Effect of Citrus Rootstocks on Soil Populations of *Phytophthora parasitica*

J. P. AGOSTINI, Graduate Assistant, L. W. TIMMER, Professor, and W. S. CASTLE, Professor, Citrus Research and Education Center, University of Florida, Institute of Food and Agricultural Sciences, 700 Experiment Station Road, Lake Alfred 33850; and D. J. MITCHELL, Professor, Department of Plant Pathology, University of Florida, IFAS, Gainesville 32611

ABSTRACT

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Soil and root samples were collected from December 1987 to February 1989 from 12-yr-old Valencia sweet orange rootstock trials near St. Cloud and Avon Park, FL. Propagule densities of *Phytophthora parasitica* were determined by plating soil on a selective medium. The lowest populations occurred on the least susceptible trifoliate orange and Swingle citrumelo and the highest on the most susceptible sweet orange, Volkamer lemon, and Palestine sweet lime in the field experiments. Average numbers of propagules per cubic centimeter of soil over this period in the field experiments ranged from 8.3 to 32.2 at St. Cloud and from 5.4 to 14.6 at Avon Park for rootstocks with the lowest and highest populations, respectively, with the highest populations occurring in summer. In a screenhouse pot test, populations were highest on sweet orange and sour orange and lowest on Swingle citrumelo and trifoliate orange but were not significantly different from the unplanted control. In experiments at St. Cloud, where roots were removed from cores of soil and new roots were allowed to grow into infested and disturbed soil, propagule densities were high and were correlated with the density of new roots formed ($r = 0.929$). Abundant immature fibrous roots, a highly susceptible rootstock, and favorable environmental conditions promote development of root rot and, consequently, high propagule densities.

Phytophthora parasitica Dastur is a soilborne fungus that commonly occurs in citrus orchards and field nurseries in Florida and is the source of several disease problems. Symptoms can appear above or below ground, and the fungus can cause foot rot of the trunk, root rot, or brown rot of the fruit (17).

Rootstocks vary in their tolerance to *Phytophthora* spp. Previously, they were rated according to their foot rot tolerance or resistance until the extent and importance of fibrous root loss caused by root rot had been established (6). Fibrous root losses have been assumed to be minimal, except perhaps on highly susceptible rootstocks such as sweet orange. In general, sweet orange and some sources of rough lemon are considered highly susceptible to infection, whereas trifoliate orange, Swingle citrumelo, and alemow are resistant (5–7). Troyer and Carrizo citranges, Cleopatra mandarin, and sour orange are intermediate between the two extremes (20).

Soil populations of *P. parasitica* in Florida citrus orchards have been estimated with the use of a selective medium for the isolation of *Phytophthora* spp. (18), and the effect of treatments with the fungicides metalaxyl and fosetyl-Al on populations has now been evaluated (14). Fungicide treatments appear to be beneficial when threshold levels of the fungus reach 10–15 propagules per cubic centimeter of soil (16). However, the biological significance of different propagule densities and the interaction of this factor with tolerant or susceptible rootstocks and citrus fibrous roots have not yet been clearly defined. Therefore, the objectives of this study were to determine the effect of rootstocks on soil populations of *P. parasitica* under screenhouse and field conditions and to determine the relationship between the density and condition of fibrous roots of different rootstocks and propagule densities of *P. parasitica* in the field.

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MATERIALS AND METHODS

Field study. Two citrus rootstock experiments with 12-yr-old trees of Valencia sweet orange (*Citrus sinensis* (L.) Osb.) on 12 rootstocks located near Avon Park and St. Cloud, FL, were selected as study sites.

