Infection Court and Factors Affecting the Expansion of Stem Canker of Avocado Caused by *Phytophthora citricola*

Z. A. EL-HAMALAWI, J. A. MENGE, and F. B. GUILLEMET, Department of Plant Pathology, University of California, Riverside 92521

ABSTRACT

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Stem wounds are the main infection court for *Phytophthora citricola* on avocado. *P. citricola* in cankers formed after inoculation of stem wounds or wounds caused by removal of suckers could move upward in the inner bark and cause infection of stem wounds above these inoculation sites. Inoculation of the root systems of either nurse seed plants or clonal rootstock plants with *P. citricola* caused infection to both root systems, but the pathogen did not move upward to the stems during the first 4 wk after inoculation. There was no direct transmission of *P. citricola* through the phloem from the infected stems of nurse seed plants to wounds made on the stems of clonal rootstock plants. *P. citricola* infected and survived in wound sites caused by removal of seed cotyledons without further advancement. *P. citricola* was isolated from healed-over cankers, but only when these cankers were scraped to reveal healthy stem tissue did *P. citricola* move into the phloem and infect distant wounds. Healed wounds and healed-over cankers were not susceptible to infection unless they were reinjured. *P. citricola* was isolated from the sugary exudate that emanated from cankers caused by *P. citricola*.

Avocado (*Persea americana* Miller) trunk canker disease caused by *Phytophthora citricola* Sawada has been found in every avocado-growing county in California. *P. citricola* causes collar rot both in mature trees and young nursery trees (8) and has great potential for limiting avocado production. *P. citricola* affects the crown, lower trunk, and sometimes the main structural roots of avocado trees (7,19). The fungus invades the host at or near the soil line and grows in the inner bark tissues causing a lesion. If the lesion is not arrested, it may encircle the tree and cause its death. In advanced stages, defoliation and twig dieback occur.

The mode of infection and the infection court most conducive for disease varies with different *Phytophthora* species. *P. infestans* invades potato tubers through young lenticels (16). Dale and Irwin (9) reported that stomata located below the cotyledons of 7-day-old chickpea seedlings are preferential infection courts for zoospores of *P. medicaginis*. Also, zoospores of *P. medicaginis* that accumulate on the root hairs of pea seedlings penetrate intercellularly between anticlinal epidermal cell walls. *P. cinnamomi* directly penetrates avocado roots (1,17,18) and eucalyptus seedlings (15). Nearly all cankers on almond trees caused by *P. syringae* are associated with pruning wounds (4).

Stem wounds are the main infection court on avocado trees for *P. citricola*, which causes trunk canker (11). Neither intact bark nor lenticels on the crown or upper stem of avocado plants are penetrated by the pathogen (11). *P. citricola* infects and survives in the adventitious roots of avocado plants without advancement beyond the root structure into the stem (11).

Many researchers have demonstrated that wounds become increasingly less susceptible to fungal pathogens with age (2,5,6,12). The disease incidence and severity in geranium cuttings caused by *Pythium ultimum* decreases as the period of time between wounding and inoculation increases (6). Pruning wounds on almond trees that initially are susceptible to infection by *P. syringae* become resistant to infection with time (10). Lignification and suberization around the bark wounds appear to be involved in resistance to canker-forming pathogens (3,10).

The objectives of our research were to evaluate: 1) the role of nurse seed plants in *P. citricola* transmission to the rootstock plant; 2) the effect of some cultural practices in avocado groves that cause wounds, such as sucker shoot removal and the accidental separation of seed cotyledons, on the susceptibility of avocado trees to *P. citricola*; 3) the susceptibility of aged wounds and healed-over cankers to infection by *P. citricola*; 4) the expansion of *P. citricola* cankers when further wounds are introduced above the cankers; and 5) the possible role of canker exudates in the spread of the stem canker pathogen.

