

Effects of Temperature on Sporulation and Growth of *Phytophthora citrophthora* and *P. parasitica* and Development of Foot and Root Rot on Citrus

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ABSTRACT

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Abundant production of sporangia by *Phytophthora citrophthora* and *P. parasitica* occurred between 20 and 30 C. *P. citrophthora* was recovered from at least 50% of tested rootlets of *Citrus jambhiri* (rough lemon) plants incubated at temperatures of 10, 15, 20, and 25 C in the presence of preformed sporangia, whereas *P. parasitica* was recovered from at least 50% of tested rootlets at 15, 20, 25, and 30 C. Lowest recovery of either pathogen from rootlets of rough lemon occurred after incubation at 10 and 35 C for *P. parasitica* and 35 C for *P. citrophthora*. Maximum recovery from rootlets of rough lemon seedlings in the presence of soil naturally infested with *P. citrophthora* and *P. parasitica* was recorded at temperature ranges of 15–25 C and 15–30 C, respectively. Greatest growth of *P. citrophthora* on cornmeal agar (CMA) occurred at 25 C, whereas maximum development of lesions on stems of rough lemon or excised root pieces of *C. aurantium* (sour orange) inoculated with this pathogen was recorded at 10–20 or 20–25 C, respectively. Radial growth of *P. parasitica* on CMA was greatest at 30 C, whereas the largest lesions on stems of rough lemon or excised root segments of sour orange inoculated with this pathogen were recorded at 15–25 or 20–25 C, respectively. Soil temperatures that were recorded during certain times of the year in a citrus orchard in Yuma, Arizona, were found to be inhibitory to sporulation and growth of *P. citrophthora* and *P. parasitica* as well as development of lesions on citrus stem and root tissues in the laboratory.

Yearly losses of citrus trees and production, attributable to *Phytophthora* spp., occur in Arizona. *Phytophthora citrophthora* (R. E. Sm. & E. H. Sm.) Leonian and *P. parasitica* Dastur, which have been shown to cause foot and root rot, have been isolated from more than 85% of sampled citrus orchard sites in Arizona (24). Infection of citrus tissue usually occurs by zoospores, which are released from sporangia when free water is available (35). Within favorable ranges of moisture and temperature, 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.

Losses attributable to *Phytophthora* foot and root rot have been reduced through the use of fosetyl Al (Aliette, Rhone-Poulenc Ag Co., Research Triangle Park, NC) and metalaxyl (Ridomil, Ciba-Geigy Corp., Greensboro, NC) (4,6,15,27,31,34). A single application of either fungicide can provide protection from colonization by *P. citrophthora* and *P. parasitica* for 2–3 mo (19). However, to maximize economic disease control with these fungicides, applications should coincide with periods favorable for pathogen activity and disease development. Temporal fluctuations in the colonization of citrus root and stem tissues

by *P. citrophthora* and *P. parasitica* have been recorded (20,23). Climate influences the development of all diseases caused by *Phytophthora* spp. (5). Extremes of temperature have been shown to limit disease development by direct effects on *Phytophthora* spp. in soil (3,8,38) or by reducing infection or subsequent disease development on several plant genera (2,3,8,12,32,33,38,39). Thus, extreme temperatures may be useful indicators of periods of pathogen inactivity or arrested disease development when fungicide applications are not needed.

The objective of this study was to examine the influence of temperature on growth and sporulation of *P. citrophthora* and *P. parasitica* and the development of root rot and cankers on citrus tissue inoculated with these pathogens. Seasonal changes in soil temperature within a citrus orchard in Arizona also were recorded for determining periods when temperature may be inhibitory to pathogen and/or disease development. A partial account of this work was reported earlier (22).

MATERIALS AND METHODS

Fungi. Two isolates each of *P. citrophthora* (C161 and C224) and *P. parasitica* (C66 and C217) recovered from diseased citrus trees in Arizona were used in the laboratory and growth chamber studies.

Sporangium formation. Two isolates each of *P. citrophthora* and *P. parasitica* were grown on V8 juice agar (25). After 5 days, five 6-mm-diameter agar disks

were removed from the edge of an actively growing culture and incubated separately in nonsterile soil extract in 60-mm-diameter plastic petri dishes (18). After a 4-day incubation period at 10, 15, 20, 25, 30, or 35 C in darkness, each of the five agar disks was examined, and all the sporangia were counted along the edge of each agar disk within one representative microscopic field at 75 \times . This experiment was repeated once.