Avon Park. The Avon Park experiment was planted in Candler fine sand, a soil typical of the central Florida Ridge area. At this site, trees were planted at a spacing of 4.5 × 6.0 m. A split-plot design with randomized complete blocks was used. The main plot treatments were preplant fumigation with methyl bromide or no fumigation. The main plot treatments were replicated four times with six trees per subplot (rootstocks). Soil samples were taken from the two central trees of each subplot with the four replications of each main plot treatment of the following five rootstocks: English Small trifoliate orange (*Poncirus trifoliata* (L.) Raf.), Swingle citrumelo (*C. paradisi* Macf. × *P. trifoliata*), Palestine sweet lime (*C. limettioides* Tanaka), Ridge Pineapple sweet orange, and Cleopatra mandarin (*C. reticulata* Blanco). Four cores were collected from each of the two trees per replicate, the eight cores were combined, and a single determination of propagule density was made for each replication.

St. Cloud. The St. Cloud rootstock experiment was planted on a site with several kinds of soil. The Pomona, Immokalee, Myakka, and St. Johns series were the most prevalent. Trees were planted in plots 4.5 × 6.0 m in a split-plot arrangement with randomized complete blocks. There were two trees per subplot (rootstock) and four replications of the two main plot treatments (irrigation by microsprinkler or no irrigation). Soil samples were taken from the two trees in each plot and from the four replications of each main plot treatment of the following five rootstocks: English Small trifoliate orange, Palestine sweet lime, Cleopatra mandarin, Swingle citrumelo, and Volkamer lemon (*C. volkameriana* Pasq.). Eight cores were collected from each tree and composited, and a single determination for propagule density was made. The propagule density for each replication was the average for the two trees.

Sample collection. Soil samples were collected periodically around the canopy drip line of each of the sampled trees from December 1987 through February 1989. An auger, which held approximately 930 cm^3 of soil (18.5 cm long × 8.0 cm diameter), was used for sampling. Cores were combined and passed through a 3-mm mesh sieve. A subsample of about 250 cm^3 of soil was collected in a plastic bag. In addition, all roots from the bulked samples were collected in a separate plastic bag.

Determination of propagule densities of *Phytophthora parasitica*. In the laboratory, each soil sample was saturated with water and then allowed to drain freely overnight. The procedure of Timmer et al (18) was used and the samples were incubated at room temperature for at least 1 day.

Table 1. Mean propagule densities of *Phytophthora parasitica* and root densities for five rootstocks at the Avon Park and St. Cloud citrus orchards

	Avon Park[w]						St. Cloud[w]					
	Propagules/cm³ of soil			Root density in soil (mg/cm³)			Propagules/cm³ of soil			Root density in soil (mg/cm³)		
Rootstocks	F[x]	UF[x]	Avg.	F	UF	Avg.	I[x]	UI[x]	Avg.	I	UI	Avg.
Pineapple sweet orange	13.4	15.8	14.6 a[y]	1.7	1.6	1.7 a	...	...	...	...	...	...
Palestine sweet lime	10.2	11.7	11.0 ab	1.4	1.3	1.4 b	28.0	36.5	32.3 a	1.9	1.6	1.7 a
Volkamer lemon	...	...	...	...	...	...	33.7	29.1	31.4 a	1.6	1.2	1.4 b
Cleopatra mandarin	10.7	6.3	8.5 bc	1.6	1.6	1.6 ab	19.3	16.4	17.9 b	1.8	1.4	1.6 a
Trifoliate orange	5.4	8.6	7.0 bc	1.6	1.4	1.5 ab	19.0	13.5	16.3 b	1.4	1.2	1.3 c
Swingle citrumelo	4.2	6.5	5.4 c	1.6	1.6	1.6 ab	9.0	7.5	8.3 c	1.8	1.5	1.7 a
Average	8.8	9.8		1.6	1.5[z]		21.7	20.6[z]		1.7	1.4[z]	

[w] Each mean is the average of five sampling times with four replications of each treatment from March 1988 through February 1989 at Avon Park and from December 1987 through December 1988 at St. Cloud.
[x] F = preplant fumigation with methyl bromide at 500 kg/ha, UF = unfumigated, I = irrigated by microsprinklers, UI = unirrigated.
[y] Mean separation in columns by Duncan's multiple range test, $P \leq 0.05$.
[z] Treatment averages significantly different, $P < 0.05$.