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MATERIALS AND METHODS

Preparation of inoculum. The isolate of *P. citricola* used in this study (cc-6) was obtained from an infected avocado tree and is maintained in the culture collection, Department of Plant Pathology, University of California, Riverside. The stock culture was maintained on slants of V8C agar (Campbell V8 juice clarified by centrifugation, 200 ml/L; $CaCO_3$, 2 g/L; agar, 15 g/L; and deionized water, 800 ml/L) and stored in the dark at 18 C. Fresh cultures were grown in V8C agar dishes at 24 C in the dark to establish uniform colonies. *P. citricola* was reisolated monthly from the bark of diseased Topa Topa avocado plants to maintain its virulence, and the identity of *P. citricola* was confirmed microscopically using the revised key of Stamps et al (14).

Inoculation of wounds caused by removing sucker shoots and seed cotyledons with *P. citricola*. Plant material included 5-mo-old avocado plants of Thomas (commonly used clonal rootstock plant) and Lula (nurse seed plant) cultivars. Sucker shoots produced on Thomas rootstock plants were removed either by cutting above or below the soil line close to the stem or by the common field practice of tearing the sucker shoots off by hand below the soil line. Wounds were induced on Lula nurse seed plants by cutting off the seed cotyledons that usually remain attached for many months after the seeds germinate. In practice, seed cotyledons occasionally detach during transplanting.

To inoculate wounds resulting from sucker shoot and seed cotyledon removal, a plug of *P. citricola* culture grown on V8C agar for 5 days was placed on the wound and wrapped with Parafilm. The inoculation sites and adjacent tissues (the area below inoculation sites and above the roots and the stem area above inoculation sites) were examined for canker development 2 wk after inoculation. The presence of *P. citricola* was detected by isolation from inoculation sites and adjacent tissues on *Phytophthora*-selective PARPH medium (13). Treatments were evaluated on 10 replicate plants for each inoculation method in each experiment. Each experiment was repeated twice.

Inoculation of roots of nurse seed plants. Generally, in the commercial production of avocado trees, a rootstock scion is first grafted onto a nurse seedling, which results in root formation on the rootstock plant. A commercial avocado scion is then grafted onto the rootstock plant. At this point the nurse

seedling roots are usually removed with a girdling ring.

Clonal rootstock plants (cv. Thomas) attached to the nurse seed plants (cv. Lula), either with or without a girdling ring placed above the graft, were used. The roots of the nurse seed plants were dipped in an aqueous suspension of zoospores of *P. citricola* (1×10^6 spores per milliliter) for 24 h, rinsed with running water, and planted in pots. The inoculated root systems of nurse seed plants were either potted and irrigated separately from the rootstock plants (group 1, Fig. 1A), or the root systems of both nurse seed plants and rootstock plants were potted together, and the water was allowed to move freely between the two root systems (group 2, Fig. 1B).

Two weeks after inoculation the roots and stems of nurse seed plants and clonal rootstock plants were examined for disease incidence. Roots and stems of both nurse seed and rootstock plants were cut and plated on PARPH medium. In both groups, wounds were made on the stem of the root-inoculated nurse seed plant below the soil line and on the stem of the rootstock plant either at the soil line or 10 cm above it. Two weeks after inoculation wounds were examined for canker development, and bark samples were plated on PARPH medium. Ten replicate plants were used for each inoculation method in each experiment. Each experiment was repeated twice.

Inoculation of stems of nurse seed plants. Clonal rootstock plants (cv. Thomas) attached to the nurse seed plants (cv. Lula) either with or without a girdling ring placed above the graft were used in this study. The stem of the nurse seed plant was inoculated by removing a disk of the bark with a 4-mm-diameter cork borer to expose the cambium onto which a 4-mm agar plug of *P. citricola* was placed and wrapped firmly with Parafilm. The inoculation site was kept below the soil line. Wounds were made on the stem of the stem-inoculated nurse seed plant below the soil line (5 cm above the inoculation site) and on the stem of the rootstock either at the soil line or 10 cm above it. After 2 and 4 wk, all inoculation and wound sites were examined for canker development. Bark samples from all inoculation and wound sites on the rootstock and the nurse seed plant stems were evaluated for the presence of *P. citricola* on PARPH media. Ten replicate plants were used for each inoculation method in each experiment, and the experiment was repeated twice.

