

Avocado Trunk Canker Disease Caused by *Phytophthora citricola*: Investigation of Factors Affecting Infection and Disease Development

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ABSTRACT

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Phytophthora citricola was able to cause stem canker of avocado only when inoculated into trunk or crown wounds. Neither intact bark nor lenticels on the crown or upper stem could be penetrated by *P. citricola*. While *P. citricola* infected and survived in the adventitious roots of avocado plants, it did not advance beyond the root base into the stem or woody root. Inoculum placed over cut wounds or injected under the bark on the crown or stem resulted in cankers in all cases. Avocado plants stressed by root pruning developed cankers more easily and at a greater rate than did nonstressed plants. The rate of disease development increased as the degree of stress increased. Younger plants were more easily predisposed to canker development by *P. citricola* than were older plants. Root pruning resulted in lower levels of soluble carbohydrates and higher levels of free amino compounds in the bark of avocado plants. Irrigation water sprayed on inoculation sites on avocado bark increased the rate of canker development more than sevenfold.

Avocado trunk canker disease, which is commonly known as 'citricola canker', is caused by *Phytophthora citricola* Sawada. This disease was first described by Fawcett (15) and Barrett (5). Subsequently, several reports have appeared in the literature redescribing the disease (22,40,41), but it was not until 1973 that Zentmyer et al identified the pathogen as *P. citricola* (42).

In recent years, *P. citricola* has caused increasing devastation in avocado (*Persea americana* Miller) groves throughout California (9,10). It affects the crown, lower trunk, and sometimes the main structural roots (10,43). The typical symptoms of the disease include bark cracking and exudation of white, sugary material, usually at the base of the trunk. Scraping the bark reveals a blackened, necrotic lesion in the inner bark and phloem which is usually confined to the

larger roots, crown, and trunk of the tree. In advanced stages, defoliation and twig dieback occur. If the canker encircles the trunk, the tree will die. *P. citricola* can be isolated from nearby soil, feeder roots, and cankers of infected avocado trees.

P. citricola has a wide host range, and in California it has been found to infect English walnut (*Juglans regia* L.), sweet cherry (*Prunus avium* (L.) L.), white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.), and red fir (*A. magnifica* Andr. Murray) (31). *P. citricola* also has been reported to cause root rot of black walnut (19), rhododendron fruit (20), strawberry root rot (28), and fruit rot of citrus (13) and guava (*Psidium guajava* L.) (24).

P. citricola readily produces thick-walled oospores in culture. It also produces sporangia which liberate motile zoospores. It is very likely that because of its ability to produce zoospores, *P. citricola* can establish itself in avocado groves or nurseries, and because of its abundant oospores it is very difficult to control. Oospores are the most resistant

spore structure produced by *Phytophthora* spp. and may survive in soil in absence of a host for more than one year (11).

Infection courts for various *Phytophthora* spp. may vary tremendously. Walmsley-Woodward et al (37) showed that *Phytophthora infestans* can invade potato tubers through lenticels and that, as the tubers develop, the lenticels gradually became more resistant to infection. Dale and Irwin (12) reported that stomata located beneath the cotyledons of 7-day-old chickpea seedlings were the preferential infection court for zoospores of *Phytophthora megasperma*. Also, they showed that zoospores which accumulated on the root hairs penetrated intercellularly between anticlinal epidermal cell walls. *P. citricola* invaded Fraser fir only after wounding by removing strips of bark in the hypocotyl region and/or by root pruning (35). Wounding also was necessary for consistent infection of avocado fruits by *P. citricola* regardless of the isolate used (31). *Phytophthora cinnamomi* apparently penetrates directly into avocado roots (2) and seedling eucalypti (36). It is of great concern in California that, while yield-damaging *P. citricola* cankers occur in less than 5% of the orchards, *P. citricola* is present and infects feeder roots in more than 20% of the avocado groves (10). The mechanisms responsible for canker formation in avocado are not yet fully understood.

