Influence of *Fusarium solani* on Citrus Root Growth and Population Dynamics of *Phytophthora parasitica* and *Phytophthora citrophthora*

L. M. Dandurand and J. A. Menge

Department of Plant Pathology, University of California, Riverside 92521.
Present address of first author: Plant Pathology Division, University of Idaho, Moscow 83843.
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ABSTRACT

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To determine the influence of *Fusarium solani* on citrus root growth and subsequent development of rhizosphere populations of *Phytophthora parasitica* or *Phytophthora citrophthora,* Troyer citrange was grown for 30 days in soil infested with *F. solani* prior to infestation with *P. parasitica* or *P. citrophthora.* Root weights, root lengths, development of root tips, percentage of roots colonized by *Fusarium,* and rhizosphere densities of *P. parasitica* or *P. citrophthora* were measured over time. Rhizosphere densities of *P. parasitica* were greater at the end of the experiment than at the beginning. Infestation of soil with *F. solani* suppressed *P. parasitica* densities in the rhizosphere of citrus by 53% but did not alter rhizosphere density fluctuations. Root lengths of plants grown in soil infested with *F. solani* were 25% less than those of plants grown in noninfested soil. The average percentage (over 28 days) of root tips that were new was lower in soil drenched with suspensions of *P. parasitica* zoospores than in nondrenched soil. However, root tip development of plants grown in soil infested with *F. solani* was no different from that of plants grown in noninfested soil. Rhizosphere density of *P. citrophthora* was not different whether soil was infested with *F. solani* or not. Rhizosphere densities of *P. citrophthora* fluctuated over 24 days but were not affected by soil infestation with *F. solani.* When citrus was inoculated with *P. citrophthora,* soil infestation with *F. solani* did not affect root length but resulted in 43% fewer new root tips.

Additional keywords: root ecology, root health, root rot

Phytophthora parasitica Dastur and *Phytophthora citrophthora* (R. E. Sm. & E. H. Sm.) Leonian are the major causes of feeder root rot of citrus in California (6,12). Infection of feeder roots by these pathogens causes a slow decline of citrus trees, which leads to decreased fruit yields (6). Rhizosphere population densities of *Phytophthora* are related to inoculum efficiency and infection levels, and significant yield losses of citrus usually occur when high populations of *Phytophthora* are present (9,11,30). Therefore, recommendations for control are based on information about the rhizosphere population densities of *P. parasitica* or *P. citrophthora* (17).

Populations of *P. parasitica* are highly sensitive to environmental factors such as soil temperature and soil moisture (8,13). Host factors, such as the quantity and composition of root exudates and time of root growth flushes, may be important determinants affecting initiation of disease cycles and population fluctuations of the pathogen. Feeder root growth of citrus begins in May when the soil starts to warm and ceases in November (14). *P. parasitica* becomes active when the soil temperature rises, and populations increase concurrently with root growth throughout the summer (7,8,13,14). Populations of *P. parasitica* are likely to be greatest where feeder roots are most dense (7,8). In contrast, *P. citrophthora* is active in the winter, when temperatures are cool (18) and citrus is not actively growing. Increases in population densities of *P. citrophthora*, therefore, probably are not concurrent with root growth but may occur in soil where feeder roots are most dense.

Microbial community effects on populations of *P. parasitica* or *P. citrophthora* have not been well studied. *Fusarium solani* (Mart.) Sacc. is the predominant fungus isolated from both the roots and the rhizosphere of citrus (2,15,23,28) and can reduce root growth (1,4,22). Reduction of root growth by a root colonizer such as *F. solani,* however, might lead to reductions in populations of *P. parasitica* or *P. citrophthora*, either directly or by affecting the growth of the host.

The first objective of this study was to examine the effects of *F. solani* on population densities of *P. parasitica* and *P. citrophthora* in the rhizosphere of citrus. Second, the development of feeder root rot in citrus co-inoculated with *F. solani* and *P. parasitica* or *P. citrophthora,* or inoculated with either *P. parasitica* or *P. citrophthora* alone, was evaluated over time.