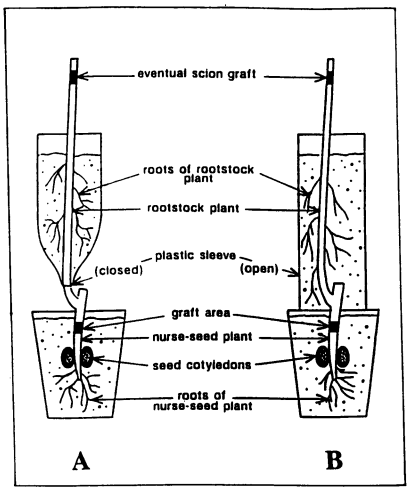

Fig. 1. Avocado nurse plant (cv. Lula) was grown from seed. A clonal rootstock (cv. Thomas) scion was grafted onto a nurse seedling. Root production was induced on the rootstock plant. Nurse seed plant roots were either left on the plant or removed with a girdling ring. **(A)** The root systems of nurse plant and rootstock plant were potted and irrigated separately. **(B)** The root systems of nurse seed plant and rootstock were potted and irrigated together.

Susceptibility of aged wounds and healed-over cankers to infection with *P. citricola*. Stems of 15-mo-old Topa Topa avocado plants were wounded at 50 cm above the soil line by removing a 2-cm-diameter disk from the bark with a cork borer to expose the cambium. The wounds were allowed to age for 4 mo. The susceptibility of aged wounds to infection with *P. citricola* was evaluated by placing a V8C agar plug (2 cm diameter) of *P. citricola* on the wound scar, followed by spraying with distilled water and wrapping with Parafilm. Fresh wounds made at the same position on a similar group of plants also were inoculated at the same time and used as positive controls. Wound susceptibility to infection by *P. citricola* was evaluated 2 wk after inoculation.

Similarly, 6-mo-old, healed-over (inactive) cankers on Topa Topa avocado plants were inoculated with either a culture plug of *P. citricola* or a fungus-free agar plug moistened with water spray and wrapped with Parafilm. Healed-over (inactive) cankers on Topa Topa avocado plants were revived by scraping the borders of cankers and removing a 2- 3-mm ring of the bark surrounding the old canker but were not reinoculated. The expansion of the old canker was assessed 2 wk after the treatment. The presence of *P. citricola* in all healed-over (inactive) cankers was tested by isolation on PARPH medium. Ten replicate plants were used in each experiment. Each experiment was repeated twice.

Effect of distant wounding above active and inactive cankers on disease development. The outer layer of the bark of 8- and 15-mo-old Topa Topa plants was cut with a razor blade 10–15 cm (distant wounding) above active as well as healed-over (inactive) cankers. *P. citricola* inoculum was not introduced onto the wounds. Preexisting cankers as well as the new wounds were examined daily for canker expansion or development. Two weeks after wounding, samples were taken from preexisting cankers, new wound sites, and the green area in between them and tested for the presence of *P. citricola* by plating on PARPH media. Samples taken from distant nonwounded areas above active as well as inactive cankers of control plants also were tested for the presence of *P. citricola*. Ten replicate plants were used for each inoculation method in each experiment. Each experiment was repeated twice.

Isolation of *P. citricola* from the sugary exudate of stem canker disease. The liquid or powdery, dry sugary exudate usually produced at the stem canker site caused by infection with *P. citricola* was collected. Droplets of the liquid exudate or 0.1-g portions of the dry exudate were plated on PARPH agar medium and incubated at 25 C. Fungal growth was examined microscopically, and the fungus was subcultured on V8C agar. Resultant cultures were used to inoculate *Persea indica* plants. Isolations made from the exudate and the subsequent cankers were examined microscopically to determine the presence and identity of *P. citricola* (14).