The method of Kannwischer and Mitchell (8) was used to determine propagule densities. Ten cubic centimeters of soil from each sample was diluted in 90 ml of 0.25% agar and shaken. From this suspension, 1-ml aliquots were spread on each of five plates of PAR medium that is selective for *Phytophthora* spp. (8). The medium was modified by adding 25 mg of hymexazol per liter. After 72 hr of incubation at 28 C, the soil residue was washed from the agar surface under a gentle stream of water and colonies in the agar were counted. Results were expressed as the number of propagules per cubic centimeter of soil.

Root measurements. All fibrous roots (those less than 2 mm in diameter) were collected on a 3-mm mesh screen and oven-dried at 45 C. Root weight was expressed as milligrams of dry weight per cubic centimeter of soil.

The capacity for root regeneration of each rootstock was determined by placing baskets, 20 cm long × 8 cm diameter, made from 6-mm mesh screen in holes from which soil samples and roots had been removed at the St. Cloud site. Four baskets were placed around each of three trees on each rootstock and filled with soil from the same hole in which they were placed. In the first experiment, the baskets were kept in the field for 1 mo (July–August 1988) and in the second experiment for 3 mo (August–November 1988). Baskets were removed carefully so as not to disturb the roots inside the core and were placed in a plastic bag for transport to the laboratory. The soil was rinsed from the baskets under water pressure and collected to determine the propagule densities. Roots in the baskets were also collected and treated as above for root density determinations. Results were expressed as milligrams of root per cubic centimeter of soil.