Environmental stress usually increases susceptibility to diseases (33), and it is hypothesized that environmental stress may predispose avocado trees to citricola canker. Water stress is considered one of the main predisposing factors in plant diseases. Water stress does not result only from lack of water, but also from other factors such as root injury due to transplanting, root rot diseases, low temper-

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atures, salinity, and fertilizer damage. Kozłowski (25) reported excess transpiration over water absorption in transplanted trees even though soil moisture was near field capacity. This physiological shock during and after transplanting was found to be due to root injury (26). Schoeneweiss (33) used a root-pruning technique of white birch (*Betula alba*) seedlings to simulate root injury occurring during transplanting. Pruned and unpruned plants were inoculated with the stem canker fungus *Botryosphaeria dothidea*, and the water potential of the plants as well as fungus colonization were evaluated throughout a 16-day period. Results indicated that the predisposition of root-pruned white birch to stem canker was due to water stress. Water stress resulted in an increase of disease incidence and the length of canker formed on aspen inoculated with *Hypoxylon pruinaum* (3). In many cases, increased susceptibility of plants to attack by nonaggressive pathogens due to water stress can be a reversible process (32). Duniway (14) concluded that water stress was a significant predisposing factor in the root rot of safflower caused by *Phytophthora cryptogea*. Schoeneweiss (33) indicated that physiological processes which limit pathogen establishment are activated in plant tissues following pathogen invasion. These resistance mechanisms may be impaired by stress. Stress may also predispose avocado to citricola canker. In the field, citricola cankers appear to be associated with minisprinklers, which spray directly on the trunk.

The objectives of this study were to investigate the infection court for *P. citricola* in avocado trees and to examine factors such as root-pruning stress and the application of irrigation water directly on cankers that may affect disease incidence and canker development.

MATERIALS AND METHODS

Host and pathogen. Seedlings of *Persea americana* 'Topa Topa' were grown from seeds planted in a soil mix (UC no. 4) in plastic liners (6.5 × 12.5 cm) with perforated bases for drainage. After 6 wk of growth in the greenhouse at 24 ± 2 C, seedlings were transplanted into 4-L pots with the same soil mix. These seedlings were used in the following experiments.

Avocado plants produce adventitious root premordia under aerobic as well as anaerobic conditions. Three-month-old seedlings were placed in vermiculite medium with frequent irrigation for 1 mo. After the appearance of root premordia, the plants were carefully removed from the media and washed with water to expose adventitious roots. After inoculation of adventitious roots, plants were returned to the vermiculite medium.

Inoculum and inoculation techniques. The isolate used in the study, designated

as AA-1 (=cc-6), was originally obtained from a citricola canker on an avocado tree in Temecula, California. The stock culture was maintained on slants of V8C agar medium (per liter: V8 juice, 200 ml; CaCO₃, 2 g; agar, 15 g; deionized water, 800 ml) stored in the dark at 18 C.

Fresh cultures were grown on V8C agar plates and incubated at 24 C in the dark to establish uniform colonies. Avocado seedlings were inoculated, and the pathogen was reisolated monthly from colonized bark tissue to maintain its virulence.

Preparation of inoculum was as follows. Two culture plates of *P. citricola* on V8C agar were comminuted in 200 ml of sterile deionized water (SDW) for 30 sec with a Sorvall Omnimixer at medium speed. The temperature of the suspension was maintained below 20 C by immersing the blender cup in an ice bath. One milliliter of the minced mycelium was transferred to a 15-ml V8C liquid medium in a petri plate and incubated at 24 C for 3–4 days in the dark. Mycelial mats were washed three times (1 hr apart) with Chen-Zentmyer (C-Z) solution (8) and incubated in C-Z solution for 3 days. The plates were examined under a stereoscopic microscope for sporangial production. Four plates with heavy sporangial production were pooled, and the mycelial mats were washed with SDW, blended with 200 ml of SDW for 1 min, and kept at 4 C to be used in inoculation experiments.

A method was developed in which a small container of inoculum was attached to intact parts of the plant such as lenticels and unwounded areas of the stem. A small plastic tube (2 cm long and 0.5 cm wide) slanted from one end was used as an inoculum container. The slanted side of the tube was attached to the site of inoculation on the plant using chewed bubble gum, which was selected because it was not toxic to either avocado plants or *P. citricola* (Fig. 1). While attached to the site of inoculation, the tube was filled with an aqueous suspension of inoculum. More fresh inoculum was added every 2 days throughout the experiment to keep a continuous supply of inoculum on the inoculation site.

An injection technique was developed to deliver inoculum of *P. citricola* to specific sites on the avocado plants. Plastic sterile hypodermic syringes were filled with an aqueous suspension of inoculum. An aliquot (0.2 ml) of the inoculum was injected through the bark at the designated sites of inoculation. Two culture plates of the fungus bearing sporangia produced enough inocula for 1,000 injections.

