Influence of Drip and Furrow Irrigation on Phytophthora Root Rot of Citrus Under Field and Greenhouse Conditions

S. J. FELD, J. A. MENGE, Department of Plant Pathology, and L. H. STOLZY, Department of Soil and Environmental Sciences, University of California, Riverside 92521

ABSTRACT

Feld, S. J., Menge, J. A, and Stolzy, L. H. 1990. Influence of drip and furrow irrigation on Phytophthora root rot of citrus under field and greenhouse conditions. Plant Dis. 74: 21-27.

The influence of drip and furrow irrigation on the distribution of populations of *Phytophthora parasitica* and citrus roots in soil was examined under field conditions and in the greenhouse and lathhouse. During a 2-yr field study in a 70-yr-old citrus orchard, the soil population of *P. parasitica* was significantly lower under drip irrigation than under furrow irrigation; however, this difference was evident only during the summer months when the fungus was most active. The abundance of citrus roots under furrow irrigation increased with distance from the furrow center. Citrus roots under drip irrigation were uniformly distributed in the area wetted by the emitter. Distribution of *P. parasitica* propagules correlated directly with the distribution of citrus feeder roots. In both greenhouse and lathhouse, Phytophthora root rot of citrus seedlings was most severe where seedlings were watered by drip irrigation or kept constantly moist by furrow irrigation. Seedlings that received water by furrow irrigation that allowed the soil to dry sufficiently between irrigations were able to produce more feeder roots than seedlings grown under drip irrigation. Data obtained from greenhouse and lathhouse studies indicate that the commonly recommended method of furrow irrigation that allows the soil to dry to −50 to −70 cb ψm between irrigations favors the host plant and reduces damage by *P. parasitica* more than the other irrigation methods investigated.

Phytophthora citrophthora R. E. Sm. & E. H. Sm. and *P. parasitica* Dastur are the main causal agents of root rot of citrus (4). The disease is favored by abundant soil moisture and is most severe in fine-textured soils where drainage is impeded (4). In sandy loam soils, the greatest destruction of feeder roots occurs in irrigation furrows, where saturated conditions favor zoospore production and movement. Roots outside the furrow often remain healthy (9).

Currently in California, root rot of citrus is controlled by fumigating and replanting with resistant varieties, reducing nutrient and water stress on healthy trees, applying systemic fungicides, and avoiding excessive application of water (2,7). Because water plays such an important role in root rot disease of citrus, precise control of *Phytophthora* spp. may be possible through careful regulation of irrigation water.

Water is applied to citrus groves using several irrigation methods: surface (flood, basin, or furrow), sprinkler, and drip or trickle irrigation. With surface and sprinkler methods, a large volume of the soil becomes saturated [soil matric potential (ψ) = 0 cb] during irrigation. The University of California Extension Service recommends that soil be allowed to dry to −50 to −70 cb between irrigations (13). Drip irrigation applies water gradually to the soil. As a result, only the soil directly under the emitter becomes saturated during irrigation. Soil matric potential in the root zone fluctuates between −10 and −25 cb throughout the irrigation cycle (12, 13).

Our study examined the effects of drip and furrow irrigation on distribution of citrus roots, *P. parasitica* populations, and Phytophthora root rot of citrus under field, greenhouse, and lathhouse conditions.

MATERIALS AND METHODS

Population of *P. parasitica* in a field soil. A furrow-irrigated, 70-yr-old grove of navel orange on sweet orange (Citrus sinensis (L.) Osbeck) rootstock at the Kiel Ranch in Highland, California, was selected as the experimental site. The soil was a Greenfield sandy loam.

The grove has a long history of root rot, and *P. parasitica* is spread fairly uniformly throughout the site. Populations of *P. parasitica* ranged from 7 to 30 propagules per gram of rhizosphere soil in two initial samplings. When propagule numbers from any combination of eight trees were compared to those for any other eight trees, no significant differences were found ($P = 0.05$).

The site consisted of four rows of 16 mature trees each. Two rows of trees remained under furrow irrigation while two nearby rows were placed under drip irrigation. Furrow treatments and drip treatments were always separated by at least one buffer row. In each experimental row, we selected eight trees with similar aboveground symptoms of root rot disease for use as data trees.

Accepted for publication 7 July 1989.

© 1990 The American Phytopathological Society

Trees receiving water by the furrow method were irrigated on the 5th and 19th days of each month. Each row received 24 hr of water at a rate of 20 L/min (120 L per tree per day). This was the normal irrigation regime for the grove. For drip irrigation, six Rainbird emitters (EM-A2 series) were placed under each test tree, three per side. The entire drip system was regulated by a Cloud 9 automatic lawn sprinkler control (a battery-operated timer). Trees under drip irrigation received water for a 3-hr period each day at a rate of 2.6 L/hr (46 L per tree per day). This was considered the optimum requirement for the grove based on evapotranspiration requirements.

Test trees were irrigated by the drip or furrow method throughout the growing season (approximately from April to November). Trees were watered naturally by precipitation during the winter months. Irrigation began in the spring when soil water matric potentials in the root zone of trees irrigated by drip irrigation reached −20 to −25 cb. Water was applied to trees under furrow irrigation on a 2-wk schedule; tensiometer readings indicated that the first irrigation occurred when the soil had dried to −10 to −15 cb. This is normal practice in the San Bernardino citrus growing region, in which canal water is provided on a 2-wk schedule.

