fluorescens* per milliliter at 50 ml/kg of seed pieces in polyethylene bags. Treated seed pieces were planted by hand. New gloves and bags were used for each treatment to avoid cross-contamination.

**Monitoring populations of *P. fluorescens* and *V. dahliae*.** In 1982, potato root and soil samples were collected in June and September, and in 1984, samples were collected in June, July, and September. Three samples were taken from the third row of each replicate. A pitchfork was used to loosen soil around each plant to minimize root damage. Samples were placed in polyethylene bags and transported to the laboratory. Populations of *V. dahliae* and *P. fluorescens* were determined as previously described. Populations of *V. dahliae* in the rhizosphere were estimated in 0.5-g samples of soil removed by shaking roots and then dilution plating. Populations of M-4 were estimated on two lateral roots (0.5 g of root) from each plant. Single colonies of M-4 isolated from each treatment were tested to verify in vitro antagonism.

**Disease measurement and potato harvest.** Incidence of Verticillium wilt was recorded as percentage of plants in one of the interior rows showing wilt symptoms in September. Potatoes were harvested in October from the second row in each plot. Total weight and percentage of U.S. No. 1 tubers were recorded.

## RESULTS

**Glasshouse studies.** Glasshouse studies were repeated twice with similar results. The data from one trial are shown. Treating seed pieces with *P. fluorescens* had no significant effect on shoot or root weight or plant height in pasteurized soil or when *V. dahliae* was initially added at 10<sup>2</sup> p/g soil (Table 1). However, in soil with *V. dahliae* at 10<sup>3</sup> p/g, there was a significant linear relationship between shoot or root weight or plant height and rate of *P. fluorescens* applied to seed pieces.

**Populations of *P. fluorescens* on roots at harvest.** Populations of *P. fluorescens* were significantly higher when applied at 10<sup>8</sup> than at 10<sup>4</sup> cfu/g dust to seed pieces (Table 2). A significant linear relationship was found between initial rate of application and final populations on roots at each inoculum density of *V. dahliae*. Populations of *P. fluorescens* in roots were 10-fold greater in pasteurized soil (0 *V. dahliae* per gram) than in soil with *V. dahliae* at the initial application rates of 10<sup>4</sup> and 10<sup>8</sup>.

Populations of *V. dahliae* in the rhizospheres of seed pieces treated with either rate of *P. fluorescens* did not differ significantly

TABLE 1. Effects on plant growth in steamed soil when *Pseudomonas fluorescens* was applied to potato seed pieces at population densities of 0, 10<sup>2</sup>, or 10<sup>3</sup> propagules of *Verticillium dahliae* per gram of oven-dried soil in glasshouse tests

<i>V. dahliae</i> (p/g)	<i>P. fluorescens</i> (cfu/g dust)	Shoot weight (g)	Root weight (g)	Plant height (cm)
0	0	32.92	9.11	34.4
	10 <sup>4</sup>	29.62	13.73	38.5
	10 <sup>8</sup>	37.49	10.81	35.5
<i>F</i> <sup>a</sup>		0.19 NS	0.17 NS	0.04 NS
10 <sup>2</sup>	0	29.03	8.80	26.1
	10 <sup>4</sup>	25.18	6.57	22.4
	10 <sup>8</sup>	31.96	8.91	29.1
<i>F</i> <sup>a</sup>		0.08 NS	0 NS	0.29 NS
10 <sup>3</sup>	0	23.45	8.73	17.5
	10 <sup>4</sup>	37.53	20.29	36.5
	10 <sup>8</sup>	55.72	27.13	38.2
<i>F</i> <sup>a</sup>		9.6**	8.25*	13.0**

<sup>a</sup>Treatment linear mean squares for the appropriate orthogonal comparison were divided by the error mean square to provide an *F* statistic. NS = nonsignificant; \* and \*\* refer to statistical significance levels at *P* = 0.05 and *P* = 0.01, respectively.

from the untreated control at either level of *V. dahliae* (Table 3). *P. fluorescens* had no effect on the number of propagules of *V. dahliae* in dried stems of plants grown in soil with  $10^2$  p/g. However, *V. dahliae* in stems was significantly less for plants treated with either rate of *P. fluorescens* in soil with *V. dahliae* at  $10^3$  p/g.