MATERIALS AND METHODS

Fungal isolates and inoculum preparation. Isolates of *F. solani* were obtained from feeder roots of citrus from groves in Highland and Visalia, California. Root segments (1 mm) were surface-sterilized for 5 min in 0.5% sodium hypochlorite, rinsed several times in sterile distilled water, and plated onto a *Fusarium*-specific medium (20). Monoconidial isolates were transferred to carnation leaf water agar and identified according to Nelson et al (21). Isolates of *F. solani* were stored in autoclaved sand with cornmeal (1%, v/v) at 9 C. Inoculum for experiments was prepared by placing particles from storage onto citrus twig agar (1) and incubating the plates under continuous fluorescent light at room temperature for 4–6 wk. Macroconidia from three isolates (H39, H41, and S5) were scraped from the surface of the twigs, suspended in sterile water, and adjusted to the desired concentration.

Isolates of *P. parasitica* and *P. citrophthora* were obtained by plating soil dilutions from citrus rhizosphere soil from Highland, California (13). Single-spore subcultures were identified by colony morphology. Zoospores of *P. parasitica* (isolates Z1 and Z5) and *P. citrophthora* (isolates M2, M77, and M183) were produced according to the methods of Menyonga and Tsao (19).

Plant material and soil. Seeds of Troyer citrange (*Poncirus trifoliata* (L.) Raf. × *Citrus sinensis* (L.) Osbeck) were planted in containers (Ray Leach Container, Canby, OR) filled with University of California potting mix II (16), which had been autoclaved twice for 2 h on consecutive days. The mix was amended with slow-release fertilizer (Osmocote 14-14-14; Sierra Chemical Co., Milpitas, CA) at a rate of 0.25 g per pot. To minimize contamination by *F. solani*, the seedlings were grown

in a walk-in growth chamber with a 16-h light period at 25–28 C and watered with sterile water as needed. Before the seeds were planted, the growth chamber was fumigated with methyl bromide.

The soil used for all experiments was a Greenfield sandy loam from a grove in Highland, California. It contained 9.4% clay, 21.1% silt, and 69.7% sand and had an electrical conductivity of 0.68 mmho/cm. Before the seedlings were transplanted, the soil was sieved through a 1-cm mesh and autoclaved at 120 C three times for 2 h on consecutive days. The soil was infested with *F. solani* at a rate of 4×10^4 macroconidia per gram of soil 24 h after being last autoclaved. Macroconidia were suspended in sterile water and sprayed onto the autoclaved soil, which was then mixed in a cement mixer for 10 min. For noninfested treatments, soil was sprayed with comparable amounts of sterile water and mixed. Soil was used immediately after infestation with *F. solani*.

Effect of precolonization of citrus by *F. solani* on root growth and rhizosphere population densities of *P. parasitica*. Six-month-old Troyer citrange seedlings were transplanted into either soil infested with *F. solani* or noninfested soil and grown under greenhouse conditions for 30 days prior to inoculation with zoospores of *P. parasitica*. Treatments were arranged in a split-plot design with infestation with *F. solani* as the main effect and sampling time as the subeffect. Water-saturated soil was infested with a suspension (10 ml per pot) containing the equivalent of 20 zoospores per gram of soil. To ensure that zoospores did not remain on the surface of the pots, pores were made in the soil with a hair pick (six teeth, 4 cm long) before the soil was drenched. In pots with noninfested soil, the soil the around the plants was drenched with an equal volume of sterile water. All pots were watered immediately after drenching the soil and thereafter were watered every other day to a matric potential of approximately 30 J/kg. Plants were harvested destructively every four days over a 28-day period. For each harvest, there were 10 replicates per treatment. The experiment was conducted in July (mean temperature 25 C) and was repeated once.