Tensiometers were placed at 30-cm and 45-cm depths to monitor soil water matric potentials in the root zone of each experimental tree. Tensiometers at 30 cm monitored matric potential fluctuation in the feeder root zone, while those at 45 cm monitored reserve soil water. Tensiometers were placed on the southwest (sunny) side of both drip-irrigated and furrow-irrigated trees; this is where the greatest fluctuation in soil moisture occurs (14). During the growing season, soil matric potential in the root zone of trees under drip irrigation ranged from −5 to −30 cb at a distance of 30 cm from the emitter. When measured at 30 cm from the center of the furrow, soil matric potential in the root zone of furrow-irrigated trees fluctuated between 0 and −15 cb.

Soil populations of *P. parasitica* under the two irrigation methods were monitored for 2 yr, beginning 6 mo after installation of the drip irrigation lines. Two soil samples were taken from the feeder root zone (7.5 to 30 cm deep) of each experimental tree once per month using a bucket auger (7-cm diameter), and then combined. To ensure that moisture conditions were similar in both furrow-irrigated and drip-irrigated soil, samples were taken 2 days after furrow irrigation and 12 hr after completing the drip-irrigation cycle; in both cases, soil matric potentials were similar at the 30-cm depth.

Soil samples were passed through a screen with a 2-mm mesh to remove large roots and rocks. A 1:10 soil dilution (20 g dry soil in 200 ml water) was made during the summer months and a 1:5 dilution (20 g dry soil in 100 ml water) was made during the winter months. Two replicate dilutions were made per sample. A 1-ml aliquot per replicate dilution was added to each of four petri plates and covered with PVPH selective medium (21). *P. parasitica* produces a readily identifiable colony morphology on this medium; nevertheless, random colonies were plated out at regular intervals and identified to ensure that *P. parasitica* colonies could be identified accurately throughout the year. After 5 days, the number of colonies per plate was counted and the population of *P. parasitica* estimated. Data were analyzed using a multifactor analysis of variance.

Distribution of citrus roots and *P. parasitica*. Soil cores were taken from various points around the drip sources and furrow centers for 2 yr after beginning the irrigation trials. Soil cores were taken 2 days after furrow irrigation and 12 hr after completing the drip-irrigation cycle to ensure that soil moisture conditions were similar (−3 to −15 cb for furrow irrigation and −5 to −30 cb for drip irrigation, both measured at 15 cm soil depth) at the time of sampling. A soil auger (7-cm diameter) was used to collect samples.

With trees under drip irrigation, core samples were taken from directly under the emitter and at distances of 10 and 20 cm from the emitter; the latter cores were taken at the corners of a rectangle centered on the emitter. Soil cores taken under the emitter and at 10 cm distance were divided into four sections according to depth: 0–5, 5–15, 15–30, and 30–40 cm. Cores taken at 20 cm from the emitter were divided into sections for 0–5 and 5–15 cm depths. With trees under furrow irrigation, soil cores were taken directly under the furrow center and at 20 and 40 cm from the center. These cores were taken in a single vertical plane, with the 40-cm core taken closest to the tree trunk. Cores from furrow-irrigated soil were divided into four sections according to depth: 0–5, 5–15, 15–30, and 30–40 cm.

Samples were taken from 15 trees under drip and furrow irrigation during July and August, 1979—the two warmest summer months. Samples were taken randomly within the tree rows. The presence or absence of roots was recorded for each soil core and the population of *P. parasitica* in each core was estimated using a soil dilution plate method and PVPH selective medium (22). *P. parasitica* frequency was monitored again the following year, with results similar to those reported here. Soil water matric potential and root frequencies were monitored for 1 yr only, since the amount of water and soil characteristics were the same for both years.

Greenhouse disease severity studies. We used chlamydospores to infest soil because they provide a measurable, uniform source of inoculum with a high survival rate (19). Chlamydospores were produced and harvested according to the methods of Tsao and Oster (23). Spore viability was determined to be 95%, and germination was 80% (20).

A field soil, Greenfield sandy loam, was autoclaved for two 2-hr periods with a 24-hr interval. *P. parasitica* could not be isolated from soil or root pieces after autoclaving. Using a cement mixer, chlamydospores were incorporated into 72 kg of autoclaved soil to achieve a final inoculum density of 450–500 spores per gram of soil. A suspension of 6×10^4 spores per milliliter was added gradually to the soil (to prevent clumping). The total volume of liquid added was 3 L (600 ml spore suspension + 2400 ml sterile water). Three liters of sterile water were added to noninfested control soil. Each soil was mixed for 30 min, which was adequate to mix the inoculum uniformly. Samples taken immediately after mixing and plated on PVPH selective medium (22) yielded populations of *P. parasitica* that were not significantly different; the average was 102 propagules per gram of soil. No fertilizer was applied at the time of mixing.

Twelve kilograms of infested or noninfested soil were placed into each 12-L plastic pot. A single mycorrhizal six-week-old sweet orange seedling (*C. sinensis 'Pineapple'*) was planted in each pot. The mycorrhizal fungus species was *Glomus deserticola* Trappe, Bloss & Menge. Pea gravel was used as a mulch to prevent cracking of the soil surface. A tensiometer was placed in each pot to monitor fluctuations in soil moisture.

