Colonization of Citrus Roots by Phytophthora citrophthora and P. parasitica in Daily Soil Temperature Fluctuations Between Favorable and Inhibitory Levels

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ABSTRACT

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Studies compared colonization of citrus rootlets by Phytophthora citrophthora or P. parasitica under constant favorable or inhibitory temperatures to root colonization under various daily combinations of favorable and inhibitory temperatures. Colonization of rough lemon rootlets after incubation for 96 h in the presence of soil naturally infested with P. citrophthora was detected at 9 through 27°C; however, the extent of colonization detected at 27°C was significantly lower than that observed at the other temperatures. In comparison, colonization of rootlets in the presence of soil naturally infested with P. parasitica was detected at constant incubation temperatures ranging from 12 to 33°C; however, the extent of colonization at 33°C was significantly lower than that observed at the other temperatures. Critical threshold temperatures, defined as thermal values at or above which colonization of rootlets was significantly restricted or prevented, were 27°C for P. citrophthora and 33°C for P. parasitica. After four consecutive 24-h periods, the magnitude of rootlet colonization by both pathogens was significantly less under incubation that included a daily time of at least 2.5 h at or above the threshold temperature when compared to rootlet colonization for 96 h at a constant favorable temperature. Significantly fewer sporangia were produced by P. citrophthora or P. parasitica at 24 h than after 48 and 72 h. The extent of root infection caused by P. citrophthora and P. parasitica at 24 or 30°C, respectively, was significantly lower at incubation periods of 4, 8, and 16 h than at periods of 24, 48, and 72 h. A fivefold increase in duration of zoospore motility was observed for P. citrophthora at 24°C than at 30°C, temperatures that respectively favor and prevent rootlet colonization; while an 11-fold increase was detected for zoospores of P. parasitica at favorable compared to inhibitory temperatures of 30 and 36°C, respectively. Temperature periods partially as well as entirely at or above the critical threshold values may reduce the degree of citrus rootlet colonization by P. citrophthora and P. parasitica by retarding the rate of sporangium formation and zoospore production and the duration of zoospore motility, compared to periods of equal duration that are entirely favorable for rootlet colonization. More efficient use of fungicides for control of Phytophthora root rot of citrus could be possible by application only when soil temperatures favor disease development.

Phytophthora citrophthora (R.E. Sm. & E.H. Sm.) Leonian and P. parasitica Dastur, which cause root rot and gummosis on citrus (4), have been isolated from orchards in Arizona. Infection of citrus usually is initiated by zoospores, which are released from sporangia when free water is available (18). Root disease is favored by abundant soil moisture, conducive soil temperatures, and the relative susceptibility of rootstocks to infection by the pathogen (4). One or more of these factors may be responsible for the high incidence of root rot in several Arizona citrus plantings.

Climate influences the development of all diseases caused by Phytophthora spp. (3). When soil moisture and temperature

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are favorable, production of sporangia and subsequent release of zoospores by P. citrophthora and P. parasitica can result in numerous new infections of citrus root and bark tissues. Temperature extremes limit disease development by direct effects on Phytophthora spp. in soil (2,5,20) or by reducing disease development on several plant genera (1,2,5,8,15,16,20,21). Additionally, temperature levels have been identified that inhibit or prevent sporangium production and infection of citrus roots (12). In this same study, soil temperatures that were recorded during certain times of the year in a citrus orchard in Yuma, Arizona, were at or above levels found to be inhibitory to sporulation and colonization of citrus roots by P. citrophthora and P. parasitica. Therefore, extreme temperatures may be useful indicators of periods of pathogen inactivity or arrested disease development and of periods when fungicides are not essential for disease control.

Temperature levels that prevent sporulation and infection of citrus roots by P. citrophthora or P. parasitica were identified under experimental conditions using constant temperature levels (12). In the field, however, temperatures fluctuate between values favorable or inhibitory to sporulation and disease development. The objectives of this study were: (i) to compare the colonization of citrus roots by P. citrophthora or P. parasitica under constant favorable or inhibitory temperatures to root colonization under various daily combinations of favorable or inhibitory temperatures; (ii) to determine the time required for sporangia formation and citrus root infection; (iii) to examine the effect of temperatures either favorable or inhibitory to sporangium formation and root colonization on the duration of zoospore motility; and (iv) to record temperatures within two citrus orchards at three different soil depths to determine possible periods of time when infection of roots by P. citrophthora or P. parasitica is not likely to occur. A preliminary account of this research was reported earlier (13).