At each harvest, plant tops were excised, oven dried, and weighed. Feeder roots were separated from taproots and weighed. Root lengths of feeder roots were determined by the line intercept method (2-cm grid) (25). New and old root tips were counted while the root lengths were being determined. Root tips that appeared white were counted as new, whereas any tips that appeared brown or rotted were counted as old. The number of new root tips as a percentage of all root tips was determined. To quantify rhizosphere populations of *P. parasitica*, the soil adhering to the root system was gently shaken into plastic bags (13). Population densities of *P. parasitica* were determined by soil-dilution plates (13). Soil samples (10 g, oven-dried basis) were placed in 250-ml flasks, and water was added to 100 ml. One milliliter of the soil suspension was pipetted into each of five petri dishes, and molten (45 C) PARPH medium (10) was added. After 7 days of incubation in the dark at room temperature, *P. parasitica* colonies were counted.

Colonization of feeder roots by *F. solani* was determined by surface-disinfesting 15 root segments (1 mm) per replicate in 0.1% sodium hypochlorite for 5 min followed by rinsing several times in sterile distilled water and plating the root segments onto selective medium (20). Plates were incubated in the dark at room temperature for 4 days before the number of root segments colonized by *F. solani* were counted.

Effect of precolonization of citrus by *F. solani* on root growth and rhizosphere population densities of *P. citrophthora*. An experiment similar to that described above was conducted to study the effect of precolonization of citrus roots by *F. solani* on population densities of *P. citrophthora*. Eight-month-old Troyer citrange seedlings were transplanted into noninfested soil or into soil infested with *F. solani*. To simulate winter conditions, the experiment was conducted in November (mean temperature 21 C), and plants were kept in a lathhouse after they were transplanted into soil. After 30 days of growth, the soil was drenched with zoospores of *P. citrophthora* as described above. At each harvest, the plants were sampled destructively as described above. There were 10 replicates for each treatment for each sampling time, and the experiment was repeated once.

Data from each experiment were analyzed by analysis of variance with the general linear models procedure of the Statistical Analysis System (27). To stabilize the variance, *Phytophthora* populations were transformed using $\log_{10}(x + 1)$. The arcsine transformation was performed on data expressed as proportions (27).

RESULTS

Effect of precolonization of citrus by *F. solani* on root growth and rhizosphere population densities of *P. parasitica*. Colonization of citrus roots by *F. solani* was greater in soil infested with *F. solani* than in noninfested soil (Table 1). Although colonization of roots by *Fusarium* was observed in some controls in noninfested soil, the treatment effect of adding *F. solani* to the soil was significant for some of the parameters measured (Tables 1 and 2). The rhizosphere density of *P. parasitica* was 43% lower in soil infested with *F. solani* than in noninfested

TABLE 1. Effects of planting Troyer citrange in noninfested soil or soil infested with *Fusarium solani* prior to inoculation with *Phytophthora parasitica*

Soil	Propagules of *P. parasitica*[x] (cfu/g soil)	Root colonization by *F. solani*[y] (% of root segments)	Root weight (g)	Root length (cm)	New root tips[y] (% of tips)
Noninfested	426.8 a[z]	30.8 a	3.5 a	242.2 a	22.4
F. solani-infested	244.9 b	59.1 b	2.6 b	172.8 b	22.7

[x] Data were transformed to $\log_{10}(x + 1)$ for statistical analysis.
[y] Data were transformed to arcsines for statistical analysis.
[z] Values for means in each column followed by different letters are significantly different according to an F test from an analysis of variance ($P \leq 0.05$).

TABLE 2. F values from analyses of variance to determine the effects of planting Troyer citrange in soil infested with *Fusarium solani* prior to inoculation with *Phytophthora parasitica*

Source	df	Root weight (g)	Root length (cm)	New root tips[x] (% of tips)	Propagules of *P. parasitica*[y] (cfu/g soil)	Root colonization by *F. solani*[x] (% of root segments)
F. solani	1	25.0 *[z]	25.2 *	0.0	36.0 *	41.0 *
Time	6	1.7	2.4 *	53.3 *	33.6 *	15.7 *
F. solani × time	6	0.7	0.5	2.2 *	0.7	1.9