Simulated drip and furrow irrigation systems were the same for both greenhouse experiments. The drip system consisted of a polyethylene main line (1.6-cm diameter) to which emitters were attached. Spaghetti tubing (10-mm diameter) ran from each emitter to its respective pot. Water was applied at a slow rate (12–15 ml/min) so as not to exceed a slow, steady drip. The simulated furrow irrigation system involved applying water to each pot by hand (4 L/min.) until the soil became saturated. Seedlings from both experiments were irrigated with a 14% Hoagland's solution lacking phosphorus.

In the first greenhouse experiment, six infested and six noninfested sweet orange seedlings were watered by either the simulated drip or simulated furrow method. Under drip irrigation, seedlings were watered every 5–7 days to maintain a soil matric potential in each pot of −5 to −30 cb. Under the furrow method, seedlings were watered weekly to establish a soil matric potential of 0 to −15 cb in each pot. Water was applied until

the tensiometers reached zero suction; the soil was then allowed to dry to −15 cb before the next irrigation. The soil matric potentials under these irrigation methods mimicked those measured under field conditions at the Highland site. This experiment was repeated once.

The irrigation methods used in the second greenhouse experiment were similar to those in the first, except that the two furrow irrigation methods used simulated those recommended by the University of California Extension Service (13). In the first furrow method, seedlings were watered every 7–10 days; the soil matric potentials in pots fluctuated between 0 and 50 cb. In the second furrow method, seedlings were watered every 10–14 days; soil matric potentials fluctuated between 0 and 70 cb. Seedlings under drip irrigation in this experiment were watered in the same way as those in the first greenhouse experiment.

Data were collected at the end of a 3-mo period, when significant differences could be visually observed. Plant dry weights were obtained and the percentage of healthy root tips was determined by visual observation. The independent observations of three raters were averaged for each plant. The population of *P. parasitica* in the rhizosphere soil was estimated from three replicate samples per pot using a soil dilution plate technique with PVPH selective medium (22). Data were evaluated using Duncan's multiple range test, two-way Anova, and *t* tests, all with similar results.

Lathhouse disease severity studies. Two lathhouse beds (1.2 × 4.6 × 0.5 m) were filled with soil from the Highland field site. The soil was covered by a tarp and then fumigated with methyl bromide at a rate of 0.65 kg per cubic meter. *P. parasitica* could not be isolated from soil samples or root pieces that had been fumigated. Treatment plots (each 1.8 m long) were established at the ends of each bed; the center section (0.9 m) was left as a buffer zone. One lathhouse bed received drip irrigation and the other received furrow irrigation.

One end of each bed received chlamydospore inoculum of *P. parasitica,* which was prepared as in the greenhouse study. Chlamydospores were incorporated into the soil by layering inoculum and soil in the bed selected for infestation. Inoculum was mixed within each 15-cm layer using a garden hoe. Final inoculum density was estimated at 30 chlamydospores per gram (dry weight) of soil by plating on PVPH selective medium (22).

Twenty-four six-week-old mycorrhizal sweet orange seedlings were planted in each treatment plot. The mycorrhizal fungus species was *G. deserticola.* During the first week, seedlings were watered manually as needed. Later, seedlings were watered by either drip or furrow irrigation. The drip system consisted of a polyethylene line (1.6-cm diameter) connected to the water source. Twelve emitters were attached to the line for each treatment plot. Seedlings under drip irrigation were watered periodically to maintain a soil matric potential of −5 to −30 cb. Under furrow irrigation, water was applied manually to furrows when the the soil matric potential reached −50 to −70 cb; water was applied until the soil was saturated. During the winter months (November–March), the seedlings were watered by precipitation only.

After 1 yr, root and total dry weight of the seedlings were measured and the amount of root rot was estimated by visual observation. The independent observations of three raters were averaged for each plant. Data was evaluated by Duncan's multiple range test, two-way Anova, and *t* tests, all with similar results. The experiment was repeated the following year, except that different beds were irrigated. The trends were identical during both years; however, only the second-year data is presented here.

RESULTS

Population of *P. parasitica* in a field soil. The soil population of *P. parasitica* associated with mature orange trees (Fig. 1) under both drip and furrow irrigation fluctuated periodically throughout the year. Propagule counts were low—essentially zero—during winter months, but they began to increase between April and May. The *P. parasitica* population reached its maximum level in July or August (32 propagules per gram in the first year; 17 propagules per gram in the second), a pattern seen in both years. There was no significant difference in population observed between irrigation methods during the cool winter months. During the warmer summer months (July–October) when the fungus was most active, however, a significant difference ($P = 0.05$) in *P. parasitica* population between the two methods was observed. In the first year, the average population of *P. parasitica* under drip irrigation during these months was 43% of that under furrow irrigation; in the second year, the average population was 54% of that under furrow irrigation (Fig. 1).

Distribution of citrus roots and *P. parasitica.* Core samples from drip and furrow irrigation sites were grouped into zones based on moisture content (Fig. 2A,C) and matric potential (Fig. 2B,D). Soil water potential values were extrapolated from a moisture release curve constructed for the soil at the field site.