Colonization of rootlets in the presence of preformed sporangia. Seedlings of *Citrus jambhiri* Lush. (rough lemon) were grown in heat-pasteurized potting mix (45% peat/45% vermiculite/10% sand, v/v/v). Three-month-old seedlings were removed carefully from the potting mix, washed thoroughly in tap water to remove potting mix adhering to the roots, wrapped in moist towels, and incubated for 30 min at test temperatures. Temperature-adjusted plants were then placed into 8-cm-diameter \times 13-cm-deep plastic cups, each containing 400 ml of distilled water adjusted to 10, 15, 20, 25, 30, or 35 C. Each cup contained a single seedling of rough lemon with roots totally immersed in water. A total of five plants were inoculated with agar disks bearing sporangia of one of two isolates of *P. citrophthora* or *P. parasitica*; procedures described previously were followed (21). Briefly, isolates of *Phytophthora* were grown on V8, then 10 6-mm-diameter agar disks were removed from the edge of an actively growing culture and incubated in nonsterile soil extract in 60-mm-diameter plastic petri dishes. Numerous sporangia formed after incubation for 6 days at 24 C and subsequently were induced to release zoospores by being chilled for 15 min at 4 C. Immediately after being chilled, 10 agar disks bearing sporangia were added to each cup containing a plant. Plants within cups then were maintained in illuminated incubators (2,000 lux) with a 12-hr photoperiod at 10, 15, 20, 25, 30, or 35 C for 24 hr; the agar disks remained on the bottom of the cups during this time.

Inoculum was quantified by microscopically counting the number of sporangia that had formed on each of eight separate agar disks for each of the two isolates of *P. citrophthora* and *P. parasitica*. The final concentrations of sporangia during inoculation of plants were approximately 66 and 48 sporangia per

milliliter of water for *P. citrophthora* and *P. parasitica*, respectively.

After the 24-hr inoculation period, seedlings of rough lemon were removed from the containers, and the contents of each cup were decanted and replaced with distilled water at the appropriate temperature. Roots of inoculated plants were placed into the water in the cups and incubated for an additional 4 days at their original temperatures. To determine the degree of root colonization by *P. citrophthora* and *P. parasitica*, we plated 10 terminal rootlets from each plant onto PARP medium (14). The number of rootlets that yielded *P. citrophthora* and *P. parasitica* was recorded. The experiment was repeated once.

Colonization of rootlets in the presence of naturally infested soil. Fourteen-month-old seedlings of rough lemon were removed from potting mix and washed in tap water to remove potting mix adhering to the roots. Soil naturally infested with *P. citrophthora* or *P. parasitica* was collected during August and September 1991 from two different citrus orchards in Arizona. A 100-cc vol of soil infested with either pathogen was placed into each of a series of 8-cm-diameter \times 17-cm-deep cups. Each cup was filled with 600 ml of distilled water adjusted to 10, 15, 20, 25, 30, or 35 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 (2,000 lux) with a 12-hr photoperiod at 10, 15,

20, 25, 30, or 35 C for 96 hr; 10 terminal rootlets from each plant were then plated onto PARP medium for determination of the extent of root colonization by these pathogens. This experiment was repeated two times.

Mycelial growth on agar. Each of the two isolates of *P. citrophthora* and *P. parasitica* was grown in four replicate petri dishes containing CMA. Radial growth (in millimeters) was measured after a 4-day incubation period at 10, 15, 20, 25, 30, or 35 C. This experiment was repeated once.

Lesion development on stems of rough lemon seedlings. Each of the two isolates of *P. citrophthora* and *P. parasitica* was grown on V8 for 6 days at 24 C. To inoculate stems of 1-yr-old containerized rough lemon seedlings, we removed 6-mm-diameter agar disks from the edge of actively growing cultures and placed them directly into 6-mm-diameter wounds approximately 5 cm above the soil surface. Bark and phloem tissue were removed completely at the wound site, and cambium was exposed. The agar disk bearing the mycelium was placed on the exposed surface and wrapped with black plastic tape. The rough lemon seedlings were irrigated thoroughly, placed in large plastic bags to retard water loss, and maintained for 7 days at 10, 15, 20, 25, or 30 C in illuminated incubators (2,000 lux) with a 12-hr photoperiod. After this, we determined disease severity by measuring the length of the lesion that developed at the inoculation site. For each temperature, five replicate plants were inoculated with each of two isolates of *P. citrophthora* or *P. parasitica*. This experiment was repeated once.

Lesion development on excised stem

pieces of rough lemon and root pieces of sour orange. We compared excised stem tissue from rough lemon trees with intact stems described earlier to determine the validity of using excised tissue for studying the effect of temperature on lesion development on plants inoculated with *P. citrophthora* or *P. parasitica*. Excised stem tissue of rough lemon or excised root tissue of sour orange was inoculated with 6-mm-diameter agar disks from the edge of actively growing cultures that were placed directly into 6-mm-diameter wounds in the middle of stem or root segments 5–10 mm in diameter by 70 mm long. Inocula of *P. citrophthora* and *P. parasitica* were grown as described for intact stem inoculation of rough lemon plants. Excised stem pieces were collected from rough lemon trees on *C. macrophylla* P. J. Wester rootstock, whereas root tissue was collected from lemon trees (*C. limon* (L.) N. L. Burm. 'Lisbon') established on sour orange rootstock. Both plantings were established in 1972 at the Yuma Agricultural Center. Stem and root pieces were collected during October and November. We removed outer tissues completely at the wound site to an approximate depth of 1 mm to expose the cambium. Excised stem and root segments were incubated for 7 and 4 days, respectively, at 10, 15, 20, 25, or 30 C (and 35 C for root pieces only) in moist chambers; after which the lengths of resulting lesions were recorded.