[x] Data were transformed to arcsines for statistical analysis.
[y] Data were transformed to $\log_{10}(x + 1)$ for statistical analysis.
[z] F values followed by an asterisk are significantly greater than zero ($P \leq 0.05$).

soil (Table 1). Populations of *P. parasitica* were greater at the end of the experiment than at the beginning ($F = 109.5$; $P = 0.0001$) (Fig. 1). Soil infestation with *F. solani* did not affect the fluctuation in densities of *P. parasitica* in the rhizosphere of citrus (i.e., the *F. solani* × time interaction was not significant; Table 2).

Both feeder root weight and root length of plants inoculated with *P. parasitica* were significantly less in soil infested with *F. solani* (26 and 29%, respectively; Table 1) than in noninfested soil. The percentage of root tips decreased regardless of whether plants were planted in noninfested or infested soil (Fig. 2).

The rhizosphere density of *P. parasitica* was positively correlated with root weight, root length, and the percentage of root tips that were old; it was negatively correlated with the percentage of root tips that were new (Table 3). However, the rhizosphere density of *P. parasitica* was not correlated with the percentage of roots colonized by *F. solani* (Table 3). The percentage of roots colonized by *F. solani* was negatively correlated with the percentage of root tips that were new and positively correlated with the percentage of root tips that were old. However, there was no significant correlation between colonization with *F. solani* and root weight or root length.

When the experiment was repeated, rhizosphere densities of *P. parasitica* from citrus planted in soil infested with *F. solani* were significantly lower than from citrus planted in noninfested soil (72%). Root weight and length and the percentage of root tips that were new were less (54, 57, and 62%, respectively) in soil infested with *F. solani* than in noninfested soil.

Effect of precolonization of citrus by *F. solani* on root growth and rhizosphere population densities of *P. citrophthora*. Although soil infestation with *F. solani* lowered rhizosphere densities of *P. parasitica*, it did not lower rhizosphere densities of *P. citrophthora* (Tables 4 and 5). However, rhizosphere densities of *P. citrophthora* increased and then decreased during the experiment (Fig. 3). As in the case of *P. parasitica,* infestation of soil with *F. solani* did not affect the fluctuation of rhizosphere densities of *P. citrophthora* (i.e., the *F. solani* × time interaction was not significant; Table 5)

The percentage of root tips that were new was 42% less in soil infested with *F. solani* than in noninfested soil, but generation of root tips did not change over time (i.e., the *Fusarium* × time interaction was not significant; Table 5). Feeder root length and weight of plants grown in infested soil were not significantly different from those of plants grown in noninfested soil (Table 4). The same results were observed when the experiment was repeated.

The rhizosphere density of *P. citrophthora* was positively cor-

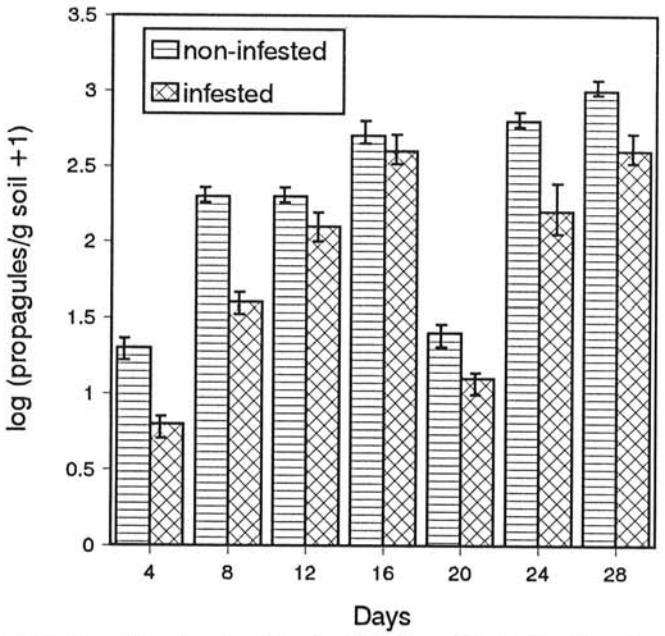

Fig. 1. Population density of *Phytophthora parasitica* in the rhizosphere of Troyer citrange in soil infested with *Fusarium solani* and in noninfested soil. The soil was drenched with *P. citrophthora* zoospores 30 days after seedlings were transplanted, and rhizosphere populations of *P. citrophthora* were sampled every 4 days for 28 days after inoculation. Means plus or minus standard errors are indicated.