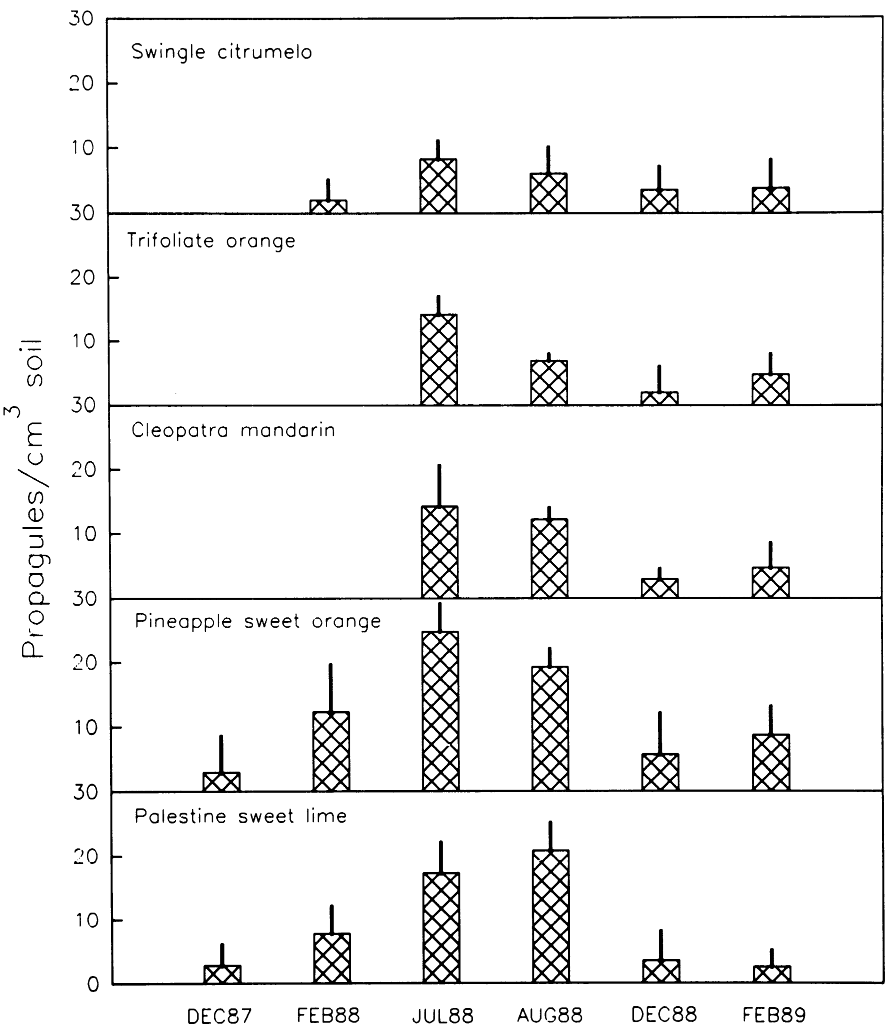

Fig. 1. Seasonal variation in populations of *Phytophthora parasitica* at the Avon Park citrus orchard from December 1987 to February 1989. The propagule density at each date is the mean of eight replications (four from fumigated and four from unfumigated plots treated preplant with methyl bromide) for indicated rootstocks. Lines on each bar represent standard deviations at each date.

Screenhouse experiment. Seedlings of Ridge Pineapple sweet orange, Cleopatra mandarin, Swingle citrumelo, sour orange (*C. aurantium* L.), and trifoliate orange were grown in a potting mix of peat-perlite (60-40, w/w) for 18 mo before use. Soil from the St. Cloud experiment was collected at five locations, thoroughly mixed, and used to fill 7.6-L plastic pots. Seedlings were rinsed free of potting medium, and one seedling was planted in each pot of field soil. Nine replications for each rootstock were used, and pots of field soil without seedlings were used for controls. Plants were arranged in a randomized complete block design and maintained in a screenhouse.

Soil samples for assessment of the number of propagules of *P. parasitica* were taken in four sectors around the seedling in each pot with an auger 2 cm in diameter. Propagule densities were determined as above. Samples for propagule determinations of *P. parasitica* were collected 1, 2, 3, 5, 6, and 8 mo after potting. At the end of the experiment, the root system of each seedling was recovered and divided into four transverse sections. The number of new root tips and the percentage of root rot were evaluated visually on 50 rootlets (10 cm in length) selected at random from each section. Total dry weight of the root system was determined.

RESULTS

***Phytophthora* spp.** The colonies that developed from the samples collected in this study all appeared to be characteristic of *P. parasitica.* No other species of *Phytophthora* was detected in any of the samples.

Avon Park. Rootstock influenced the number of propagules of *P. parasitica* per cubic centimeter of soil (Table 1). The average across all sampling dates was higher on Ridge Pineapple sweet orange than on Cleopatra mandarin, trifoliate orange, or Swingle citrumelo. Swingle citrumelo also had significantly lower levels than Palestine sweet lime. Root density of Ridge Pineapple sweet orange was significantly greater than that of Palestine sweet lime, but no other differences were observed in root densities among rootstocks.

Soil populations of *P. parasitica* in the Avon Park experiment were highest during the summer; propagule densities varied from overall means of 15.8 propagules per cubic centimeter of soil in July to only 3.6 propagules per cubic centimeter of soil in the winter (Fig. 1). The root dry weight increased in March, peaked during summer, and remained constant until December (*data not shown*).

As anticipated, there was no significant effect of fumigation 12 yr earlier on propagule densities at any individual sampling date nor when the overall means across sampling dates were considered (Table 1). Thus, for rootstock effects through the season, the means for each rootstock were averaged across fumigated and unfumigated treatments. Root dry weight density was significantly higher in the fumigated than in unfumigated plots across all rootstocks and sampling dates.

St. Cloud. The propagule densities of *P. parasitica* in soil and overall root weights were higher in the St. Cloud experiment than at Avon Park on all sample dates, but the seasonal variations were similar at the two sites (Table 1, Fig. 2).

Soil from Volkamer lemon and Palestine sweet lime had the highest overall propagule densities, with intermediate densities in the soils surrounding Cleopatra mandarin and trifoliate orange, and the lowest densities occurred around trees on Swingle citrumelo rootstock (Table 1). The populations of *P. parasitica* peaked in late spring or early summer, and the lowest propagule densities for all rootstocks occurred during the winter with values of two to six propagules per cubic centimeter of soil (Fig. 2).

Irrigation did not affect populations of *P. parasitica* at St. Cloud when sampling dates were analyzed separately. However, the overall mean was higher for the irrigated than for the unirrigated treatments across all sample dates and rootstocks (Table 1). There was a significant interaction for irrigation vs. rootstock treatments on only one sample date.