RESULTS

Sucker shoot and cotyledon removal sites as infection courts. Wounds caused by removal of sucker shoots on Thomas rootstock plants became infected with *P.*

Table 1. Evaluation of wounds resulting from sucker and seed cotyledon removal from avocado plants as courts of infection of *Phytophthora citricola*

Wound site	Canker[a]	*P. citricola*[b]
Sucker removal		
Inoculation site[c]	+	+
Area between inoculation site and roots	+	+
Stem above inoculation site	+	+
Seed cotyledon removal		
Inoculation site[c]	+	+
Area between inoculation site and roots	−	−
Stem above inoculation site	−	−

[a] Inoculation sites were examined for canker development 2 wk after inoculation.
[b] The presence of *P. citricola* was tested by isolation on selective PARPH (13) medium: + = presence of canker or fungus in all 30 replicate samples tested; − = absence of canker or fungus in all 30 replicate samples tested.
[c] A V8C agar plug of *P. citricola* culture was placed on wound caused by the removal of either suckers or seed cotyledons, sprayed with water, and wrapped with Parafilm.

citricola in all cases. The canker expanded from the inoculation site upward onto the stem and downward into the area between inoculation site and roots of the avocado plant (Table 1). Small brown lesions appeared on Lula nurse seed plants at the inoculated sites where the seed cotyledons had been removed, but *P. citricola* did not progress upward onto the stem or downward between the inoculation site and roots. Isolation from all symptomatic sites tested positive for the presence of *P. citricola* (Table 1). Isolations from the region between the root and the inoculation site yielded *P. citricola* only where sucker shoots had been removed (Table 1).

Role of nurse seed plants in infection of clonal rootstock plants by *P. citricola*. Necrotic lesions developed on feeder roots and wounds on the stems of only nurse seed plants after inoculation of nurse seed plant roots with *P. citricola* when roots of nurse seed plants and rootstock plants were potted and irrigated separately (Table 2). Symptoms did not develop on either feeder roots or stems of clonal rootstock plants. *P. citricola* was not recovered from the feeder roots of rootstock plants or from stems of both nurse seed and rootstock plants but was recovered from infected feeder roots and wounded stems of the nurse seed plants. Wounds made on the stems of the rootstock plants at the soil line or 10 cm above did not develop into cankers, and *P. citricola* was not recovered from the wounds when feeder roots of the nurse seed plants were inoculated with *P. citricola* (Table 2).

Feeder roots of both plants were infected when roots of nurse seed plants were inoculated and potted with the roots of rootstock plants. Despite the fact that the feeder roots of the nurse seed and the rootstock plants were infected with *P. citricola*, cankers did not form on the stems of either plant. *P. citricola* was not recovered from the bark of the stems of both nurse and rootstock plants even though roots were infected. Wounds made on the stems of root-inoculated nurse seed plants (below the soil line) and rootstock plants (at the soil line) became infected with *P. citricola*; however, there was no sign of infection, and *P. citricola* was not recovered from wounds located 10 cm above the soil line (Table 2).

The effect of inoculation of the stems of nurse seed plants on the transmission of *P. citricola* to the rootstock plant either when root systems were potted and irrigated together or separately is given in Table 3. Restricted necrotic lesions developed around the inoculation sites on the stems of nurse seed plants beneath the soil line, and *P. citricola* was recovered after 2 wk of inoculation. *P. citricola*, however, was not recovered from the stem of the rootstock plant either in the presence or absence of girdling rings below the graft union between the nurse seed plant and the rootstock plant. Wounds made on the stem of the rootstock plant at the soil line became infected with the fungus, but no infection occurred, and *P. citricola* was not recovered from wounds located 10 cm above the soil line.

Evaluation of aged wounds and healed-over cankers as courts of infection. Placing V8C agar plugs of *P. citricola* on aged wounds did not result in pathogen colonization of the bark, and *P. citricola* was not recovered from these aged wounds after inoculation. Four-month-old healed wounds were resistant to infection by *P. citricola*. Healed-over (inactive) cankers (6-mo-old) covered with a fungus-free agar plug and sprayed with water to maintain a high level of moisture did not result in canker revitalization. Inoculation of inactive, intact cankers with *P. citricola* did not reactivate canker development. Scraping of inactive cankers resulted in reactivation and expansion of the canker to new areas of the bark. *P. citricola* isolated on PARPH medium confirmed the presence and viability of the fungus in the inner layers of the previously inactive, healed-over cankers (Table 4).