Excised stems of rough lemon and root pieces of sour orange were not surface-sterilized before inoculation. Uninoculated controls were prepared by placing agar disks without mycelium into wounds on stem and root tissue. For each temperature, five excised stem pieces of rough lemon or root segments of sour orange were inoculated with each of two isolates of *P. citrophthora* or *P. parasitica*. These experiments were repeated once.

Soil temperatures. Soil temperatures at 8 a.m. and 5 p.m. were recorded daily from 1 January 1987 to 31 December 1988 at the 10 cm depth in a citrus orchard at the Yuma Agricultural Center. Temperatures were recorded at one site either under the dense canopy of a mature orchard or outside the tree canopy to the south of the planting.

Data analysis. Values obtained from each execution of an experiment were analyzed by analysis of variance (ANOVA). Homogeneity of variances between runs of an experiment as well as between values for each isolate of *P. citrophthora* and *P. parasitica* was determined by Bartlett's test. When variances were homogeneous, a combined ANOVA was performed on pooled data from all runs of an experiment. Duncan's multiple range test was used for determining differences between mean values. All data were processed with the

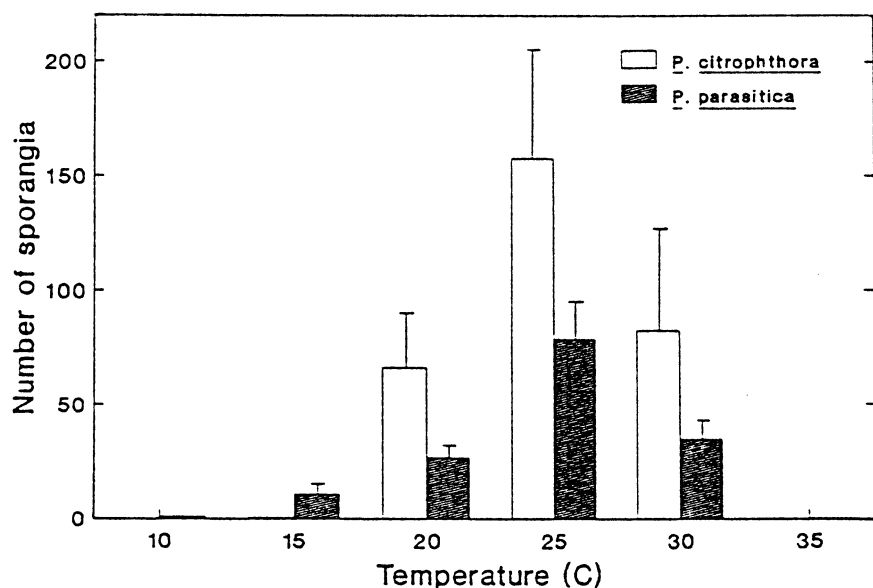


Fig. 1. Sporangium formation by *Phytophthora citrophthora* and *P. parasitica* on V8 juice agar disks incubated in soil extract for 96 hr at various temperatures. For each species of *Phytophthora*, bars represent the mean number of sporangia formed along the edge of each agar disk within one microscope field at 75 \times from two experiments; five replicate counts of each of two isolates for a total of 10 replicate counts per temperature per experiment were used. Vertical lines represent the upper half of 95% confidence levels.

MSTAT-C Statistical Software Package (Michigan State University) (26). The 95% confidence levels were developed according to methods described by Bailey (1) and Geng and Hills (9).

RESULTS

Sporangium formation. Abundant sporangia were produced by *P. citrophthora* and *P. parasitica* at 20, 25, and 30 C (Fig. 1). Only 8% of the total sporangia formed by *P. parasitica* under our test conditions were produced outside the 20–30 C temperature range, whereas no significant production of sporangia by *P. citrophthora* was observed outside the same range of temperature.

Colonization of rootlets in the presence of preformed sporangia. When rootlets of rough lemon were inoculated with zoospores produced from sporangia preformed at 24 C, *P. citrophthora* was isolated from at least 50% of the tested 1-cm-long terminal rootlets incubated at 10, 15, 20, and 25 C, whereas *P. parasitica* was isolated from at least 50% of terminal rootlets at 15, 20, 25, and 30 C (Fig. 2A). The lowest recovery of *P. citrophthora* occurred when plants were incubated at 35 C, whereas minimum recovery of *P. parasitica* was observed after inoculation at 10 and 35 C. In the presence of preformed sporangia of *P. citrophthora*, 94% of the total rootlets colonized occurred at 10–25 C, whereas 87% of rootlets colonized by *P. parasitica* occurred at treatment temperatures of 15–30 C.