MATERIALS AND METHODS

Colonization of rootlets at constant and variable temperatures. Twelvemonth-old seedlings of Citrus jambhiri Lush. (rough lemon) were removed from wooden flats and washed in tap water to remove potting mix adhering to the roots. Soil naturally infested with P. citrophthora or P. parasitica was collected from two different citrus orchards. A 100-cm³ volume of soil infested with either pathogen was placed into each of a series of 8-cmdiameter × 17-cm-deep plastic cups. For the constant temperature root colonization study, each of five cups containing soil infested with P. citrophthora was filled with 600 ml of distilled water adjusted to 6, 9, 12, 15, 18, 21, 24, 27, 28, or 30°C, while cups containing soil infested with P. parasitica were filled with water adjusted to 9, 12, 15, 18, 21, 24, 27, 30, 33, 34, and 36°C. A seedling was placed into each cup, and the stem was secured within a hole in each lid so that the roots were suspended in the water and did not touch the soil in the bottom of the cup. Five plants within cups containing soil infested with P. citrophthora or P. parasitica were maintained in illuminated incubators under a photosynthetic photon flux density (PPFD) of 53 to 74 µmol·m⁻²·s⁻¹ with a 12-h photoperiod at the test temperatures for 96 h. To determine the degree of root colonization by P. citrophthora and P. parasitica, 10 terminal rootlets about 1 cm in length from each seedling were dipped into 70% ethanol, dried on a paper towel, and plated onto pimaricin ampicillin rifampicin pentachloronitrobenzene (PARP) medium (9). The percentage of rootlets that yielded each pathogen was recorded for each incubation temperature.

For the root colonization tests using variable temperatures, cups containing 100 cm^3 of soil naturally infested with P. citrophthora were filled with 600 ml of distilled water adjusted to 30°C. After a rough lemon seedling was placed into each cup as described earlier, plants in cups were placed in an illuminated incubator set at 30°C. At various times, a group of five plants was transferred to an incubator set at 24°C, so that within a 24-h period, plants were incubated for 4, 8, 12, 16, or 20 h at 30°C and the remainder of the 24-h period at 24°C. This schedule was maintained for 96 h. Two additional groups of five plants were maintained at constant temperatures of 24 and 30°C for 96 h. The same procedures were used for the root colonization

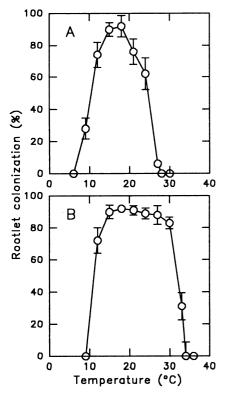


Fig. 1. Colonization of rootlets of Citrus jambhiri (rough lemon) at several constant temperatures after incubation for 96 h in the presence of soil naturally infested with (A) Phytophthora citrophthora or (B) P. parasitica. Each data point represents the average percentage of sampled rootlets per plant from which either pathogen was recovered. For each species of Phytophthora, data points are the means of two experiments, each of which contained five replicate plants per treatment. A square root transformation of the data was performed prior to analysis. Error bars represent 95% confidence intervals.

tests at variable temperatures involving soil naturally infested with *P. parasitica*, except that incubation temperatures were 30 and 36°C. At the end of the incubation period, 10 terminal rootlets from each plant were surface sterilized in 70% ethanol, then plated onto PARP medium for determination of the extent of root colonization by each pathogen. Each root colonization test was conducted twice.