Effect of distant wounding above active and inactive cankers on disease development. Cankers developed on wounds introduced 10–15 cm from pre-existing active cankers, but no cankers developed in wounds that were introduced distant from healed-over (inactive)

Table 2. Effect of inoculation[a] nurse seed plant roots with *Phytophthora citricola* on pathogen transmission to clonal rootstock plant

Site tested	Canker[b]	*P. citricola*[c]
Separate potting and irrigation		
Roots of nurse seed plant	+	+
Roots of rootstock plant	−	−
Stem of nurse seed plant	−	−
Wound on stem of nurse seed plant under soil line	+	+
Stem of rootstock plant	−	−
Wound on stem of rootstock plant at soil level	−	−
Wound on stem of rootstock plant 10 cm above soil	−	−
Combined potting and irrigation		
Roots of nurse seed plant	+	+
Roots of rootstock plant	+	+
Stem of nurse seed plant	−	−
Wound on stem of nurse seed plant	+	+
Stem of rootstock plant	−	−
Wound on stem of rootstock plant at soil level	+	+
Wound on stem of rootstock plant 10 cm above soil	−	−

[a]The roots of the nurse seed plant were dipped in an aqueous suspension of zoospores of *P. citricola* (1×10^6 spores per milliliter) for 24 h then planted in pots.
[b]Inoculation sites were examined for canker development 2 wk after inoculation.
[c]*P. citricola* was isolated on selective PARPH (13) medium: + = presence of symptoms or fungus in all 30 replicate samples tested; − = absence of symptoms or fungus in all 30 replicate samples tested.

Table 3. Effect of inoculation[a] of the stem of nurse seed plants with *Phytophthora citricola* on pathogen transmission to clonal rootstock plants

	Canker[b]		*P. citricola*[c]	
Site tested	2 wk	4 wk	2 wk	4 wk
Separate potting and irrigation				
Roots of nurse seed plant	−	+	−	+
Roots of rootstock plant	−	−	−	−
Stem of nurse seed plant	+	+	+	+
Wound on stem of nurse seed plant	+	+	+	+
Stem of rootstock plant	−	−	−	−
Wound on stem of rootstock plant at soil level	−	−	−	−
Wound on stem of rootstock plant 10 cm above soil	−	−	−	−
Combined potting and irrigation				
Roots of nurse seed plant	−	+	−	+
Roots of rootstock plant	−	+	−	+
Stem of nurse seed plant	+	+	+	+
Wound on stem of nurse seed plant	+	+	+	+
Stem of rootstock plant	−	+	−	+
Wound on stem of rootstock plant at soil level	−	+	−	+
Wound on stem of rootstock plant 10 cm above soil	−	−	−	−

[a]A V8C agar plug of *P. citricola* culture was placed on the inoculation site and wrapped with Parafilm.
[b]Inoculation sites were examined for canker development 2 and 4 wk after inoculation.
[c]*P. citricola* was isolated on selective PARPH (13) medium 2 and 4 wk after inoculation: + = presence of symptoms or fungus in all 30 replicate samples tested; − = absence of symptoms or fungus in all 30 replicate samples tested.

cankers. *P. citricola* was recovered from the green area between the new wounds and the active cankers but not from the green area between new wounds and inactive cankers. *P. citricola* was not recovered from distant nonwounded areas 10–15 cm above active and inactive cankers in control plants (Table 4).

Detection of *P. citricola* in the sugary exudate of stem cankers. *P. citricola* was recovered from both the liquid and dry sugary exudate that emanated from stem cankers. Cultures of *P. citricola* isolated from canker exudate caused stem cankers when tested on wounds of avocado plants. The reisolation of *P. citricola* from these cankers confirmed that *P. citricola* isolates obtained from sugary exudates of trunk cankers are pathogenic.