Core samples from furrow-irrigation sites were grouped into four moisture zones (Fig. 2A,B). Zone 1 contained cores taken at a depth of 0–5 cm and a distance of 9 and 20 cm from the furrow center. Their average moisture content was 23% (0 to −5 cb). Zone 2 contained cores taken at a depth of 0–5 cm and a distance of 40 cm from the furrow center, and cores taken at a depth of 5–15 cm and distances of 0 and 20 cm from the furrow center. The average moisture content of these cores was 17% (−3 to −15 cb). Zone 3 contained cores taken at a depth of 5–15 cm and a distance of 40 cm from the furrow center, and cores taken at a depth of 15–30 cm and distances of 0 and 20 cm from the furrow center. Their average moisture content was 15% (−15 to −40 cb). Zone 4

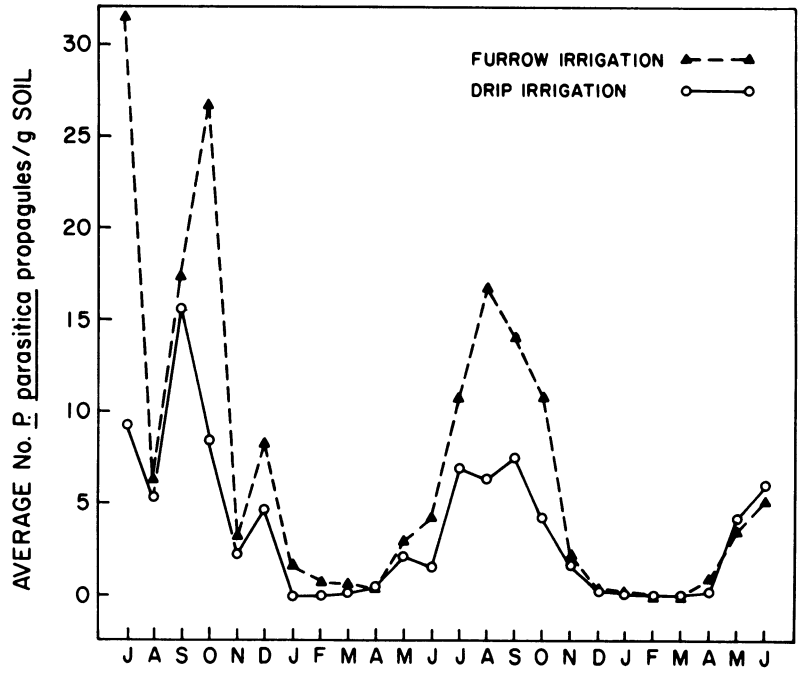

Fig. 1. Soil population of *Phythophthora parasitica* in a 70-yr-old citrus grove as influenced by drip and furrow irrigation over a 2-yr period. A significant difference ($P = 0.05$) was observed between treatments only during the period July–October for both years.