Sporangium formation as a function of time. Two isolates each of *P. citrophthora* and *P. parasitica* collected from citrus orchards in Arizona were grown on V8 juice agar (14). After 5 days, 6-mm-diameter agar disks, which contained mycelia but no sporangia, were removed from the edge of an actively

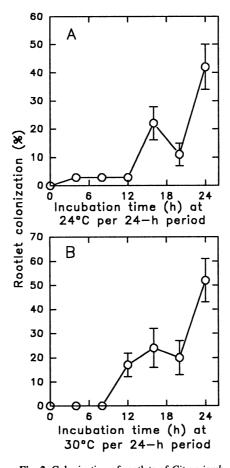


Fig. 2. Colonization of rootlets of Citrus jambhiri (rough lemon) after four consecutive 24-h periods under a series of daily temperature combinations, with one value (24 and 30°C for Phytophthora citrophthora and P. parasitica, respectively) favoring and one value (30 and 36°C for P. citrophthora and P. parasitica, respectively) preventing rootlet colonization under constant temperature conditions for 96 h. Each data point represents the average percentage of sampled rootlets per plant exposed to soil infested with (A) P. citrophthora or (B) P. parasitica from which either pathogen was recovered. For each species of Phytophthora, data points are the means of two experiments, each of which contained five replicate plants per treatment. A square root transformation of the data was performed prior to analysis. Error bars represent 95% confidence intervals.

growing culture and incubated separately in 7 ml of nonsterile soil extract within 60-mm-diameter plastic petri dishes (11) at 24 or 30°C for *P. citrophthora* or *P. parasitica*, respectively. After 4, 8, 12, 16, 20, 24, 48, and 72 h, five agar disks for each of the two isolates of each pathogen were examined, and all the sporangia were counted along the edge of each agar disk within one representative microscope field at 75×. This experiment was conducted twice.

Root colonization as a function of time. A 100-cm³ volume of naturally infested soil was placed into each of a series of 8-cm-diameter × 17-cm-deep plastic cups, followed by the addition of 600 ml of distilled water adjusted to 24 or 30°C for cups containing P. citrophthora or P. parasitica, respectively. A 12-month-old seedling of rough lemon was placed into each cup in the same manner as described earlier. Five plants within cups containing soil infested with P. citrophthora or P. parasitica were maintained in illuminated incubators under a PPFD of 53 to 74 µmol·m⁻ ²·s⁻¹ with a 12-h photoperiod at the test temperatures for 4, 8, 16, 20, 24, 48, or 72 h; 10 terminal rootlets from each plant were surface-sterilized in 70% ethanol, then plated onto PARP medium for determination of the extent of root colonization. This experiment was conducted twice.

Zoospore motility. The same two isolates each of P. citrophthora and P. parasitica used in the sporangium formation study were grown on V8 juice agar. After 5 days, three 6-mm-diameter agar disks were removed from the edge of an actively growing culture and incubated in 7 ml of nonsterile soil extract within a series of 60mm-diameter plastic petri dishes for 8 days at 24 or 30°C for P. citrophthora or P. parasitica, respectively. Sporangia that formed from the mycelium on the agar disks were induced to produce zoospores by incubation at 5°C for 20 min. Dishes containing sporangia and zoospores of P. citrophthora subsequently were incubated at 24 or 30°C, and those of P. parasitica were incubated at 30 or 36°C. Zoospore suspensions were observed regularly, and the duration of zoospore motility for each pathogen at each temperature was recorded. This experiment was conducted twice with four replicate determinations of zoospore motility for each species of Phytophthora for each trial.

Soil temperature. Soil temperatures were recorded during 1992 and 1993 in two commercial citrus orchards: a tangelo (Citrus reticulata Blanco × C. paradisi Macf. 'Orlando') planting established in 1968 in western Arizona (Yuma) and a navel orange (C. sinensis (L.) Osbeck) planting established in 1975 in central Arizona (Surprise). At each location, hourly soil temperatures were recorded under the tree canopy (in full shade) and south of the tree canopy (in full sun) using thermistor

probes (Ryan Instruments, Redmond, WA) buried in soil at 10, 30, and 60 cm.