Root density was affected by rootstock

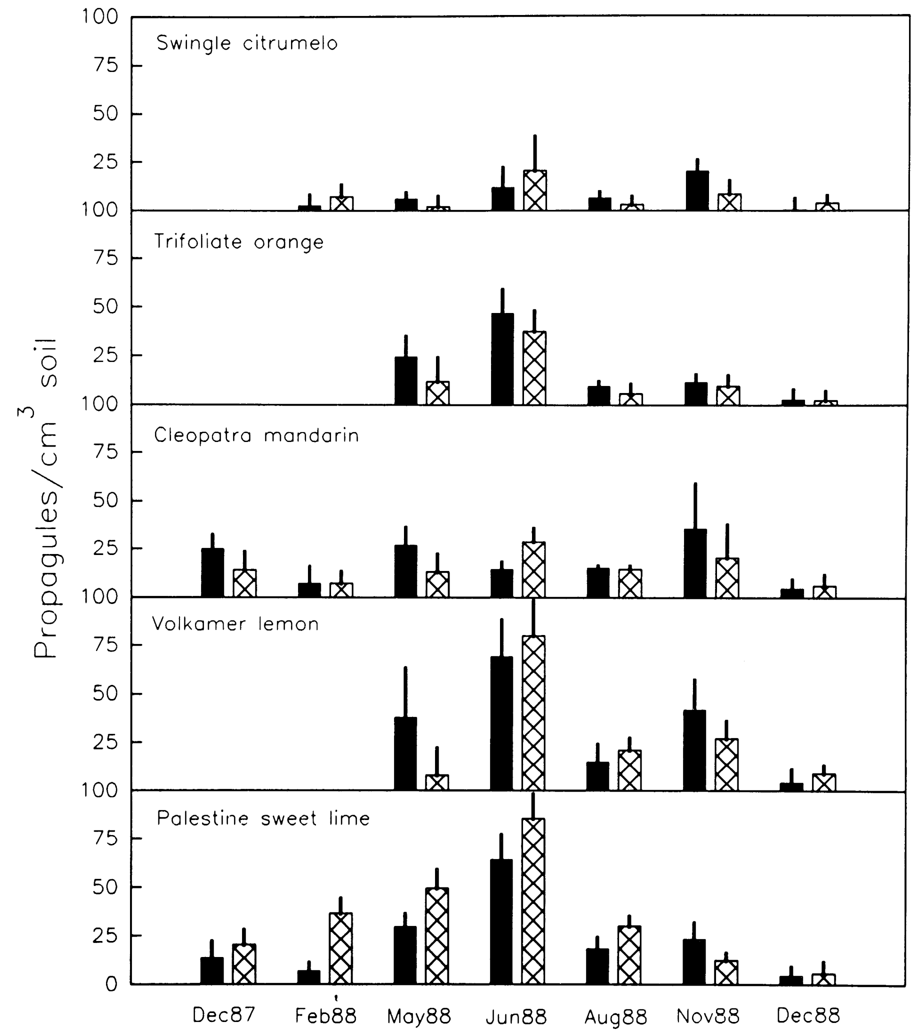

Fig. 2. Seasonal variation in soil populations of *Phytophthora parasitica* at the St. Cloud citrus orchard from December 1987 to December 1988. The propagule density for each date is the mean of eight soil samples per tree with four replications each for irrigated by microsprinklers (solid bars) and unirrigated treatments (cross-hatched bars) for the indicated rootstocks. Lines on each bar represent standard deviations at each date.