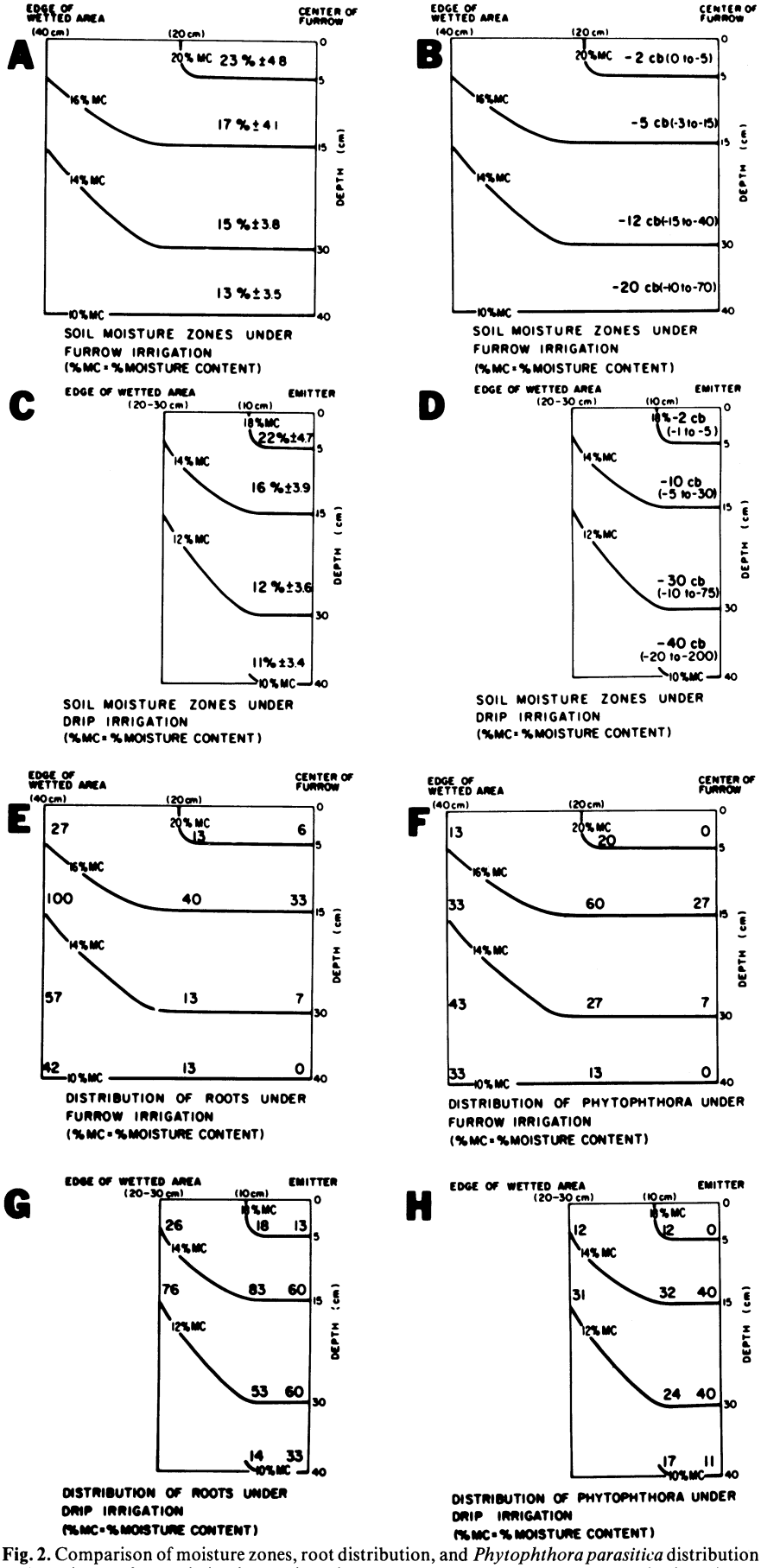

Fig. 2. Comparison of moisture zones, root distribution, and *Phytophthora parasitica* distribution under drip and furrow irrigation. Soil moisture zones are based on percentage of soil moisture or matric potential under furrow **(A,B)** and drip **(C,D)** irrigation. Root frequency **(E,G)** = number of samples where roots were observed/total number of samples for any position × 100. *P. parasitica* frequency **(F,H)** = number of samples where *P. parasitica* was observed/total number samples for any position × 100.

contained cores taken at a depth of 30–40 cm and a distance of 0, 20, and 40 cm from the furrow center, and cores taken at a depth of 15–30 cm and a distance of 40 cm from the furrow center. Their average moisture content was 13% (–10 to –70 cb). Starting at the surface, boundaries between the zones were established at 20, 16, 15 and 10% average moisture content.

Cores from drip irrigation sites were also grouped into four moisture zones (Fig. 2C,D). Zone 1 contained cores taken at a depth of 0–5 cm and distances of 0 and 10 cm from the emitter; the average moisture content was 22% (−1 to −5 cb). Zone 2 contained cores taken at a depth of 0–5 cm and a distance of 20–30 cm from the emitter (the border of the wetted area), and cores taken at a depth of 5–15 cm and distances of 0 and 10 cm from the emitter. Their average moisture content was 16% (−5 to −30 cb). Zone 3 contained cores taken at a depth of 5–15 cm and a distance of 20–30 cm from the emitter, and cores taken at a depth of 15–30 cm and distances of 0 and 10 cm from the emitter. The average moisture content of these cores was 12% (−10 to −75 cb). Zone 4 contained cores taken at a depth of 30–40 cm and distances of 0 and 10 cm from the emitter. Their average moisture content was 11% (−20 to −200 cb). Boundaries between the zones were established at 18, 14, 12, and 10% average moisture content.

Figure 2 (E,F,G,H) shows the distribution of citrus roots and *P. parasitica* within the moisture zones described above. Frequencies shown in the figure were calculated by dividing the total number of core samples into the number of times that roots or *P. parasitica* were observed in those samples, and then multipling the result by 100. Under furrow irrigation (Fig. 2E), the greatest root frequency occurred in moisture zone 2 (−3 to −15 cb; 27, 40, and 33%) and in cores taken 40 cm from the furrow center at any depth (27, 100, 57, and 42%). Few core samples taken directly under the furrow center contained roots; cores taken 40 cm under the center contained no roots. Under drip irrigation (Fig. 2G), root frequency was high, indicating a concentration of roots in the small wetted zone. Roots were also more uniformly spread throughout the moisture zones than they were under furrow irrigation. Few roots were found near the soil surface (0–5 cm depth) under drip irrigation.

Under furrow irrigation, *P. parasitica* was isolated most frequently in moisture zone 2 (27, 60, and 13%) and in soil cores taken 40 cm from the furrow center (13, 33, 43, and 33%) (Fig. 2F). *P. parasitica* was not found in soil cores taken from the furrow center at the 0–5 or 30–40 cm depths (Fig. 2F). The frequency of *P. parasitica* isolation under drip irriga-

tion was similar in distribution to root frequency (Fig. 2H). The highest frequency of the fungus was found in the soil directly under the emitter at a depth of 5–30 cm (−3 to −40 cb) and in moisture zone 3 (−15 to −40 cb). The frequency decreased as depth and distance from the emitter increased.

Because the positions sampled under the different irrigation methods were not identical, it is difficult to determine how a particular method affected *P. parasitica* frequency. A comparison of wetted areas, however, shows that *P. parasitica* was isolated from 23% of the furrow-irrigated sites and 22% of the drip-irrigated sites.