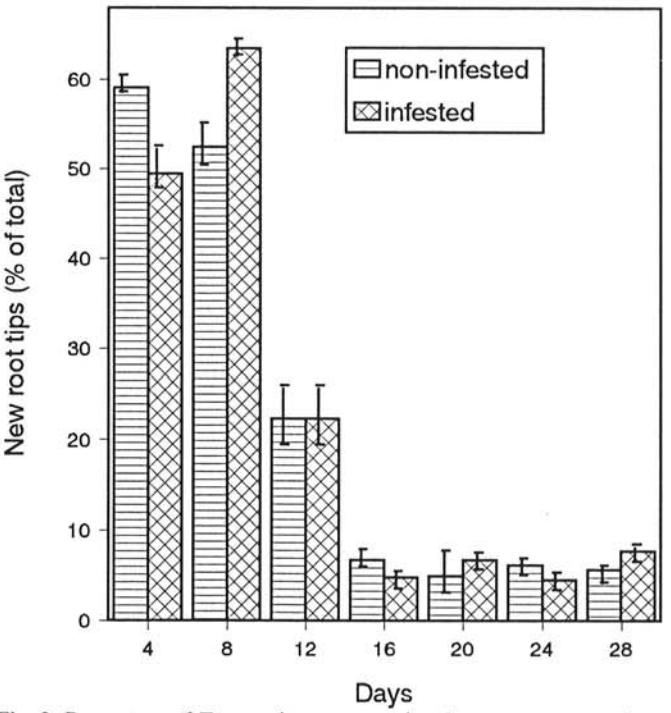

Fig. 2. Percentage of Troyer citrange root tips that were new on plants grown in noninfested soil or in soil infested with *Fusarium solani* and inoculated with *Phytophthora parasitica*. The soil was drenched with *P. parasitica* zoospores 30 days after seedlings were transplanted, and plant roots were sampled every 4 days for 28 days after inoculation. Means plus or minus standard errors are indicated.

TABLE 3. Correlation coefficients[x] for feeder root weight, feeder root length, percentages of root tips that were new or old, propagules of *Phytophthora parasitica* and *P. citrophthora*, and percentage of roots colonized by *Fusarium solani*

	Propagules of *P. parasitica*[y] (cfu/g soil)	Root colonization by *F. solani*[z] (% of root segments)	Propagules of *P. citrophthora*[y] (cfu/g soil)	Root colonization by *F. solani*[z] (% of root segments)
Root weight	0.27 *	−0.09	0.15	−0.20 *
Root length	0.29 *	−0.11	0.20 *	−0.25 *
New tips (%)[y]	−0.42 *	−0.27 *	0.08	−0.50 *
Old tips (%)[y]	0.42 *	0.28 *	−0.09	0.53 *
Propagules of *P. parasitica* or *P. citrophthora* (cfu/g soil)[c]		0.04		0.04

[x] Correlation coefficients were calculated from values of 10 replicates sampled every 4 days for 28 days for *P. parasitica* ($n = 140$) and every 4 days for 24 days for *P. citrophthora* ($n = 120$). Values followed by an asterisk are significantly greater than zero ($P \leq 0.05$).
[y] Data were transformed to $\log_{10}(x + 1)$ for statistical analysis.
[z] Data were transformed to arcsine for statistical analysis.