Colonization of rootlets in the presence of naturally infested soil. Recovery of *P. citrophthora* occurred from rootlets of rough lemon incubated at 10, 15, 20, and 25 C in the presence of soil naturally infested with this pathogen, whereas *P. parasitica* was recovered from rootlets incubated in the presence of soil naturally infested with this pathogen at 15, 20, 25, 30, and 35 C (Fig. 2B). Maximum recovery of *P. citrophthora* from rootlets occurred at 15 and 20 C, whereas no significant difference in recovery of *P. parasitica* from rootlets was observed within the temperature range of 15–30 C. The degree of recovery of *P. parasitica* at 35 C was significantly less than that observed at 25 and 30 C. Of the total amount of rootlets from which *P. citrophthora* was recovered, 88% originated from treatments at 15, 20, and 25 C, whereas 94% of the rootlets from which *P. parasitica* was recovered were incubated between 15 and 30 C.

Mycelial growth on agar. The highest rates of growth for *P. citrophthora* and *P. parasitica* on CMA occurred at 25 and 30 C, respectively (Fig. 3). Appreciable growth by *P. parasitica* was observed at 35 C, whereas no growth by *P. citrophthora* was detected at the same temperature.

Lesion development on stems of rough lemon seedlings. Maximum development of lesions on stems of rough lemon seed-

lings inoculated with *P. citrophthora* was recorded at 10, 15, and 20 C, whereas maximum development of lesions on stems inoculated with *P. parasitica* was recorded at 15, 20, and 25 C (Fig. 4A). Of the total lesion length recorded on stems of rough lemon seedlings inoculated with *P. citrophthora* and incubated at 10–30 C, 88% occurred within 10–20 C. Eighty-six percent of the total lesion length recorded on stems of rough lemon inoculated with *P. parasitica* and incubated at 10–30 C occurred within 15–25 C.

Lesion development on excised stem pieces of rough lemon and root pieces of sour orange. Maximum development of lesions on excised stems of rough

lemon inoculated with *P. citrophthora* was recorded at 10, 15, and 20 C, whereas maximum growth of lesions on the same plant material inoculated with *P. parasitica* occurred at 15, 20, and 25 C (Fig. 4B). Of the total lesion length recorded on excised stems of rough lemon from 10–30 C, 83% occurred within 10–20 C on tissue inoculated with *P. citrophthora*, whereas 88% developed within 15–25 C when the pathogen was *P. parasitica*.

Larger lesions were observed at 15, 20, and 25 C than at all other incubation temperatures tested on excised sour orange root segments inoculated with *P. citrophthora*, whereas lesion growth on root tissue inoculated with *P. parasitica*