Greenhouse disease severity studies. Under greenhouse conditions, sweet orange seedlings grew equally well in infested soil under simulated drip (ψm = −5 to −30 cb) or simulated furrow (ψm = 0 to −15 cb) irrigation (Table 1). Total plant and root dry weights of *P. parasitica*-infected plants were reduced significantly compared to dry weights of noninfected plants. Seedlings grown in infested soil under either method had fewer healthy roots than did the control plants. Final populations of *P. parasitica* in infested soil under the two irrigation methods were comparable. Results were similar when this experiment was repeated.

In the second greenhouse experiment, sweet orange seedlings grown in *P. parasitica*-infested soil under simulated drip (ψm = −5 to −30 cb) or simulated furrow irrigation (ψm = 0 to −50 cb, ψm = 0 to −70 cb) had total dry weights significantly less than those of control plants grown in noninfested soil. Weights were reduced by 64% under drip irrigation; by 58% under the first furrow system (0 to −50 cb); and by 54% under the second furrow system (0 to −70 cb) (Table 2). Similar reductions occurred in root dry weight, with no significant differences between irrigation methods.

Under all irrigation methods, the percentage of healthy roots was lower in infested soil than in noninfested soil. The fewest healthy roots (33%) occurred in seedlings grown in infested soil under simulated drip irrigation. More healthy roots (46%) were found on seedlings grown in infested soil under the first furrow system (0 to −50 cb), and significantly more roots (66%) were present under the second furrow system (0 to −70 cb). Irrigation method did not significantly affect the populations of *P. parasitica* in soil surrounding infected seedlings; main effects accounted for most of the variation observed. There was, however, a significant interaction (P = 0.05) between *P. parasitica* and irrigation method with respect to the percentage of healthy roots.

Lathhouse disease severity studies. In the lathhouse, total dry weights of sweet orange seedlings grown under drip irrigation were reduced 67% by *P. parasitica,* while dry weights of seedlings grown under furrow irrigation (ψm = 0 to −70 cb) were reduced by only 37% (Table 3). Only 34% of the roots of drip-irrigated seedlings were healthy, compared to 50% for the furrow-irrigated seedlings. Plants grown in noninfested soil grew equally well under both irrigation methods; no significant difference was observed in plant dry weight or percentage of healthy roots. Again, there was a significant interaction (P = 0.05) between *P. parasitica* and irrigation method.

DISCUSSION

Excess soil moisture has been related consistently to incidence of Phytophthora root rot of citrus (6, 8, 9, 17, 21). It is generally accepted that saturated soil conditions stimulate the production and release of zoospores and provide the medium in which zoospores move (3, 5, 10). Saturated conditions may also increase root damage by reducing the host's ability to produce new roots to replace those lost to disease (17).

Our study demonstrates that the soil population of *P. parasitica* in the field can be significantly greater under furrow irrigation than under drip irrigation. This difference in population may be due to the greater numbers of zoospores released under furrow irrigation. Most *Phytophthora* spp. require saturated or nearly saturated conditions to release zoospores. During irrigation, soil around the root zone of furrow-irrigated trees reaches saturation (12, 13). This is not the case with trees watered by the drip method; only the soil immediately below the emitter becomes saturated (12). As a result, the roots of drip-irrigated trees may receive considerably less zoospore inoculum.

P. parasitica is known as a warm-temperature *Phytophthora;* in vitro, the fungus grows best at 30–32 C (14). At the field site, soil temperatures below 10 C were recorded from November to January. Temperatures began to increase in February, reaching maximum levels (25+ C) during July, August and September. In October, temperatures slowly declined. The high soil population of *P. parasitica* during the summer and the low, essentially nondetectable population during the winter correlate directly to these changes in soil temperature. This fluctuation occurred under both irrigation methods. Our findings are consistent with those of Marks et al. (11), who were able to correlate soil temperature with a population density index (PDI) and disease hazard for the *P. cinnamomi-Eucalyptus* system. Although the population of *P. citrophthora* was not monitored, the only colonies of this species isolated from the soil were found during

Table 1. Growth of sweet orange seedlings in *Phytophthora parasitica*-infested and noninfested soil under two soil irrigation methods in the greenhouse[x]

Irrigation method	Dry weight/plant (g)		Healthy roots (%)[y]	*P. parasitica* population[z]
	Total plant	Roots		
Simulated drip (-5 to -30 cb)				
Noninfested soil	6.8 a	1.9 a	98.5 a	0.0 b
Infested soil	1.8 b	0.7 b	31.3 b	9.0 a
Simulated furrow (0 to -15 cb)				
Noninfested soil	6.4 a	2.3 a	98.6 a	0.0 b
Infested soil	2.4 b	0.9 b	21.8 b	7.0 a

[x]Each value is a mean of six observations; values followed by the same letter are not significantly different (P = 0.05).
[y]Percentages were arc sine transformed before analysis to stabilize the variance.
[z]Propagules per gram of dry soil.