Data analysis. Values obtained from each experiment were analyzed by analysis of variance (ANOVA). When appropriate, a square root or common logarithm transformation of data was used prior to analysis. When variances were homogeneous, a combined ANOVA was performed on pooled data from multiple runs of an experiment. All data were processed with the SigmaStat statistical software package (Jandel Scientific, San Rafael, CA). Error bars in figures represent 95% confidence intervals. Means with nonoverlapping 95% confidence intervals were considered significantly different (7). Student's t test was used to determine differences between zoospore motility values.

RESULTS

Colonization of rootlets at constant and variable temperatures. Colonization of rootlets of rough lemon by P. citrophthora was detected at constant incubation temperatures of 9, 12, 15, 18, 21, 24, and 27°C; however, the degree of colonization detected at 27°C was significantly lower than that observed at the other temperatures (Fig. 1A). No rootlet colonization was noted at 6, 28, or 30°C in soil infested with P. citrophthora. Colonization of rootlets of rough lemon by P. parasitica was detected at constant incubation temperatures of 12, 15, 18, 21, 24, 27, 30, and 33°C (Fig. 1B). Colonization was reduced significantly at 33°C compared to other tested temperatures where rootlet colonization was observed. No rootlet colonization was observed at 9, 34, and 36°C.

Colonization of rootlets of rough lemon incubated for four 24-h periods at a constant temperature of 24°C with soil containing P. citrophthora was significantly greater than that occurring when each 24-h period included incubation at 30°C for 4, 8, 12, 16, or 20 h or a constant incubation at 30°C, which reduced the incubation period at 24°C to 20, 16, 12, 8, 4, or 0 h, respectively (Fig. 2A). Rootlet colonization with daily incubation temperature combinations of 4 h at 24°C and 20 h at 30°C, 8 h at 24°C and 16 h at 30°C, and 12 h each at 24 and 30°C was significantly lower than that observed with daily temperature combinations of 16 h at 24°C and 8 h at 30°C, 20 h at 24°C and 4 h at 30°C, and a constant incubation at 24°C.

Colonization of rootlets incubated for four 24-h periods at a constant temperature of 30°C with soil containing *P. parasitica* was significantly greater than that occurring when each 24-h period included an incubation interval at 36°C for 4, 8, 12, 16, or 20 h or a constant incubation at 36°C, resulting in an incubation at 30°C for 20, 16, 12, 8, and 4, and 0 h, respectively (Fig. 2B). Rootlet colonization with daily incubation temperature combinations of 12 h each at 30 and 36°C, 16 h at 30°C and 8 h at 36°C, and 20 h at 30°C and 4 h at 36°C

was lower than that observed at a constant incubation of 30°C. No rootlet colonization resulted with a constant incubation period of 36°C or with daily incubation temperature combinations of 4 h at 30°C and 20 h at 36°C, or 8 h at 30°C and 16 h at 36°C.

When rough lemon seedlings were moved from a 24 to 30°C environment for soil infested with P. citrophthora or from 30 to 36°C for soil infested with P. parasitica, there was a 2.5-h lag until the soil water temperature reached the respective critical threshold temperatures of 27 or 33°C, which were identified as thermal values at or above which colonization of rootlets was significantly restricted compared to lower favorable levels. Likewise, when plants were moved from 30 to 24°C or from 36 to 30°C, there was a 1-h lag before the soil water temperatures dropped below the critical thresholds. Therefore, incubation periods of 4, 8, 12, 16, and 20 h at 30 or 36°C for rootlets exposed to P. citrophthora and P. parasitica, respectively, translate to actual rootlet exposure times of 2.5, 6.5, 10.5, 14.5, and 18.5 h at or above the respective critical thermal values.

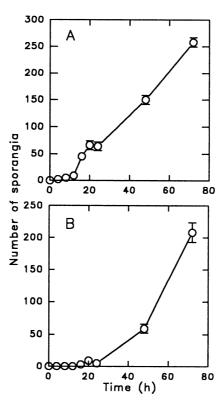


Fig. 3. Sporangium formation by (A) Phytophthora citrophthora and (B) P. parasitica on V8 juice agar disks incubated at 24 and 30°C, respectively, for various lengths of time. For each species of Phytophthora, data points represent the mean number of sporangia formed along the edge of each agar disk within one microscope field at 75× from two experiments. Five replicate counts of each of two isolates for a total of 10 replicate counts per incubation time period per experiment were used. A common logarithm transformation of the data was performed prior to analysis. Error bars represent 95% confidence intervals.