A third method of inoculating avocado plants through wounds was also used in this study. Small wounds of the same size as plant lenticels were made in the bark with a sterile razor blade. The inoculum was applied to the wound area

using the attached container technique as described above. This technique insured a continuous source of inoculum limited to the wound site. To confirm that the developed cankers resulted from infection by *P. citricola*, samples taken from the canker tissues of infected plants were plated onto a selective medium, PARPH (per liter of corn meal agar medium: pimaricin (Delvocid), 0.02 g; ampicillin, 0.25 g; rifampicin, 0.01 g; pentachloronitrobenzene, 0.10 g; and hexazole, 0.075 g). Plates were incubated at 24 C in the dark. Disks of *P. citricola* on PARPH were subcultured on V8C agar medium plates and incubated at 24 C in the dark.

Infection-court study. All avocado plants used in this study were the same age (unless otherwise indicated) and were kept in the greenhouse under the same environmental conditions before and throughout the course of the experiment. Ten replicate avocado plants were used for each infection-court treatment. All sites tested were inoculated at the same time using one inoculum preparation. All experiments were repeated, and the combined results are described.

Lenticels located below the soil line, in the crown area, and in the upper stem area were inoculated with *P. citricola*. Inoculum was also applied to lenticel-free areas of the bark. To ensure continuous contact of the inoculum to the specific sites, the attached container technique was used as described above. Inoculum was kept in contact with the sites for 15 days.

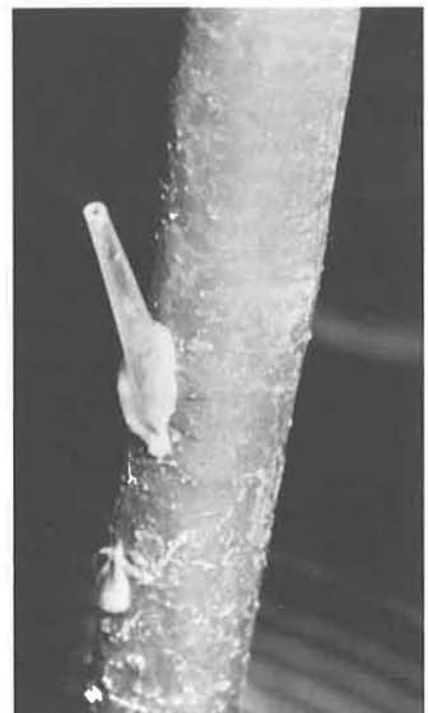


Fig. 1. The inoculum was inserted in a small plastic tube which was cut at an angle and attached with bubble gum adhesive to the site of inoculation on the stem.

To determine if wounding was necessary for infection, small wounds of the same size as the lenticels were introduced to the tested sites of the bark with a sterile razor blade. The inoculum was introduced and kept in contact with the wound site for 15 days using the attached container technique described above.

Root premordia also were tested as a possible infection court. Inoculum was applied to the root premordia and kept in contact with the inoculation site for 15 days using the attached container technique.

The injection method of inoculation was introduced to the plant on the crown and stem without wounding except for the needle hole resulting from the inoculum injection.

Avocado stems with heavy lenticel production were cut, and the ends were sealed with wax. The cuttings were then soaked in a water soluble stain solution (Toluidine blue 0.05%) for 24 hr under vacuum to determine whether the stain could penetrate the lenticels or surrounding areas.

The presence of cankers at the test sites indicated infection courts. All cankers were confirmed to be caused by *P. citricola* by isolation on agar media 15 days after inoculation.

Effect of stress on infection. Stressed plants were produced by a root-clipping technique. The experiment was carried out on 5-mo-old avocado plants and 10-mo-old plants. Each experiment was repeated twice. Either 25 or 50% of the roots were clipped to produce moderately and highly stressed plants, respectively. One day after root clipping, 12 replicate plants from each treatment and control plants were inoculated with *P. citricola* using the injection technique described above. Disease assessment was carried out 10, 20, 30, and 40 days from the time of inoculation by measuring the area of the expanding cankers in square centimeters. The rate of disease development (cm^2/day) was calculated. Treatment means were tested for differences by Fisher's least significant difference.

Table 1. Effect of root-pruning stress on the rate of canker development in Topa Topa avocado plants infected with *Phytophthora citricola*

Treatment	Area canker/day (cm^2)	
	5 ^w	10 ^w
Nonstressed (control)	0.14 a ^x	0.11 a
Moderately stressed ^y	1.07 b	0.86 b
Highly stressed ^z	2.36 c	1.36 c

^w Age of plant in months.