Table 2. Propagule densities of *Phytophthora parasitica* and root regeneration for five rootstocks measured in baskets of soil buried at the St. Cloud citrus orchard

Rootstocks	Root density in baskets[w] (mg/cm^3)	Propagules/cm^3 of soil in baskets[x]	Propagules/cm^3 of soil at random[y]
Swingle citrumelo	2.44 a[z]	74.0 a	14.4 bc
Palestine sweet lime	1.50 ab	38.3 ab	17.8 bc
Volkamer lemon	1.77 ab	53.7 ab	34.6 a
Trifoliate orange	1.50 ab	52.7 ab	10.6 c
Cleopatra mandarin	1.03 b	27.8 b	27.8 ab

[w] Mean root growth in four baskets per tree and three replications for each rootstock. Baskets were buried in the St. Cloud experiment from August through November 1988.
[x] Mean number of propagules in soil in baskets for each rootstock after 3 mo in the field.
[y] Mean of number of propagules in soil taken from around the tree for each rootstock at the regular sampling date in November.
[z] Mean separation in columns by Duncan's multiple range test, $P \leq 0.05$.

and irrigation treatments, but there was a great deal of variation among sample dates. Trifoliate orange had the lowest root density in this experiment. Mean fibrous root density was greatest during summer (2.4 mg/cm^3 of soil).

Relationship of propagule numbers to root density. If propagule densities were expressed on the basis of root weight rather than soil volume, the effect of rootstock on propagule density was not altered. The ranking of the rootstocks in St. Cloud and in Avon Park were the same with both means of expression, but there were fewer differences between means on a root weight basis. Root regeneration was measured as the weight of new roots that grew into baskets placed in holes made with the auger in the field. The differences among rootstocks were small (Table 2). Only Swingle citrumelo had a significantly greater root weight than Cleopatra mandarin. These new roots apparently resulted in an increase in the concentration of propagules of *P. parasitica* in the surrounding soil to more than four times that in the regular soil samples taken periodically from trees on Swingle citrumelo and trifoliate orange rootstocks. The root densities of all rootstocks and the number of propagules per cubic centimeter of soil were highly correlated ($r = 0.929$).

Screenhouse experiment. Among the potted rootstock seedlings, the propagule densities of *P. parasitica* in soil remained stable for about 2 mo after potting (Fig. 3). Subsequently, soil populations were higher for Ridge Pineapple sweet orange, sour orange, and, to a lesser extent, for Cleopatra mandarin. Populations of *P. parasitica* on these rootstocks remained high until the last sample date, 8 mo after planting. The number of propagules in soil where Swingle citrumelo and trifoliate orange seedlings were planted remained low through time. Populations in control pots without plants decreased after 2 mo. However, a few propagules per cubic centimeter of soil were recovered from these pots even after 8 mo in the screenhouse.

Containers with seedlings of Ridge Pineapple sweet orange and sour orange had the highest populations of *P. parasitica* in soil (Table 3). Average propagule densities with seedlings of trifoliate orange and Swingle citrumelo were not significantly higher than those in the unplanted control. Propagule numbers on Cleopatra mandarin were intermediate.

The percentage of root rot was also measured and the rootstocks were ranked in an order similar to that for propagule density in soil. Sweet orange had the most root rot, sour orange had less, and Cleopatra mandarin, trifoliate orange, and Swingle citrumelo had the least root rot. Ridge Pineapple sweet orange had fewer new root tips per rootlet than did all other rootstocks except sour orange. The rootstocks with the highest percentages of root rot and greatest number of propagules per cubic centimeter of soil had the lowest ability to regenerate new root tips.

DISCUSSION

In this study, significant differences were detected in numbers of propagules of *P. parasitica* per cubic centimeter of soil in samples from several rootstocks at two locations. The rootstocks that were considered most resistant to root rot in previous investigations (6), such as Swingle citrumelo and trifoliate orange, generally supported lower populations of *P. parasitica* in the field and screenhouse experiments than did rootstocks reported to be more susceptible. Although sour orange and Cleopatra mandarin are relatively tolerant to gummosis (15,17), they had high populations associated with them when compared with Swingle citrumelo and trifoliate orange.