**Field studies.** In 1982, treating seed pieces with a liquid suspension of *P. fluorescens* resulted in  $10^3$  cfu/g of root in June and September (Table 4). In 1984, populations of *P. fluorescens* were  $1 \times 10^4$  cfu/g in June and increased significantly to  $4 \times 10^4$  cfu/g in July. In September, however, only  $7 \times 10^2$  cfu/g of root were detected.

TABLE 2. Population densities of *Pseudomonas fluorescens* on potato roots at harvest as influenced by initial rate of application to potato seed pieces in soil infested with 0,  $10^2$ , or  $10^3$  propagules of *Verticillium dahliae* per gram of oven-dried soil in glasshouse tests

Initial <i>P. fluorescens</i> (cfu/g dust)	<i>P. fluorescens</i> on roots <sup>a</sup> ( <i>V. dahliae</i> in soil [p/g])		
	0 <sup>b</sup>	$10^2$	$10^3$
0	0	0	0
$10^4$	4.98	3.29	3.92
$10^8$	5.13	4.41	4.74
<i>F</i> <sup>c</sup>	97.2**	112.2**	132.4**

<sup>a</sup>  $\log_{10}(x + 1)/g$ .

<sup>b</sup> Steam-pasteurized soil.

<sup>c</sup> Treatment linear mean squares for the appropriate orthogonal comparison were divided by the error mean square to provide an *F* statistic; \*\* = statistical significance at *P* = 0.01.

TABLE 3. Effects of *Pseudomonas fluorescens* applied to seed pieces on populations of *Verticillium dahliae* in potato stems and rhizospheres in soil with 0,  $10^2$ , or  $10^3$  propagules of *V. dahliae* per gram of soil in glasshouse tests

<i>V. dahliae</i> (p/g)	<i>P. fluorescens</i> (cfu/g dust)	<i>V. dahliae</i> <sup>a</sup>	
		Stems	Rhizospheres
$10^2$	0	2.3	2.5
	$10^4$	2.5	2.4
	$10^8$	3.1	2.4
<i>F</i> <sup>b</sup>		1.5 NS	0 NS
$10^3$	0	3.6	3.3
	$10^4$	1.6	3.0
	$10^8$	1.6	3.6
<i>F</i> <sup>b</sup>		8.0*	1.3 NS

<sup>a</sup>  $\log_{10}(x + 1)/g$ .

<sup>b</sup> Treatment linear mean squares for the appropriate orthogonal comparison were divided by the error mean square to provide an *F* statistic, NS = nonsignificant, \* = statistical significance at *P* = 0.05.

TABLE 4. Population densities of *Pseudomonas fluorescens* on roots of potatoes and influence of *P. fluorescens* on population densities of *Verticillium dahliae* in potato rhizospheres, Verticillium wilt incidence, potato yields, and tuber quality in 1982 and 1984 field tests

Treatments	<i>P. fluorescens</i> on roots <sup>1</sup>			Population densities of <i>V. dahliae</i> <sup>1</sup>			Wilted plants <sup>2</sup>	Yield (q/ha) <sup>3</sup>	U.S. No. 1 tubers <sup>4</sup>
	Jun.	Jul.	Sept.	Jun.	Jul.	Sept.			
1982									
<i>P. fluorescens</i> <sup>x</sup>	4.2 a <sup>y</sup>	— <sup>z</sup>	4.0 a	2.7 b	—	2.4 b	64 a	810 a	64 a
Untreated check	0.0	—	0.0	3.5 a	—	3.4 a	62 a	787 a	63 a
1984									
<i>P. fluorescens</i> <sup>x</sup>	4.0 b	4.6 a	2.8 c	0.8 a	2.1 a	1.5 a	35 a	1,030 a	54 a
Untreated check	0.0	0.0	0.5 d	1.2 a	2.8 a	2.0 a	52 a	965 a	43 a

<sup>1</sup>  $\log_{10}(\text{cfu} + 1)/g$  root.