^x Values in each column followed by identical letters are not significantly different according to Waller-Duncan's *t* test ($P = 0.05$).

^y 25% Of the roots were pruned.

^z 50% Of the roots were pruned.

Effect of water mist on the inoculation site. Water spray from a microsprinkler system was directed toward inoculation sites on avocado stems. The system was attached to a timer set to spray water for about 3 sec every hour. Control plants were given a similar amount of water, but the spray was not directed at the inoculation site. The experiment was done using 10 plants per treatment and repeated twice. The water-spraying system started 5 days after inoculation, and the experiment lasted 30 days. Disease was assessed by measuring the canker area in square centimeters 10, 20, and 30 days from the time of inoculation. The rate of disease development (cm^2/day) was calculated.

Determination of total soluble carbohydrates and amino acids. Samples taken from the bark of the stressed avocado plants were chemically analyzed for total soluble carbohydrates and amino acids. Bark samples were cut into small pieces, treated with liquid nitrogen, ground, and air-dried. The dried samples were extracted with acetone in a Soxhlet apparatus to remove lipids and colored plant materials such as chlorophyll that might interfere with the chemical determinations. Two grams of the defatted samples were extracted with 200 ml of 80% (v/v) ethanol in a water bath at 100 C for 2 hr under a reflux condenser. The ethanol was removed by evaporation under vacuum, and the solution was adjusted to a known volume. Aliquots of the extract were used for soluble carbohydrate determination by the anthrone method as described by Allen et al (1). Results were calculated as milligram glucose equivalents per gram dry sample using glucose as a standard. The total amino compounds were determined in the same extract by the ninhydrin method as described by Fry (16). The results were calculated as milligram leucine equivalents per gram dry sample using the amino acid leucine as a standard.

RESULTS AND DISCUSSION

Lenticels located below the soil line, in the crown area, and in the upper stem, as well as lenticel-free areas of the bark of avocado plants, were not infected with *P. citricola* despite being in contact with inoculum for a 15-day period. The results were in agreement with Walmsley-Woodward et al (37), who indicated that development rendered the lenticels of potato tubers resistant to *P. infestans*. This suggests that *P. citricola* lacks the ability to penetrate the waxy cuticle of the bark and the structural barrier of the lenticels. These results were supported by the fact that the structure of lenticels and lenticel-free areas of the bark formed an impermeable barrier to stains in water.

Placing the inoculum of *P. citricola* on wounded areas or using the inoculum injection technique resulted in 100% infection of the avocado plants. These

results indicated that wounding was necessary for infection, as the pathogen was unable to penetrate unwounded areas of the plant. The results were in agreement with those reported by Ouimette et al (31), who found that wounding was necessary for consistent infection of avocado fruits by *P. citricola*, regardless of the isolate used. Shew and Benson (35) also showed that wounding by removing strips of the bark in the hypocotyl region and by root pruning was required for the infection of Fraser fir by *P. citricola*.

In avocado orchards, wounding the trunk, crown, or large roots should be avoided. Wounds are commonly created in the crown area of avocados by the removal of sucker shoots, and this may be a major infection court. Wounds created by removing sucker shoots should be covered by a protective fungicide. Since the disease could be transmitted by contaminated clippers (*unpublished observation*), it is advisable to disinfect cutting tools with alcohol or bleach after each cut. Other wounds which could result in *citricola* cankers include gopher and vole injury and staking wounds in young trees.

Adventitious roots inoculated with *P. citricola* using the attached inoculum container technique were killed, but the pathogen remained localized in the areas around the base of these roots without further movement. These results indicate that adventitious roots are probably not an infection court for the stem canker disease in avocado.

Root-pruned stressed plants in this study were designed to simulate plants in the field that could be vulnerable to infection by *P. citricola*. The rate of disease development over a 40-day period from the time of inoculation was significantly higher in stressed plants compared with nonstressed plants (Table 1). Highly stressed plants showed much higher rates of canker development than did moderately stressed plants over a 40-day period (Table 1). The rate of disease development was significantly higher ($P = 0.05$) in younger plants (5 mo) than in older plants (10 mo). Interestingly, canker size after 10 days was significantly lower (0.05) in the stressed plants than in the nonstressed plants (Fig. 2).