On all sampling dates, propagule densities were consistently higher at the St. Cloud location than at Avon Park. Populations were higher in the screenhouse test than at either field site. The soils at St. Cloud have higher percentages of clay and organic matter and higher

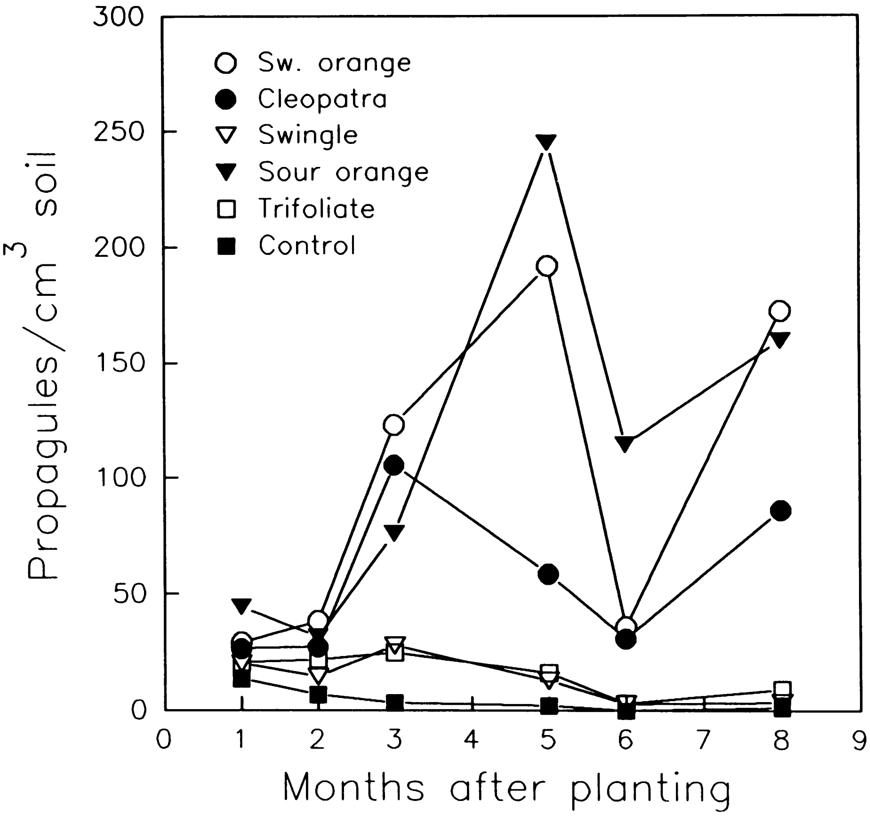

Fig. 3. Propagule densities of *Phytophthora parasitica* for five seedling rootstocks (Ridge Pineapple sweet orange, Cleopatra mandarin, Swingle citrumelo, sour orange, and trifoliate orange) and an unplanted control during an 8-mo screenhouse experiment from July 1988 (month 1) to February 1989 (month 8) in naturally infested soil collected from the St. Cloud rootstock experiment. Propagule densities at each sampling date are the mean of nine replications.

Table 3. Mean propagule densities of *Phytophthora parasitica* and percentage of root rot for five rootstocks and unplanted controls in the screenhouse experiment

Rootstocks	Propagules/cm^3 of soil[w]	Root density (mg/cm^3 of soil)[x]	Root rot (%)[xy]	New root tips/ rootlet (no.)[xy]
Pineapple sweet orange	102.2 a[z]	3.49 b	74.4 a	4.2 d
Sour orange	86.6 a	4.62 a	55.4 b	5.4 cd
Cleopatra mandarin	48.8 b	3.12 b	26.4 c	6.8 bc
Trifoliate orange	14.2 c	2.00 c	13.5 c	9.9 a
Swingle citrumelo	13.6 c	4.66 a	12.8 c	8.6 ab
Control	7.4 c	...	...	...

[w] Means for each rootstock and the control are the average of seven sampling dates with nine replications each from June 1988 through March 1989.

[x] Root measurements made at the end of the experiment in March 1989.

[y] Determined at the end of the experiment by separating the root system of each seedling into four sections and determining percentages of root rot and number of new root tips in 50 rootlets about 10 cm long for each section.