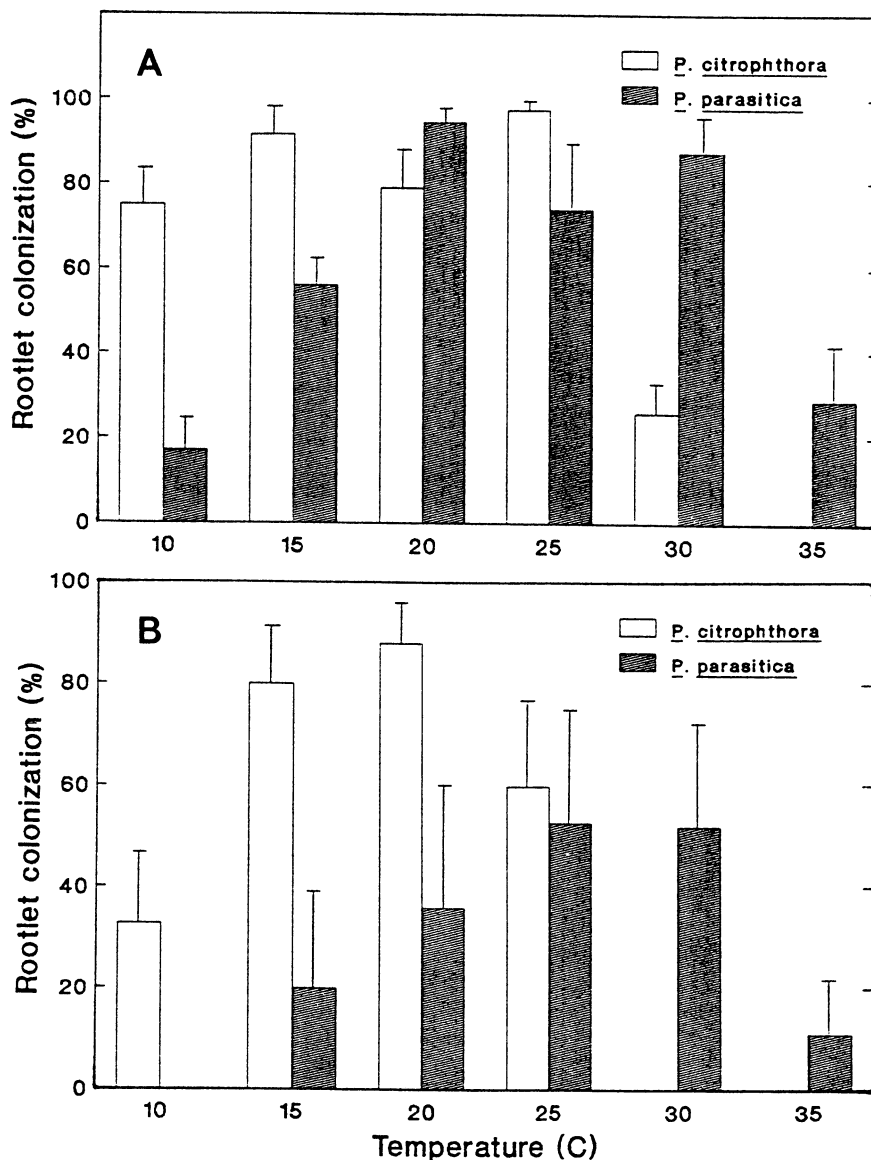


Fig. 2. Colonization of rootlets of *Citrus jambhiri* (rough lemon) at various temperatures (A) by zoospores from preformed sporangia of *Phytophthora citrophthora* and *P. parasitica* or (B) in the presence of soil naturally infested with these pathogens. Each bar represents the average percentage of sampled rootlets per plant from which either pathogen was recovered. In (A), for each species of *Phytophthora*, values are the means of two experiments; five replicate plants were inoculated with each of two isolates for a total of 10 replicate plants per treatment per experiment. In (B), values are the means of three experiments; five replicate plants per treatment per experiment were used. Vertical lines represent the upper half of 95% confidence levels.

was greater at 15, 20, 25, and 30 C than at other temperatures tested (Fig. 4C). Of total lesion length observed on excised roots of sour orange at 10–30 C, 89 and 85% occurred within 15–25 C on tissue inoculated with *P. citrophthora* and *P. parasitica*, respectively.

Soil temperatures. The mean temperatures recorded 10 cm below the soil surface in Yuma, Arizona, during the 24 mo in 1987 and 1988 in a mature citrus orchard either with a dense canopy or outside the tree canopy (exposed to full sunlight) are illustrated in Figure 5. The mean temperature of soil under a full tree canopy ranged from a low of 12.3 C in January to a maximum of 28.6 C in August, whereas the temperature of the soil at the same site outside the tree canopy ranged from a low of 12.7 C in January to a maximum of 33.9 C during July.

DISCUSSION

Temperature has a large influence on growth (7) and sporulation of *P. citrophthora* and *P. parasitica* and is an important physical factor that affects the development of *Phytophthora* foot and root rot. Similar effects of temperature on other species of *Phytophthora* in soil (3,38,39) as well as the diseases caused by these pathogens (2,12,33,38) have been described.

Of all the stages in the life cycle of soilborne species of *Phytophthora*, sporangium formation and resultant zoospore release provide the opportunity for an explosive increase in the numbers of infective propagules and increased disease (13). In our studies, no more than 1% of total sporangium production by *P. citrophthora* and *P. parasitica*

occurred below 15 or above 30 C. Although the studies focused on sporangia, they are not the only propagule of *Phytophthora* that is of concern in citrus orchards. In addition to sporangia and zoospore cysts, Lutz and Menge (16) found oospores and chlamydospores in citrus orchard soils containing *P. parasitica*. The effect of temperature on the activity of these propagules was not part of this study, because these more persistent structures are considered important forms of primary inoculum (10) and alone are probably not responsible for the rapid infection and disease development attributable to secondary inoculum, which includes sporangia and zoospores (5,36). Also, chlamydospores and oospores that persist in soil may form sporangia and zoospores upon germination (28,29).

Colonization of rough lemon rootlets by *P. citrophthora* and *P. parasitica* in the presence of preformed sporangia occurred to a higher degree over a broader temperature range than that observed when rootlets of seedlings were in the presence of naturally infested soil. Rootlets did not come into contact with the infested soil but were maintained in the water covering the soil; presumably, rootlet colonization resulted primarily from zoospore infections, which also occurred when rootlets were incubated in the presence of preformed sporangia. Perhaps the number of motile zoospores produced from pathogen propagules in the naturally infested soil was considerably lower than the concentration of zoospores originating from the preformed sporangia; this would result in decreased or undetectable levels of rootlet colonization at the lowest and

highest temperatures tested.