Plants 5 and 10 mo old showed the same response to root pruning, as shown by total soluble carbohydrates (TSC) and free amino acids (AA) evaluations. Results (Table 2) indicated that root-pruning stress resulted in an initial decrease in TSC and AA in the stem phloem. The limited colonization and necrosis accompanying the pathogen after 10 days could be attributed to unfavorable low levels of nutrients present in the phloem of the stressed plants (Table 2). Grainger (17,18) found that low disease potential could be correlated with low carbohydrate content, while high carbohydrate content was asso-

ciated with high disease potential. TSC increased in both stressed and non-stressed control plants at 40 days, but the stressed plants were still lower in TSC than the controls. The initial decrease in TSC and AA after root pruning could be explained on the basis of the "source-sink" concept described by Wareing and Patrick (38). The source-sink concept is now widely recognized as a vehicle for describing fluxes of materials from centers of production (sources) to centers of utilization (sinks) within the plants (27). Barlow and Boersma (4) and Bunce (7) also reported greater increase in soluble carbohydrates with stress in sink than in source leaves. The damaged roots may have attracted TSC and AA from the stem phloem, resulting in low levels of TSC and AA in the stem phloem at 1-10 days. The increase in TSC observed after 40 days (Table 2) in both control and root-pruned plants was consistent with the normal carbohydrate cycling reported in avocado trees by Scholefield et al (34) and Whiley et al (39). They demonstrated that carbohydrate levels were at their lowest after the summer vegetative flush and just prior to floral initiation in the autumn. Levels increased over winter during the period of floral development and reached maximum levels in early spring. The stress experiment in our study was started late in the autumn during the low carbohydrate period and continued into the winter during the high carbohydrate period. The stressed avocado plants showed a considerable degree of recovery 40 days after the root clipping. These results are in agreement with Hsiao (23), who noted that when maize was water stressed by cooling the roots, growth recovered gradually through accumulation of soluble carbohydrates.

On the other hand, in our study the total free amino acids increased dramatically in root-pruned plants compared to the control. Hsiao (23) reported that the total free amino acids were often increased in leaves if rather severe water stress lasted for several days, but proline showed the most pronounced rise. This dramatic rise during severe stress from initial low amino acid content takes place only when adequate carbohydrates are in the tissue, because they are the source of the carbon skeleton for many amino acids. Because carbohydrates are essential for amino acid synthesis, the increase of the total free amino acids in the stressed avocado plants was at the expense of the soluble carbohydrates in the phloem tissue. That explains the lower level of total soluble carbohydrates in the stressed avocado plants compared to the nonstressed.

Our results showed strong positive correlation between the content of amino acids and the rate of disease development. The rate of disease development and the total free amino acids were sig-

nificantly higher in root-pruned stressed plants compared to the control. These results are in agreement with those of Hoitink et al (21), who reported a significant linear correlation between nitrogen concentration in juvenile leaf tissue of rhododendron and susceptibility to *Phytophthora dieback*. At low (deficient) nitrogen concentrations, lesions remained tiny and the number of visible lesions produced was low. At higher nitrogen concentrations, lesions expanded, the number of lesions was high, and plants died (21). The increase in total amino

compounds in root-pruned stressed Topa Topa plants is similar to that reported by Nevin and Lovatt (29,30). They provided evidence that $\text{NH}_3\text{-NH}_4^+$ accumulates in avocado leaves in response to water deficit and low temperature stress. In a similar study by Schoeneweiss (33), European white birch (*B. alba*) seedlings were root pruned in a manner similar to that which occurs during field transplantation. Water potential measurements supported the idea that water stress is a main component of transplant shock. It was concluded that greater