[z] Mean separation in columns by Duncan's multiple range test, $P \leq 0.05$.

cation exchange capacities than those at Avon Park (2). Greater water retention in St. Cloud soils could have promoted the higher populations of *P. parasitica* there. Moreover, average root densities across all sampling dates were greater at St. Cloud than at Avon Park. Sandler et al (14) suggested that high populations of *P. parasitica* may result from the presence of abundant fibrous roots, which provide substrate for multiplication of the pathogen. Thus, populations of *P. parasitica* also could have been higher at St. Cloud partially because of higher root densities. The high populations in the screenhouse experiment may have been attributable to conducive conditions such as frequent irrigation, higher soil temperatures, and higher root densities than in the field.

Any effect of preplant fumigation on *P. parasitica* populations was not apparent after 12 yr at Avon Park. Fumigated areas may be rapidly reinfested with *P. parasitica* when there is a nearby source of the fungus (13). Yield and tree size in this experiment were affected by fumigation only during the first few years (W. S. Castle, *personal communication*). Propagule densities were slightly higher in the irrigated than in the unirrigated plots at St. Cloud. This may have been attributable to more root rot occurring at higher moisture levels, but it could also have been attributable to the higher root densities under irrigation (Table 1), which provided more substrate for the fungus.

Soil populations of *Phytophthora* spp. associated with perennial plants may fluctuate with the season of the year (12). Higher propagule densities typically occur at times when environmental conditions are optimal for the formation of zoospores. In Florida, high optimum temperature and high rainfall during the summer season are conducive for growth and sporulation of *P. parasitica*, whereas lower populations should occur during the winter months under colder and drier soil conditions. Menge et al (11) found this type of seasonal effect on *P. parasitica* populations in studies carried out in California citrus orchards. However, Timmer et al (19) reported that propagule densities of *P. parasitica* were not related to the time of year, soil temperature, or soil water content at sampling time. Thus, if current temperature and soil water content do not affect the activity of *P. parasitica*, changes in populations of the pathogen are probably the result of the amount of root rot that occurred previously.

Root growth of Florida citrus trees occurs from February to November with most intense growth occurring when temperatures are above 27 C (3). The lower populations of *P. parasitica* during the winter in this study could have been related to the absence of new root tips or to dormancy of *P. parasitica* spores induced by low soil temperatures (10). Dormancy should not have been a factor because soil temperatures in Florida citrus orchards are seldom low and the preincubation period at room temperature used in this study should have allowed detection of most propagules (9,18).

The propagule densities in soil taken from the baskets buried near trees on Swingle citrumelo and trifoliate orange rootstocks were more than four times higher than those from undisturbed soil at the same sampling time. The number of propagules in the soil and the amount of new roots were highly related. Root tips and the region of elongation appear to be susceptible to *P. parasitica* on all rootstocks; even on resistant rootstocks, the pathogen can multiply readily when abundant new roots are present.

Under Florida conditions, most fibrous root rot probably occurs during summer and early fall when rainfall is abundant and temperatures are high. Propagules detected in soil assays probably persist for some time, thus, there is little effect of environmental conditions at specific sampling times on measured densities (19). In resistant species, only the highly susceptible root tips are rotted (4), and further invasion of the root cortex may be inhibited by phytoalexins or other inhibitory compounds (1). Thus, fewer propagules are produced on resistant stocks such as trifoliate orange and Swingle citrumelo and populations survive at only low levels. On susceptible sweet orange, root rot may be extensive at times and result in high populations when conditions are favorable, but propagule densities eventually diminish during extended unfavorable periods.

The use of fungicides such as metalaxyl and fosetyl-Al at the end of spring or early in the summer in conjunction with root flushes on susceptible rootstocks may minimize root disease. They may enhance formation of fibrous roots in susceptible rootstocks for better performance of the trees. In resistant rootstocks, however, the level of root rot was probably minimal even during the summer. Populations on the most resistant rootstocks, such as Swingle citrumelo and trifoliate orange, seldom reached the threshold levels suggested for fungicide treatment. Thus, orchards on these rootstocks should seldom, if ever, need to be treated with fungicides in Florida.

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