Sporangium formation as a function of time. Negligible production of sporangia occurred when V8 juice agar disks containing mycelia of *P. citrophthora* were incubated in nonsterile soil extract at 24°C for 4, 8, or 12 h. Increasing numbers of sporangia were formed as the time of incubation progressed from 16 to 72 h (Fig. 3A). Few sporangia of *P. parasitica* were formed after 24 h of incubation of pathogen mycelia in nonsterile soil extract at 30°C; however, significant production of sporangia was noted after 48- and 72-h incubation periods (Fig. 3B).

Root colonization as a function of time. In the presence of soil infested with *P. citrophthora* or *P. parasitica* at an incubation temperature of 24 or 30°C, respectively, less than 10% of rootlets of rough lemon seedlings were colonized by each pathogen after 4- and 8-h incubation periods. The extent of root infection caused by both pathogens was significantly lower at incubation periods of 4, 8, and 16 h compared to 24, 48, and 72 h (Fig. 4A and B).

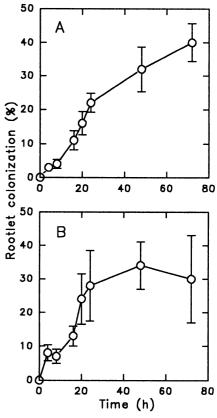


Fig. 4. Colonization of rootlets of Citrus jambhiri (rough lemon) after incubation in the presence of soil naturally infested with (A) Phytophthora citrophthora or (B) P. parasitica for various lengths of time at a temperature of 24 or 30°C, respectively. Each data point represents the average percentage of sampled rootlets per plant from which either pathogen was recovered. For each species of Phytophthora, data points are the means of two experiments, each of which contained five replicate plants per treatment. A square root transformation of the data was performed prior to analysis. Error bars represent 95% confidence intervals.

Zoospore motility. Zoospores of P. citrophthora incubated in a 1.5% soil extract at 24°C, which favors rootlet colonization, remained motile more than five times longer than those incubated at 30°C. which prevents colonization. Likewise, zoospores of P. parasitica incubated at 30°C, which favors rootlet colonization, remained motile more than 11 times longer than those incubated at 36°C, which prevents colonization by this pathogen (Table 1).

Soil temperature. For each site and soil depth, soil temperature profiles recorded in 1992 did not differ appreciably from those obtained in 1993; therefore, only temperatures for 1992 are shown (Fig. 5). For both years, the temperature of soil at depths of 10 and 30 cm exposed to full sunlight was at or above 27°C for ≥50% of the time in Yuma from May through October and in Surprise from June through September. For the same time and soil depths in full sunlight, soil temperature was at or above 30°C for ≥50% of the time in Yuma from June through September and in Surprise from July through September. In full sunlight, soil temperature in Yuma at or above 33°C for ≥50% of the time was recorded during various months from June through September, depending on soil depth and year. Soil temperature at or above 33°C for ≥50% of the time was not recorded in Yuma under the tree canopy in full shade or in Surprise in full sun or shade. As expected, the number of months during 1992 and 1993 when the percentage of hourly soil temperatures in Yuma and Surprise were at or above 27, 30, or 33°C for ≥50% or ≥90% of the time was always greater in soil exposed to full sunlight than in soil in full shade under the tree canopy. The number of months when hourly soil temperature readings at or above 27, 30, and 33°C occurred ≥50% or ≥90% of the time was consistently higher in the Yuma citrus planting, located in western Arizona, than in the Surprise orchard, 396 km away in central Arizona.