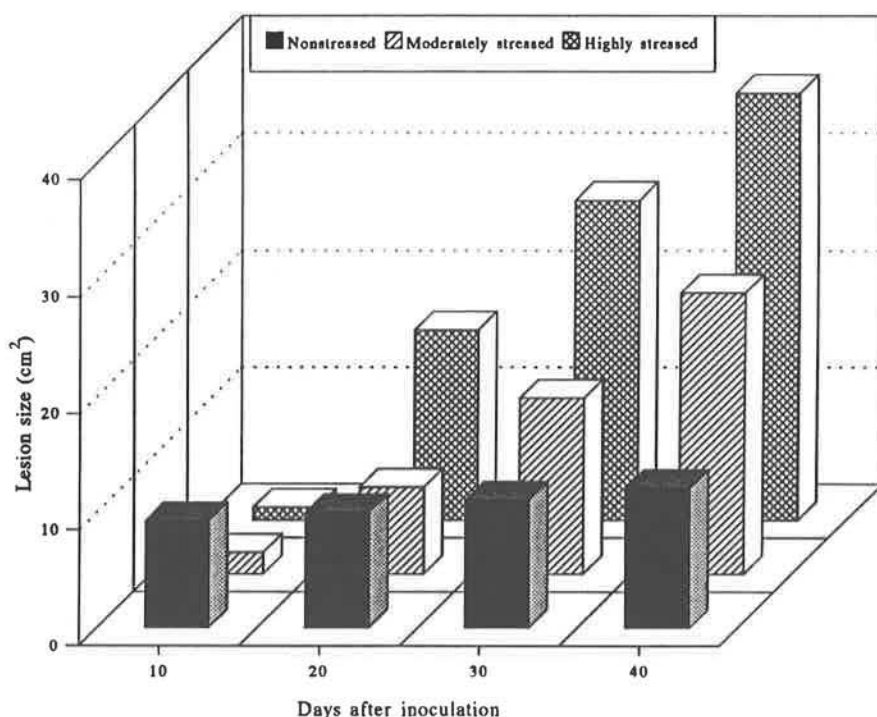


Fig. 2. Effect of root pruning stress on canker development caused by *Phytophthora citricola* on 10-mo-old avocado plants.

Table 2. Effect of root-pruning stress on total soluble carbohydrates and total soluble amino compounds in the phloem tissue of 5-mo-old Topa Topa avocado plants

Treatment	Total soluble carbohydrates (mg glucose/g dry wt)			Total amino compounds (mg leucine/g dry wt)		
	1 Day ^w	40 Days ^w	LSD (5%) ^x	1 Day ^w	40 Days ^w	LSD (5%) ^x
Control	21.30 ^y	145.5	20.7	2.82	0.53	0.60
Moderate pruning	8.15	120.7	10.3	0.53	0.92	0.49
Severe pruning	2.15	88.5	6.6	0.29	5.17	1.32
LSD (5%) ^z	2.75	17.16		0.48	1.00	

^w Days after pruning.

^x Used to compare values within rows.

^y Each value is the mean of two experiments with six replicate plants each.

^z Used to compare values within columns. Statistically, the results of total soluble carbohydrates and total amino compounds were treated separately.

Table 3. Effect of mist application onto inoculation site on disease development in Topa Topa avocado plants infected with *Phytophthora citricola*

Treatment	Lesion size (cm ²) ^y			
	10 Days ^z	20 Days	30 Days	Row LSD (5%)
Mist application	10.79	14.08	17.45	3.12
Control	1.87	2.2	2.70	1.02
Column LSD (5%)	1.95	2.3	2.47	

^y Each value is the mean of three experiments with 10 replicate plants each.

^z Days after inoculation.

moisture loss from root-pruned or transplanted plants was due to water adsorption from the roots by surrounding dry soil. The frequent association of stem canker and diebacks with transplanted plants suggests that disease predisposition due to water stress is a common occurrence.

A second mechanism by which root-pruning stress increases susceptibility of avocado plants to canker expansion may result from an impairment of normal host-defense mechanisms. Plants respond to pathogens in numerous ways that function to block, slow, or prevent the pathogen from its successful establishment or spread in host tissue (6). One effect of physiological stress which has been hypothesized following drought stress is interference with the biosynthesis of compounds involved in normal resistance reactions (33). Although root pruning is outside the norm of what plants would encounter in the field, the use of this technique has provided evidence that stress due to root damage would increase the susceptibility of avocado trees to invasion by *P. citricola*. Under field conditions, stress of avocado plants could be attributed to factors such as water deficiency, salinity, excess fertilization, low temperatures, or root-rot disease caused by *P. cinnamomi*. The root-rot disease affects about 60–75% of the acreage in southern California alone (10).

The sprinkler system used in avocado groves could be one of the main factors in enhancing canker development. It is observed frequently in the avocado groves with *P. citricola* cankers that water from the sprinkler system hits the trunks of the trees. Results from this study (Table 3) indicated that frequent exposure of the inoculation site to water enhanced the rate of canker development by more than sevenfold compared to the control. The depth of the canker into the phloem was also larger in the plants sprayed with water compared to the control. When irrigating avocado trees in the field, it would be advisable to prevent irrigation water from wetting the trunk to avoid canker development by *P. citricola*.

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