Table 2. Growth of sweet orange seedlings in *Phytophthora parasitica*-infested and noninfested soil under three soil irrigation methods in the greenhouse[x]

Irrigation method	Dry weight/plant (g)		Healthy roots (%)[y]	*P. parasitica* population[z]
	Total plant	Roots		
Simulated drip (-5 to -30 cb)				
Noninfested soil	16.3 a	5.5 a	95.0 a	0.0 b
Infested soil	6.0 b	2.0 b	33.3 c	14.0 a
Simulated furrow (0 to -50 cb)				
Noninfested soil	15.6 a	5.3 a	93.3 a	0.0 b
Infested soil	6.5 b	2.1 b	45.5 bc	8.2 a
Simulated furrow (0 to -70 cb)				
Noninfested soil	18.8 a	6.0 a	95.8 a	0.0 b
Infested soil	8.7 b	3.5 b	65.8 b	8.0 a

[x]Each value is a mean of six observations; values followed by the same letter are not significantly different (P = 0.05).
[y]Percentages were arc sine transformed before analysis to stabilize the variance.
[z]Propagules per gram of dry soil.

the cooler months of the year. *P. citrophthora* grows best at temperatures of 24–28 C (14).

Under furrow irrigation, host roots were found with greatest frequency in the drier zones and farthest from the furrow center. Roots in these areas appeared to be the safest from attack by *P. parasitica,* since the ratio of root frequency to *P. parasitica* frequency was the highest (Fig. 2E,F,G,H). Although these areas became saturated during irrigation, they dried much more rapidly than areas closest to the furrow center. Results presented here and those from similar greenhouse studies conducted by Stolzy et al. (17) indicate that new feeder roots develop to compensate for those lost to infection during irrigation, provided that the soil is allowed to dry sufficiently before additional irrigations. Constantly-wet, *P. parasitica*-infested soil, such as that close to the furrow center or in "overwatered" pots of the greenhouse experiment, is not conducive to root tip regeneration. Eventually, feeder root numbers decrease in these locations due to repeated infections during irrigation. Under drip irrigation, feeder roots are more uniformly spread throughout the moisture zones, a type of root development consistent with the more constant soil moisture levels maintained during the irrigation cycle. Under either irrigation method, the distribution of *P. parasitica* corresponds to the distribution of feeder roots; high concentrations of *Phytophthora* spp. are more likely to be found in areas with high concentrations of feeder roots.

Results from one lathhouse and three greenhouse experiments indicate that citrus root rot caused by *P. parasitica* is favored by overirrigated soil under furrow irrigation (ψm = 0 to −15 cb) and consistently moist soil under drip irrigation (ψm = −5 to −30 cb). Roots growing in soil watered by either of these irrigation methods produced very few new feeder root tips to replace diseased ones. Under these conditions, the entire root system can eventually be destroyed by the fungus. When citrus seedlings were grown under a furrow-irrigation method that allowed the soil to dry sufficiently between irrigations (ψm 0 to −70 cb), new feeder roots were continually produced and the plants were significantly healthier than those grown under other methods. Significant (P = 0.05) interactions between irrigation and *P. parasitica* and citrus occurred only when the soil was allowed to dry to −70 cb. Timmer and Leyden (18) also found a higher incidence of disease under drip irrigation than under flood irrigation in a Texas field study. As in our study, irrigation methods did not appear to influence root development in non-infested soil. The influence of irrigation on root development is seen only when the host and pathogen interact.

Using a method of watering citrus seedlings in containers that closely resembles our "overwatering" furrow method (ψm = 0 to −15 cb), Tsao and Garber (21) found that periodic waterlogging of the soil was very conducive to root infection if that soil was infested by *Phytophthora* spp. Their conclusions agree with our results. Stolzy et al. (16) developed several watering methods that enhance root decay by *P. parasitica.* They found that soil saturation was the key factor in increasing root decay and that length of saturation time was more critical than frequency of saturation. Their method of saturating the soil three times per month resembles our "overwatering" furrow method and it led to a high percentage of root decay. Their method of saturating the soil twice per month resembles the University of California-recommended furrow method (ψm = 0 to −70 cb) that we used; it led to a low percentage of root decay. These data agree with the results of our study.

Stolzy et al. (16, 17) went on to show that soil aeration is a contributing factor in root decay. A low oxygen supply in soil prevents growth and regeneration of roots, even in the absence of pathogens. Irrigation methods used in our study did not appear to limit soil oxygen. All allowed the citrus seedlings to produce an ample supply of roots in the absence of *Phytophthora.* Without the presence of *Phytophthora*, a decrease in soil oxygen can perhaps be tolerated by citrus. When *Phytophthora* is present, however, citrus roots become more susceptible to oxygen reduction. *Fusarium solani*, a ubiquitous saprophyte on citrus roots, may also be involved in the interaction between irrigation, oxygen, and *Phytophthora*; *F. solani* is known to inhibit root development in citrus. *F. solani* may initiate infection only when roots are first injured either by low oxygen or by *P. parasitica* (1).

In conclusion, good irrigation practices are essential to reduction of the effects of citrus root rot. Although drip irrigation and overwatering by furrow irrigation does not harm seedlings in soil free from *P. parasitica,* these methods of irrigation could be damaging where *P. parasitica* is a problem. Drip irrigation may help prevent the spread of *P. parasitica,* since it apparently leads to a reduction in the formation and movement of zoospores. From our greenhouse and lathhouse studies, watering citrus using the commonly recommended method of furrow irrigation (ψm from 0 to −70 cb) greatly aids the host in overcoming root damage caused by *P. parasitica,* despite the fact that this method may increase the spread of the pathogen.