DISCUSSION

Earlier studies documented the effects of constant temperatures on growth (4) and

Table 1. Motility of zoospores of Phytophthora citrophthora and P. parasitica at temperatures found to be favorable or inhibitory to colonization of Citrus jambhiri (rough lemon) rootlets by each pathogen

Phytophthora species	Temp. (C)	Duration of motility (min)
P. citrophthora	24	527 a²
	30	100 b
P. parasitica	30	315 a
	36	25 b

² Each value represents the means of two experiments, with four replicate determinations of zoospore motility per experiment. For each species of Phytophthora, means followed by a different letter are significantly different (P =0.05) according to Student's t test.

sporulation of P. citrophthora and P. parasitica, as well as the development of gummosis and root rot on citrus (12). Similar effects of constant temperatures have been described for other species of Phytophthora in soil (2,20,21), as well as for the diseases caused by these pathogens (1,16,20). Critical threshold temperatures of 27°C for P. citrophthora and 33°C for P. parasitica have been identified as values at or above which colonization of roots in the presence of soil naturally infested with either pathogen either does not occur or is significantly reduced compared to optimum temperatures (Fig. 1). In the experimental procedures used to derive these temperatures, rootlets did not come into contact with infested soil but were maintained in the water covering the soil. Under these conditions, rootlet colonization may have resulted primarily from infections by zoospores; the critical threshold temperatures for each species of *Phytophthora* may affect sporangium formation and subsequent zoospore differentiation, release, and motility. In addition to sporangia and zoospores, chlamydospores of P. citrophthora and P. parasitica and oospores of P. parasitica may be found in orchard soils (10,17); however, these more persistent structures are considered important forms of primary inoculum (6) and alone are probably not responsible for rapid infection and disease development attributable to secondary inoculum, which includes sporangia and zoospores.

Alternating between favorable and unfavorable temperatures resulted in substantially less citrus rootlet colonization by P. citrophthora and P. parasitica than did a constant favorable temperature. A partial explanation may involve the production and activity of zoospores under a combination of favorable or inhibitory temperatures. Sporangium and subsequent zoospore production for each of these pathogens, as well as rootlet colonization, was a function of time (Figs. 3 and 4). When agar disks containing mycelia of P. citrophthora or P. parasitica were incubated at 24 or 30°C, respectively, significantly fewer sporangia developed after a 24-h incubation period than after incubation periods of 48 or 72 h. Likewise, colonization of rough lemon roots was significantly less in the presence of soil infested with either pathogen at incubation periods of 4, 8, and 16 h compared to 24, 48, and 72 h. Furthermore, the duration of motility for zoospores incubated at a temperature that prevented root colonization was reduced 80 and 90% for P. citrophthora and P. parasitica, respectively, compared to that at temperatures that favored rootlet colonization. A period of at least 2.5 h at a temperature that prevents rootlet colonization within each 24-h day may result in reduced levels of rootlet infection by reducing the duration of zoospore motility, which in turn diminishes the opportunity

for zoospores to contact and penetrate host tissue. Additionally, the presence of one or more time intervals at which the temperature prevents sporangium formation within a time favorable for sporangium production may act to retard the rate of sporangium development and maturation compared to a similar constant time interval that is always favorable.

In addition to the critical threshold temperatures of 27 and 33°C for citrus rootlet colonization by P. citrophthora and P. parasitica, respectively, another study (12) showed that incubation at or above 30°C significantly restricted development of cankers on excised sour orange root segments compared to incubation at 10, 15, 20, and 25°C for P. citrophthora and 20 and 25°C for P. parasitica. An examination of soil temperature data from two Arizona citrus plantings reveals that the duration of time at which the orchard soil was at or above these critical temperature levels was dependent on the particular site and the occurrence of shading, as well as soil depth. New or young citrus plantings, where the orchard floor is exposed to full sunlight and not shaded by the tree canopy, could receive the most benefit from resulting high soil temperatures during the warmest months of the year. On the other hand, as a citrus planting matures, the increased development of tree canopy and resultant increase in orchard floor shading would lead to lower soil temperatures, which may not restrict the activity of Phytophthora. Therefore, fungicide application for young trees should be performed with caution, when temperatures are favorable for disease development. Knowledge of critical threshold temperatures that restrict root colonization or canker development within host tissue, in addition to a record of soil temperatures in a particular citrus planting, could facilitate the development of a simple method for predicting times when pathogen activity and disease development are either probable or unlikely. Unfortunately, the accuracy of such a predictive procedure would be somewhat diminished by the fact that soil temperature generally decreases with soil depth, so that citrus rootlets at the 10-cm depth may be at or above the critical soil temperature for pathogen activity, while rootlets at a depth of ≥60 cm may be in soil at a temperature that favors pathogen activity. However, since a significantly higher quantity of citrus roots was found at a soil depth above 23 cm compared to the amount below this soil depth (19), a substantial portion of citrus rootlets may be at a soil depth where critical soil temperatures are met or exceeded and where useful predictions of pathogen activity and disease development are possible.