TABLE 4. Effects of planting Troyer citrange in noninfested soil or soil infested with *Fusarium solani* prior to inoculation with *Phytophthora citrophthora*

Soil	Propagules of *P. citrophthora*[x] (cfu/g soil)	Root colonization by *F. solani*[y] (% of root segments)	Root weight (g)	Root length (cm)	New root tips[x] (% of tips)
Noninfested	15.5	8.4 a[z]	3.1	387.5	47.2 a
F. solani-infested	31.8	71.2 b	2.8	347.0	27.6 b

[x] Data were transformed to $\log_{10}(x + 1)$ for statistical analysis; pretransformed arithmetic means are shown.
[y] Data were transformed to arcsines for statistical analysis; pretransformed arithmetic means are shown.
[z] Values for means in each column followed by different letters are significantly different according to an F test from an analysis of variance ($P \leq 0.05$).

TABLE 5. F values from analyses of variance to determine the effects of planting Troyer citrange in noninfested soil or soil infested with *Fusarium solani* prior to inoculation with *Phytophthora citrophthora*

Source	df	Root weight (g)	Root length (cm)	New root tips[x] (% of tips)	Propagules of *P. citrophthora*[y] (cfu/g soil)	Root colonization by *F. solani*[x] (% of root segments)
F. solani	1	1.8	3.2	131.8 *[z]	2.3	165.7 *
Time	5	3.5 *	1.1	1.7	3.6 *	2.6 *
F. solani × time	5	0.6	1.3	0.7	0.3	0.4

[x] Data were transformed to arcsines for statistical analysis.
[y] Data were transformed to $\log_{10}(x + 1)$ for statistical analysis.
[z] F values followed by an asterisk are significantly greater than zero ($P \leq 0.05$).

related with root length but was not correlated with root weight, the percentage of root tips that were old, or the percentage of root tips that were new (Table 3). It was also not correlated with the percentage of roots colonized by *F. solani* (Table 3). Colonization of roots by *F. solani* was negatively correlated with root weight, root length, and the percentage of root tips that were new, and positively correlated with the percentage of root tips that were old.

DISCUSSION

In the field, high populations of *P. parasitica* are associated with areas with dense masses of feeder roots (8). *F. solani* is weakly pathogenic to feeder roots (1,4,22–24,26,29). Thus, a reduction in feeder root mass when feeder roots are colonized by *F. solani* might be expected to lead to decreased populations of *P. parasitica.* In these experiments, root weights and lengths were less when plants were planted in soil infested with *F. solani* than when they were planted in noninfested soil, and populations of *P. parasitica* were suppressed. Despite the lower density (43%), infestation of soil with *F. solani* did not significantly influence fluctuation of *P. parasitica* populations in the rhizosphere. The rhizosphere density of *P. parasitica* was greater at the end of the experiment than at the beginning in either *Fusarium*-infested or noninfested soil. Thus, several generations were produced, but regeneration was suppressed when soil was infested with *F. solani.* Like others (8), we are unable to explain the short-term fluctuations in rhizosphere densities of *P. parasitica.*

In addition to root mass, the amount of healthy root tips generated by a plant may influence population densities of *P. parasitica.* In our first experiment conducted with *P. parasitica,* the percentage of root tips that were new was not diminished when soil was infested with *F. solani.* When the experiment was repeated, however, the reduction in the percentage of root tips that were new was significant. The presence of root tips is important to densities and population increases of *Phytophthora* because encystment and infection by zoospores usually occurs just behind the root tip in the zone of elongation (31). Fewer new root tips may have contributed to the suppression of rhizosphere densities of *P. parasitica* when soil was infested with *F. solani.* We also hypothesize that colonization of roots by a root colonizer such as *F. solani* might effectively reduce microsites available for encystment and infection by *P. parasitica* and thereby influence densities in the rhizosphere. Indeed, roots colonized by *F. solani* have been shown to have significantly fewer zoospores encysted on them than noncolonized roots (3).