Significant formation of sporangia *in vitro* was limited to narrower ranges of temperature (20–30 C for *P. citrophthora* and 15–30 C for *P. parasitica*) than the temperature ranges in which infection of rootlets of rough lemon occurred, which presumably resulted from zoospores released from preformed sporangia (10–30 C for *P. citrophthora* and 10–35 C for *P. parasitica*) or from zoospores produced by pathogen propagules in naturally infested soil (10–25 C for *P. citrophthora* and 15–35 C for *P. parasitica*). Essentially no sporangia formed from agar disks bearing mycelium of *P. citrophthora* at 10, 15, or 35 C or *P. parasitica* at 10 or 35 C, whereas significant infection of rough lemon rootlets occurred in the presence of preformed sporangia of these pathogens at the same temperatures. Apparently, these temperatures inhibit sporangium formation but do not totally suppress zoospore motility and infectivity. On the other hand, abundant sporangia were produced by *P. citrophthora* at 30 C, whereas no colonization of rootlet tissue occurred at the same temperature in the presence of soil naturally infested with this pathogen. In this case, 30 C may have prevented indirect germination of sporangia to produce zoospores, thus, preventing colonization of rootlets (28).

The phrase “root colonization” as used in this paper refers to incipient invasion of citrus rootlet tissue by zoospores of *P. citrophthora* or *P. parasitica*. The continued development of root rot after the initial invasion of tissue is affected by the tolerance of the citrus rootstock to disease development. Tolerance in this sense is the condition in which plants are infected but show little or no net root loss, either because infected roots do not rot or because root mass is maintained by root regeneration (11).

In an earlier report documenting the effect of temperature on growth of *P. citrophthora* and *P. parasitica*, Fawcett (7) assumed that similar relationships would hold for growth of the pathogen in bark tissue. To the contrary, we found that temperatures associated with optimal or minimal lesion development on stems of rough lemon and root tissue of sour orange inoculated with *P. citrophthora* and *P. parasitica* did not correspond to temperatures associated with optimal or minimal radial growth of these pathogens on CMA. Temperature affects only the physiology of the pathogen when grown on CMA. On the other hand, the development of lesions on citrus tissue is the resultant, cumulative effect of temperature on the physiological processes of the pathogen as well as the host. Apparently, growth of *P. citrophthora* and *P. parasitica* at various temperatures on agar media offers no predictive value for the rate of lesion development on citrus tissue

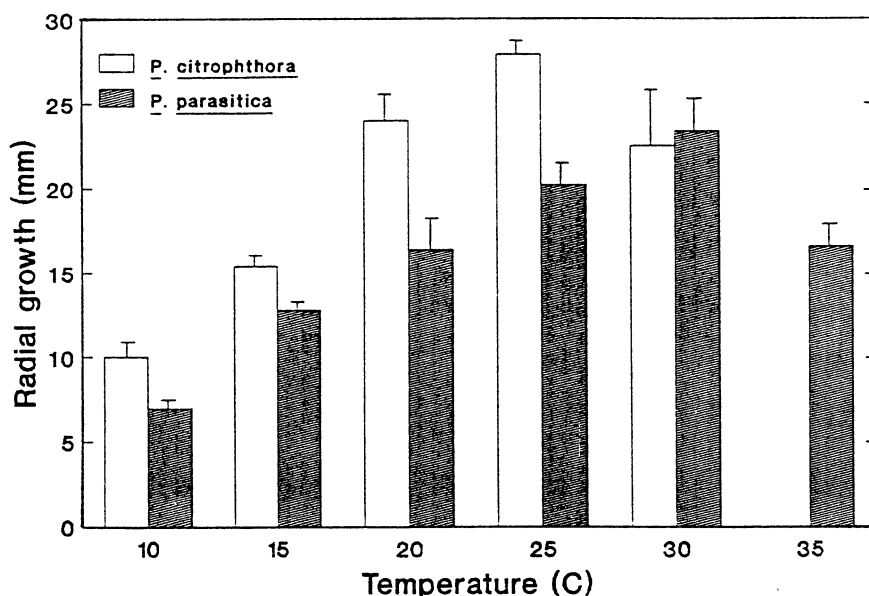


Fig. 3. Radial growth of *Phytophthora citrophthora* and *P. parasitica* on cornmeal agar after a 96-hr period of incubation at various temperatures. For each species of *Phytophthora*, bars represent the means of two experiments; four replicate plates of each of two isolates for a total of eight replicate plates per temperature per experiment were included. Vertical lines represent the upper half of 95% confidence levels.

caused by the same pathogens at the same temperatures.