Significant reduction of rootlet colonization in a citrus planting can occur only if soil temperatures are maintained at or above the critical threshold value during and immediately after an irrigation or significant rainfall, when soil moisture is favorable for zoospore release, movement, and rootlet colonization. If irrigation or rainfall provides adequate soil

moisture and lowers soil temperature to a level favorable for sporangium formation and zoospore release and mobility for approximately 20 to 24 h or more, then rootlet colonization would be expected to proceed at normal or unrestricted levels.

Critical high-threshold thermal values have been identified at or above which rootlet colonization and canker formation

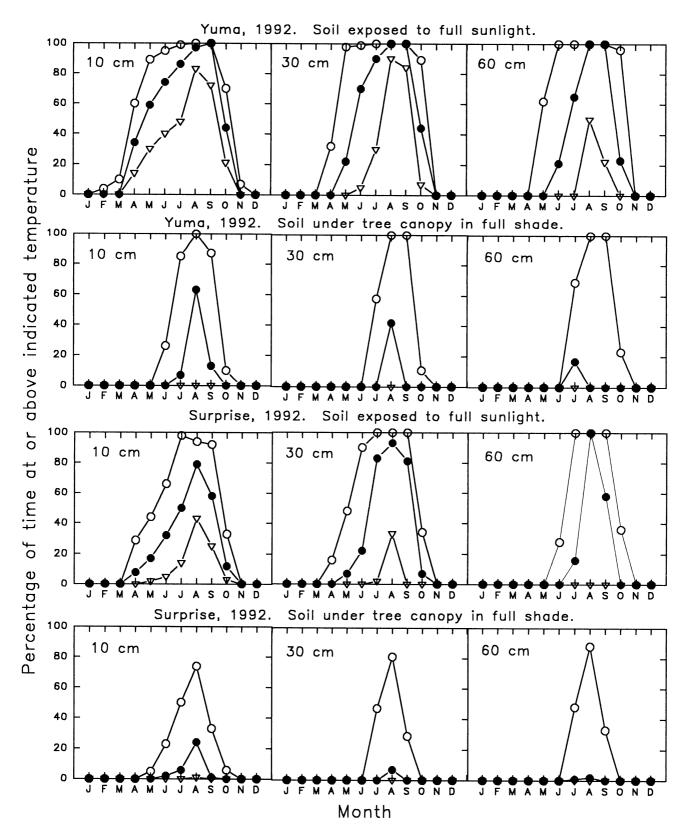


Fig. 5. Percentage of hourly temperatures per month during 1992 in a tangelo orchard in Yuma and a navel orange orchard in Surprise, Arizona, when temperatures for soil either exposed to full sunlight or shaded under the tree canopy were at or above 27°C (○), 30°C (●), or 33°C (▽), which are critical threshold temperatures at or above which rootlet colonization by Phytophthora citrophthora, canker development on roots inoculated with mycelia of P. citrophthora and P. parasitica, and rootlet colonization by P. parasitica were significantly restricted, respectively.

are significantly restricted compared to lower, more favorable temperatures for these components of disease development. These threshold values were met or surpassed for varying periods of time in two Arizona citrus plantings, depending upon the species of Phytophthora present, soil depth, geographical location, and degree of soil shading by the tree canopy. More efficient use of fungicides for control of Phytophthora root rot of citrus could be possible by having these materials in place only when soil temperatures favor disease development. A similar strategy may be feasible in regions where soil temperatures drop low enough in the winter to stop or substantially reduce pathogen activity.

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