DISCUSSION

Wounding, caused by removal of sucker shoots on rootstock plants, enhanced infection by *P. citricola*. This finding is in agreement with an earlier report indicating that wounding was necessary for the infection of avocado plants with *P. citricola* (11). Since wounds that result from the removal of sucker shoots in the field are usually located at or below the soil line, they are exposed to *P. citricola*-infested soil. Such wounds created by standard cultural practices should be covered by a protective material (12). The infection of seed cotyledon removal sites and plant root systems of either nurse seed or rootstock plants with *P. citricola* is limited to areas below the soil and, therefore, does not directly result in potentially lethal stem cankers. However, *P. citricola* can survive as a source of inoculum at these locations and may spread to wounded areas of the stem of the plant by indirect means, such as release of zoospores in irrigation water.

P. citricola did not move from stems of the nurse seed plants to stems of clonal rootstock plants through the inner bark tissue. This suggests that cankers that formed on stems of nurse seed plants were not involved in direct infection of wounds on the stems of clonal rootstock plants, but *P. citricola* might be transmitted indirectly by means of zoospores released in irrigation water. Only when an active canker and newly introduced distant wounds were located on the stem of the same plant did *P. citricola* move from the infection site to distant wounds.

Aged, healed wounds on avocado stems were resistant to infection by *P. citricola*. In this study as well as in our earlier studies, it was shown that wounds became resistant to infection in approximately 2 wk (12). Aged bark wounds became infected only when they were reinjured (12). The mechanism of wound healing involves suberization and production of antifungal compounds. Doster and Bostock (10) indicated that phenolic polymers such as lignin increase in almond bark wounds over time and are correlated with an increase in resistance to the canker-forming pathogen *Ceratocystis fimbriata*. The process that leads to healing of cankers in avocado could involve the production of a strongly lignified zone and a suberized periderm in the outer bark around the canker area, resulting in the arrest of the pathogen.

Scraping the surface of healed-over (inactive) cankers and introducing new wounds around the canker resulted in reactivation and spread of the canker. *P. citricola*, which remained latent until the tissue was broken, moved upward from the reactivated canker and infected newly introduced distant wounds. This information helps explain why attempts by growers to remove cankers by scraping, actually allows cankers to expand. Scraping aged wounds and healed-over cankers results in the disruption of a physical barrier, allowing *P. citricola* to advance, as well as exposing fresh bark areas to infection.

P. citricola can persist in the liquid or dry sugary exudate from infected stem tissues. It is possible that canker exudate may facilitate pathogen transmission and spread. We have observed in avocado groves that the sugary exudate attracts a number of insects, such as ants and beetles. The possible role of insects in transmission of *P. citricola* to wounded stem areas or through damage caused by insects is now under investigation.

Table 4. Role of aged wounds and latent inoculum of *Phytophthora citricola* in healed-over (inactive) cankers on the infection of avocado plants

Site tested	Canker[a]	*P. citricola*[b]
Fresh wounds		
Inoculation with *P. citricola*[c]	+	+
Aged wounds[d]		
Inoculation with *P. citricola*[c]	−	−
Active cankers		
Canker	+	+
Wounds 10–15 cm above canker (distant)	+	+
Area between distant wound and canker	−	+
Nonwounded area 10–15 cm above canker (control)	−	−
Healed-over (inactive) cankers[d]		
Fungus-free agar	−	+
Inoculation with *P. citricola*[c]	−	+
Wounds 10–15 cm above canker (distant)	−	−
Area between distant wound and canker	−	−
Scraped canker	+	+
Wounds 10–15 cm above scraped canker (distant)	+	+
Area between distant wound and scraped canker	−	+
Nonwounded area 10–15 cm above canker (control)	−	−

[a] Inoculation sites were examined for canker development 2 wk after inoculation.
[b] *P. citricola* was isolated on selective PARPH (13) medium: + = presence of symptoms or fungus in all 30 replicate samples tested; − = absence of canker or fungus in all 30 replicate samples tested.
[c] A V8C agar plug of *P. citricola* was placed on the inoculation site and wrapped with Parafilm.
[d] Fifteen-month-old avocado plants with 4-mo-old healed wounds or 6-mo-old, healed-over cankers were used.

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