Maximum lesion development on rough lemon seedlings was observed at 10, 15, and 20 C for stems inoculated with *P. citrophthora* and 15, 20, and 25 C for stems inoculated with *P. parasitica*. Similar results were recorded when excised stem tissue of rough lemon was inoculated. Evidently, excised stem tissue reacts similarly to intact stem tissue with respect to lesion development as a function of incubation temperature. Because intact root tissue was not available in a size that could be incubated in our temperature-controlled chambers, we inoculated excised sour orange root segments and assumed that excised material would react similarly to intact root tissue. One notable difference between lesion development on sour orange root and rough lemon stem pieces was that maximum lesion expansion on sour orange root segments inoculated with *P. citrophthora* occurred at 20 and 25 C, whereas maximum development on rough lemon stem pieces inoculated with the same pathogen was observed at 10, 15, and 20 C. These differences could be attributable to physiological variation between the two species of *Citrus* to colonization by *P. citrophthora* and resultant development of lesions or to physiological distinctions in root compared to stem tissue.

During some periods, temperatures recorded 10 cm below the soil surface in a citrus orchard in Yuma for two consecutive years were similar to those that suppressed sporangium formation by *P. citrophthora* and *P. parasitica* as well as colonization of rootlets and lesion development on citrus tissue by these pathogens. The time and duration of these inhibitory temperatures would depend on the age of the citrus planting, the normal yearly variations in temperature, as well as the identity of the species of *Phytophthora* present. In a newly planted citrus orchard, the absence of a well-developed leaf canopy could result in higher soil temperatures than those recorded in a mature orchard with a full leaf canopy that shades the orchard floor and moderates soil temperatures. Because rootlet colonization and lesion growth are at maximum and minimum levels at different ranges of temperature for *P. citrophthora* and *P. parasitica*, knowledge of whether one or both pathogens are in an orchard would be necessary before a determination could be made of time and duration of temperatures inhibitory to pathogen activity and disease development.

One concern about the use of soil temperature in predicting activity of soilborne plant pathogens is that this parameter changes with distance from the soil surface. The soil temperature at the 10 cm depth during the summer may inhibit sporulation of *P. citrophthora*