<sup>2</sup> Percentage of plants in 6.1-m row showing wilt symptoms in September.

<sup>3</sup> Calculated from the weight of tubers from a 6.1-m row.

<sup>4</sup> Percentage by weight of U.S. No. 1 tubers.

<sup>x</sup> Applied to potato seed pieces as liquid suspension in 3% methylcellulose at  $10^8$  cfu/ml.

<sup>y</sup> Different letters within each year denote significant differences according to Duncan's multiple range test (*P* = 0.05). The root populations (repeated measures over time) were analyzed as a split block.

<sup>z</sup> Not sampled.

**Effects of *P. fluorescens* on populations of *V. dahliae*.** In 1982, population densities of *V. dahliae* in the rhizospheres of potatoes treated with *P. fluorescens* were significantly lower than in the untreated check in both June and September (Table 4). In 1984, there were no significant differences in population densities of *V. dahliae* at any of the sampling dates.

**Effects of *P. fluorescens* on incidence of Verticillium wilt and potato production.** Treating seed pieces with *P. fluorescens* had no significant effect on the incidence of Verticillium wilt, potato yield, or the percentage of U.S. No. 1 tubers in either the 1982 or 1984 field trials (Table 4).

## DISCUSSION

*P. fluorescens* strain M-4 does not appear to promote plant growth in pasteurized soil, even though the bacterium colonized roots to significantly greater population densities than in soil infested with *V. dahliae*. This agrees with other reports comparing growth responses in sterile or pathogen-free natural soil (7,12).

Plant growth responses observed in this study appear to be related to both the inoculum density of *V. dahliae* in the soil and the initial rate of application of *P. fluorescens* to potato seed pieces. In glasshouse tests or 1984 field plots with an average of only 200 propagules of *V. dahliae* per gram, treatments of *P. fluorescens* had no effect on plant growth, tuber yield, or quality. Verticillium wilt was not severe in these tests. However, in glasshouse tests where soil had more than 1,000 propagules of *V. dahliae* per gram, shoot and root weights and plant heights were significantly greater for plants treated with *P. fluorescens*. Untreated plants were chlorotic and wilted after 5 wk but Verticillium wilt was less severe for plants treated with *P. fluorescens*.

Variability in colonization of roots by *P. fluorescens* (8,12) would not explain the variation in plant response in this work. Both dust and liquid treatments of *P. fluorescens* to seed pieces in glasshouse and field tests resulted in populations of  $10^3$  to  $10^5$  cfu/g of root, depending on the initial rate of application of *P. fluorescens*. Applying *P. fluorescens* to seed pieces at  $10^8$  compared with  $10^4$  cfu/g resulted in only a 10-fold (one log) increase in root colonization, thus there appeared to be a maximum colonization of  $10^5$  cfu/g of root for this strain. These populations are similar to populations of pseudomonads antagonistic to *E. carotovora* isolated by Xu and Gross (15) on roots of potatoes grown in the Columbia Basin in Washington.

*P. fluorescens* appears to prevent or delay penetration by *V. dahliae* because the number of propagules of *V. dahliae* in dried, ground stems of treated plants grown in soil with  $10^3$  p/g was significantly lower than in untreated plants. Roots of untreated plants were discolored and deteriorated, consistent with other reports of the adverse effect of *V. dahliae* on root health (9,10). In contrast, roots of plants treated with *P. fluorescens* appeared

healthy with fresh weights comparable to roots of plants grown in pasteurized soil.

*P. fluorescens* appears to protect roots from extensive colonization by *V. dahliae* in soil heavily infested with the pathogen. However, infection was not prevented and plants treated with *P. fluorescens* eventually developed wilt symptoms. In 1982 field trials, the number of propagules of *V. dahliae* averaged  $10^3$  p/g soil and Verticillium wilt was more severe than the 1984 trial, yet treatments with *P. fluorescens* had no effect on incidence of wilt or tuber yield or quality. Optimum cultural practices such as crop rotation, fertilization, and irrigation suppress Verticillium wilt in Russet Burbank potatoes most years. Results of this study suggest that bacterization will have no effects on plant growth or yields in the field regardless of cultural practices.

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