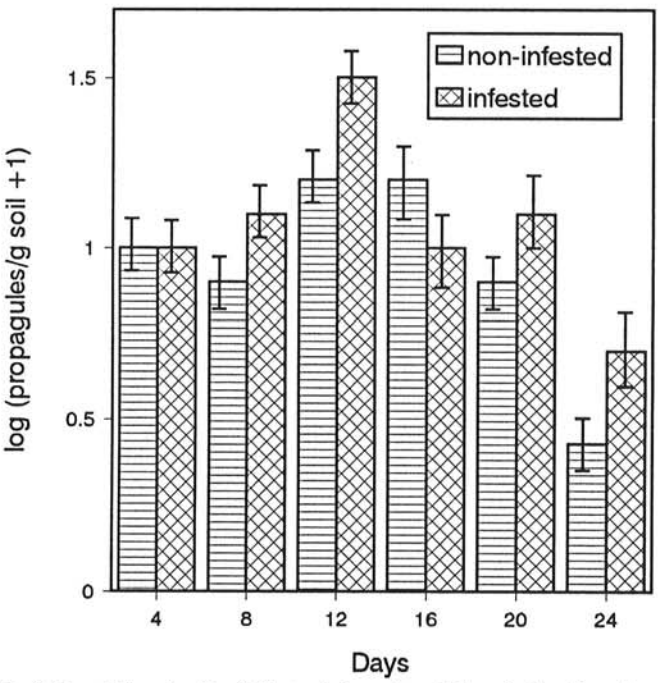

Fig. 3. Population density of *Phytophthora citrophthora* in the rhizosphere of Troyer citrange in soil infested with *Fusarium solani* and in noninfested soil. The soil was drenched with *P. citrophthora* zoospores 30 days after seedlings were transplanted, and rhizosphere populations of *P. citrophthora* were sampled every 4 days for 24 days after inoculation. Means plus or minus standard errors are indicated.

Numbers and lengths of roots of tobacco were not altered when soil was amended with a composite of rhizosphere organisms comprising *Trichoderma harzianum, Aspergillus carbonarius, Aspergillus terreus, Penicillium steckii,* and *Pseudomonas putida* (5). Likewise, root infection by *Phytophthora parasitica* var. *nicotianae* was not lower in soil infested with this composite, nor were population densities of *P. p. nicotianae* in nonrhizosphere soil influenced by the composite. Unlike *F. solani,* however, the organisms used in the composite are not dominant on the root surface but predominate in the rhizosphere.

Rhizosphere densities of *P. citrophthora* associated with roots of citrus were not affected by *F. solani.* There was no significant difference in population fluctuations of *P. citrophthora* whether

or not plants were grown in soil infested with *F. solani*. In southern California, *P. citrophthora* is active in the winter, when soil temperatures are cool (18). At that time, roots of Troyer citrange are dormant. When citrus was planted in soil infested with *F. solani* and inoculated with *P. citrophthora*, the percentage of root tips that were new was less than that for plants grown in noninfested soil. Populations of *P. citrophthora* were not likewise suppressed when plants were planted in soil infested with *F. solani*. An actively growing root system is therefore not important to the infection process of *P. citrophthora*.

The reasons for the different responses in population densities of *P. parasitica* and *P. citrophthora* to colonization of citrus roots by *F. solani* are not clear. However, colonization of roots by *F. solani* suppressed population densities of *P. parasitica* but did not have an influence on population densities of *P. citrophthora*. Determinants that influence the infection processes and population increases differ for *P. parasitica* and *P. citrophthora*. *P. parasitica* is active in the summer and responds to root flushes. *P. citrophthora* is active in the winter and does not respond to root growth (18). *F. solani* is active in the summer as well as in the winter but may be more detrimental to citrus growth when citrus is quiescent than when it is actively growing (1). We propose that *F. solani* suppresses populations of *P. parasitica* by a combination of 1) reducing the availability of infection sites as a result of root dieback and 2) decreasing the number of microsites available for encystment and infection. These particular determinants appear to be less important for population increase in *P. citrophthora*, and thus *F. solani* had little influence on *P. citrophthora* rhizosphere density.

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