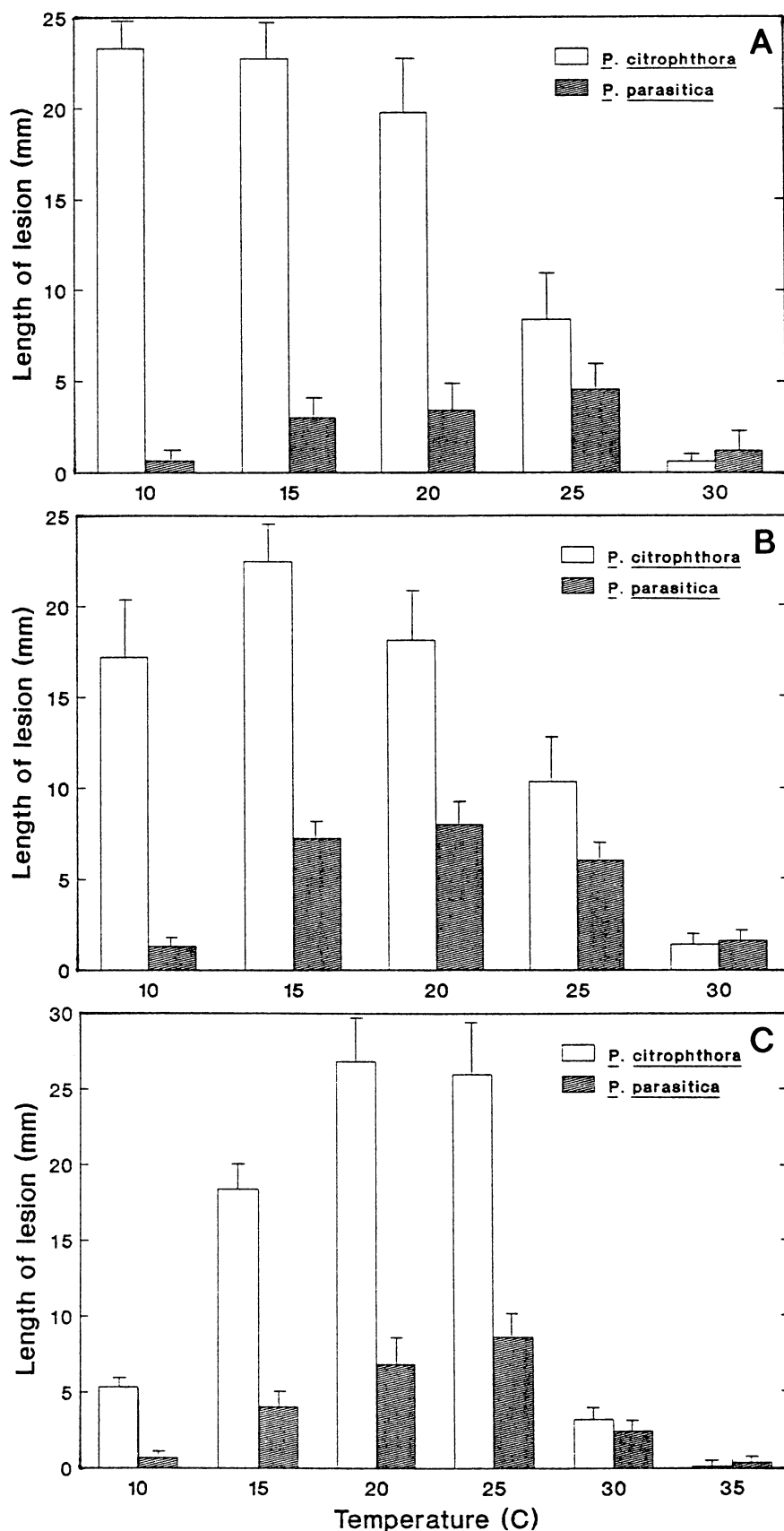


Fig. 4. Lesion development on (A) intact stems of *Citrus jambhiri* (rough lemon) seedlings or (B) excised stem segments of *C. jambhiri* and (C) excised root segments of *C. aurantium* (sour orange) 5–10 mm in diameter by 70 mm long wound-inoculated with an agar disk containing mycelium of *Phytophthora citrophthora* or *P. parasitica* and incubated for (C) 4 or (A,B) 7 days at various temperatures. Vertical lines represent the upper half of 95% confidence levels.

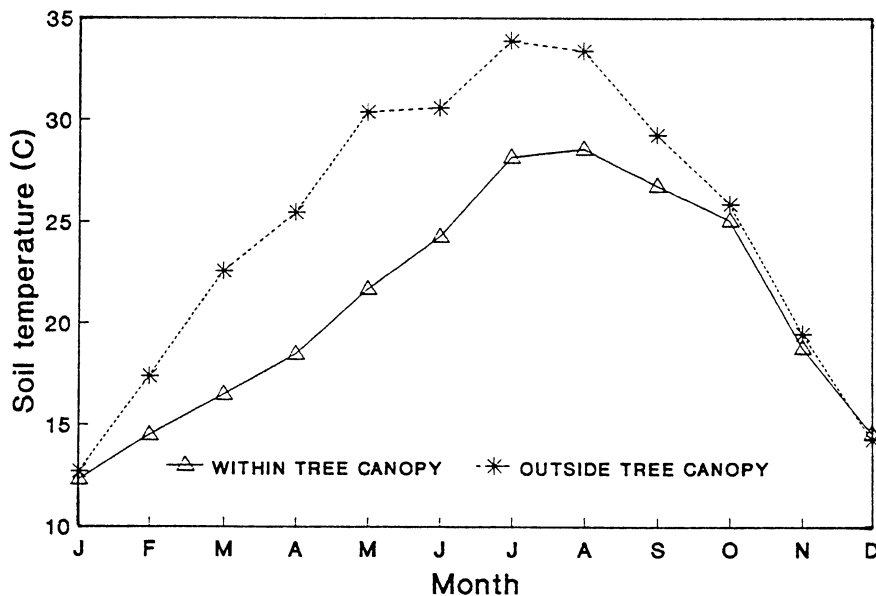


Fig. 5. Average soil temperature during 1987 and 1988 in Yuma, Arizona, 10 cm below the soil surface in a mature citrus orchard with a dense canopy or at the same depth outside the tree canopy.

and *P. parasitica* and resultant infection of rootlets, but the temperature at the 30–90 cm depth may be conducive to sporulation and disease development. Root density studies of Valencia orange trees (*C. sinensis* (L.) Osbeck) on rough lemon rootstock in Yuma County revealed that the highest density of roots was located between 0 and 30 cm below the soil surface (30), although roots were found to a depth of at least 120 cm. The utility of soil temperature as an indicator of pathogen activity or of potential development of root rot could be enhanced if the vertical distribution of the pathogens and roots of the target citrus rootstock as well as the temperature at various soil depths was known. Such studies are now in progress. However, ambient air temperature as well as the temperature of soil at the 10 cm depth should be useful in predicting periods of time when development of gummosis and foot rot is either unlikely or imminent.

The preliminary findings presented here suggest that the soil temperature could be used to time fungicide applications or other disease control measures so that they coincide with periods when the threat of sporulation by the pathogen and subsequent disease development is high. Suppressive temperatures may not occur in all regions where citrus is grown commercially but could be expected in areas subject to high summer temperatures as found in Arizona. To facilitate accurate timing of applications of fungicides or other disease control measures, more in-depth information is needed on the effect of alternate periods of favorable and unfavorable temperatures on subsequent sporulation and disease development. Population and growth of a pathogen are related more to the relative extent of favorable and unfavorable

temperatures than to the mean daily temperature (37). Germination of propagules of *P. parasitica* was correlated directly with accumulation of heat units from 0 to 150 degree-days (17). The heat unit concept also may be useful for predicting the onset of favorable periods for disease development in citrus orchards.

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