Table 3. Growth of sweet orange seedlings in *Phytophthora parasitica*-infested and noninfested soil under two soil irrigation regimes in lathhouse beds[y]

Irrigation method	Dry weight/plant (g)		Healthy roots (%)[z]
	Total plant	Roots	
Drip (-5 to -30 cb)			
Noninfested soil	7.5 a	37.5 a	85.7 a
Infested soil	3.6 c	12.4 c	34.0 c
Furrow (0 to -70 cb)			
Noninfested soil	7.7 a	33.1 a	86.5 a
Infested soil	5.6 b	20.8 b	49.7 b

[y] Each value is a mean of 24 observations; values followed by the same letter are not significantly different (P = 0.05).
[z] Percentages were arc sine transformed before analysis to stabilize the variance.

LITERATURE CITED

1. Bender, G. 1985. Dry root rot of citrus: factors which increase the susceptibility of trees to infection by *Fusarium solani.* Ph.D. thesis. University of California, Riverside. 204 pp.
2. Calavan, E. C. 1957. Three major root rot diseases of citrus. Calif. Citrog. 42:431-432.
3. Duniway, J. M. 1979. Water relations of water molds. Annu. Rev. Phytophathol. 17:431-460.
4. Fawcett, H. S. 1936. Citrus Diseases and Their Control. McGraw-Hill Book Co., New York. 656 pp.
5. Gisi, U., Zentmyer, G. A., and Klure, L. J. 1980. Production of sporangia by *Phytophthora cinnamomi* and *P. palmivora* in soils at different matric potentials. Phytopathology 70:301-306.
6. Ioannou, N., and Grogan, R. G. 1984. Water requirements for sporangium formation by *Phytophthora parasitica* in relation to bioassay in soil. Plant Dis. 68:1043-1048.
7. Klotz, J., DeWolfe, T. A., and Miller M. P. 1969. Control of *Phytophthora* problems. Calif. Citrog. 54:228-229.
8. Klotz, L. J., Stolzy, L. H., Labanauskas, C. K., and DeWolfe, T. A. 1971. Importance of *Phytophthora* spp. and aeration in root rot and growth inhibition of orange seedlings. Phytopathology 61:1342-1346.
9. Klotz, L. J., Stolzy, L. H., Letey, J., Labanauskas, C. K., Valoras, N., and DeWolfe, T. A. 1966. Root decay of citrus as affected by soil moisture and aeration. Calif. Citrog. 51:296-299.
10. MacDonald, J. D. 1978. Influence of soil water on the sporangia and zoospores of three root-infecting species of *Phytophthora.* Ph.D. thesis. University of California, Davis. 109 pp.
11. Marks, G. C., Kassaby, F. Y., and Fagg, P. C. 1975. Variation in population levels of *Phytophthora cinnamomi* in *Eucalyptus* forest soils of eastern Victoria. Aust. J. Bot. 23:435-449.
12. Marsh, A. W. 1973. Irrigation. Pages 230-279 in: Reuther, W., ed. The Citrus Industry. Vol. 3. University of California Press, Berkeley. 528 pp.
13. Marsh, A. W. 1975. Questions and answers about tensiometers. Ext. Leafl. Univ. Calif. Ext. Serv. 2264. 10 pp.
14. Ribeiro, O. K. 1978. A Sourcebook of the Genus *Phytophthora.* J. Cramer, Hirschberg, Germany. 417 pp.
15. Stolzy, L. H., Marsh, A. W., Puffer, R. E., and Baier, D. C. 1960. Placement of tensiometers as guides to irrigation practices. Calif. Agric.

14:11-12.
16. Stolzy, L. H., Letey, J., Klotz, L. J., and DeWolfe, T. A. 1965. Soil aeration and root-rotting fungi as factors in decay of citrus feeder roots. Soil Sci. 99:403-406.
17. Stolzy, L. H., Letey, J., Klotz, L. J., and Labanauskas, C. K. 1965. Water and aeration as factors in root decay of *Citrus sinensis*. Phytopathology 55:270-275.
18. Timmer, L. W., and Leyden, R. F. 1976. Effect of irrigation and soil management practices on the incidence of *Phytophthora* foot rot of citrus. J. Rio Grande Val. Hortic. Soc. 30:19-25.
19. Tsao, P. H. 1971. Studies on the saprophytic behavior of *Phytophthora parasitica* in soil. Proc. Int. Citrus Symp. 1st. 3:1221-1230.
20. Tsao, P. H. 1971. Chlamydospore formation in sporangium-free liquid cultures of *Phytophthora parasitica*. Phytopathology 61:1412-1413.
21. Tsao, P. H., and Garber, M. J. 1960. Methods of soil infestation, watering, and assessing the degree of root infection for greenhouse in situ ecological studies with citrus phytophthoras. Plant Dis. Rep. 44:710-715.
22. Tsao, P. H., and Guy, S. O. 1977. Inhibition of *Mortierella* and *Pythium* in a *Phytophthora*-isolation medium containing hymexazol. Phytopathology 67:796-801.
23. Tsao, P. H., and Oster, J. J. 1981. Relation of ammonia and nitrous acid to suppression of *Phytophthora* in soils amended with nitrogenous organic substances. Phytopathology 71:53-59.