

Phytophthora–Diaprepes Weevil Complex: *Phytophthora* spp. Relationship with Citrus Rootstocks

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ABSTRACT

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Diaprepes abbreviatus (Coleoptera: Curculionidae) is a root weevil, introduced from the Caribbean Basin into Florida in 1964. The larval stage feeds on fibrous and structural roots of citrus, predisposing the injured root system to infection and girdling by *Phytophthora* spp. In citrus orchards, the rootstocks trifoliolate orange (*Poncirus trifoliata*) and hybrid 'Swingle' citrumelo (*Citrus paradisi* × *P. trifoliata*) are resistant to the complex of *P. nicotianae* with *D. abbreviatus*, while 'Cleopatra' mandarin (*C. reticulata*) is susceptible to this complex. When *Phytophthora palmivora* is coincident with *P. nicotianae* in fine-textured, poorly drained soils, Swingle citrumelo is more vulnerable to attack by the complex with *P. palmivora* than is Cleopatra mandarin. Infestation of 9-month-old seedlings with zero, two, or five neonate larvae resulted in a wide range of fibrous root and taproot damage of trifoliolate orange and Cleopatra mandarin. Leakage of reducing sugars increased sharply as injury to the roots exceeded 75%. The relationship between feeding damage and root leakage was similar for the two rootstocks. Thus, reduced root damage was not based on host resistance to larval feeding. Root infection and rhizosphere populations of *P. nicotianae* were higher on Cleopatra mandarin than on trifoliolate orange. Root rot by *P. nicotianae* did not increase with severity of feeding injury on either rootstock. Root infection and root rot by *P. palmivora* was more severe on trifoliolate orange than on Cleopatra mandarin and increased with severity of larval damage. *P. palmivora* infected and rotted the taproot of both rootstocks if predisposed by larval feeding, but *P. nicotianae* did not. Commercial rootstocks are severely damaged by larvae of *D. abbreviatus*; therefore, tolerance of the *Phytophthora–Diaprepes* weevil complex should be based on resistance of rootstocks to each *Phytophthora* sp.

Additional keywords: insect–fungus complex, *Phytophthora nicotianae*, *P. palmivora*, sour orange

Diaprepes abbreviatus L. (Coleoptera: Curculionidae) is a polyphagous root weevil introduced into Florida from the Caribbean Basin that attacks *Citrus* spp. and other agricultural crops. Since discovery of *D. abbreviatus* in Orange County in 1964, the weevil has been dispersed primarily by nursery stock into 22 counties and now infests more than 66,000 ha of commercial agriculture, including approximately 12,000 ha of commercial citrus (8). *D. abbreviatus* larvae feed and reproduce on all commercial rootstocks budded with *Citrus* spp. At larger developmental stages, the larvae strip the bark from the taproot

and structural roots, causing girdling and eventual death of trees (16). Due to lack of early detection methods and availability of effective management options, much of the weevil-infested acreage of citrus is in severe decline or out of production (8).

As *Diaprepes* weevil infestations grew in scope over the last three decades, citrus production managers noted that trees in lower-elevation, wetter areas of the orchards were the first to decline. Trees on rootstocks such as sour orange (*Citrus aurantium* L.) and 'Cleopatra' mandarin (*C. reticulata* Blanco), susceptible to the root rot pathogen *Phytophthora nicotianae* Breda de Haan (syn. *P. parasitica* Dastur), declined more rapidly than in adjacent orchards on rootstocks more resistant to this pathogen, like 'Swingle' citrumelo (*C. paradisi* Macfad. × *Poncirus trifoliata* (L.) Raf.) (3,22). Based on these observations, citrus producers began augmenting the management program for *Diaprepes* weevil with one or more fungicide applications to control *Phytophthora nicotianae* (13). Management costs for the weevil and the complex with *Phytophthora* root rot combined are estimated to be as much as \$500 to 600 per hectare (14).

In 1996 to 1997, a survey of weevil-affected orchards confirmed that *Phytophthora* spp. were associated with larval feeding injury on structural roots of all commercial rootstocks (5). Excavation of root systems revealed sloughing of root bark where *Phytophthora* spp. entered the injuries created by larval feeding, referred to as root etching or channeling of the bark. Infection of the wounds accelerated the girdling and collapse of roots from the crown of the tree outward. Greenhouse studies confirmed that larval feeding predisposed fibrous roots of seedlings to greater infection by *P. nicotianae* and promoted infection and higher rhizosphere populations of the pathogen (17). Subsequent investigations demonstrated that *P. nicotianae* was more severe on susceptible Cleopatra mandarin than on resistant trifoliolate orange (*Poncirus trifoliata*) selection DPI 50-7 (17,22). Severity of root rot caused by the *Phytophthora–Diaprepes* complex was not due to differences between the rootstocks in susceptibility to larval feeding because damage to Cleopatra mandarin and trifoliolate hybrid rootstocks Swingle citrumelo and 'Carrizo' citrange (*C. sinensis* (L.) Osbeck × *Poncirus trifoliata*) was similar (18,19).

The association of *Phytophthora* spp. with root damage by larvae was named the *Phytophthora–Diaprepes* complex (5). The potential importance of the complex in the decline of trees on different rootstocks prompted a survey of the east coast of Florida near Vero Beach (Indian River County) and Ft. Pierce (St. Lucie County), where trees rapidly declined despite aggressive management of the weevil. More severe damage was encountered where *P. palmivora* (Butler) Butler was the predominant pathogen in the complex with *D. abbreviatus* (5,7). The *P. palmivora–Diaprepes* complex was associated with fine-textured, poorly drained soils on rootstocks normally resistant to or tolerant of *P. nicotianae*, Swingle citrumelo and Carrizo citrange. In these situations, structural roots moderately damaged by larvae were extensively infected with *P. palmivora*. Bark infection caused rapid collapse of structural roots and expression of a gummy residue in the bark.

In the most recent surveys of *Diaprepes*-infested areas on the east coast (1,4), trees on Swingle citrumelo and Carrizo citrange rootstocks supported higher soil populations of *P. palmivora* and declined more

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rapidly than trees in adjacent blocks on Cleopatra mandarin and sour orange. This raised concern, because Swingle citrusmelo is being used heavily as the rootstock for replanting of orchards on sour orange that are declining due to *Citrus tristeza virus* in this production area (4). These surveys were the first indication that rootstocks with trifoliolate orange hybrid parentage might be more susceptible to the *P. palmivora*-*Diaprepes* sp. interaction. Susceptibility to *P. palmivora* was unexpected because the resistance of most commercial and experimental rootstocks to *Phytophthora* root rot is based on hybrids with trifoliolate orange (6).

Hybrids appear to be more vulnerable to attack by *P. palmivora*; therefore, trifoliolate orange, as well as Cleopatra mandarin, were compared for their relative resistance to the complex with each *Phytophthora* sp. We report the disease development of *P. nicotianae* and *P. palmivora* on these two rootstocks in the greenhouse after seedlings were infested with neonate larvae to establish a range of feeding damage.

MATERIALS AND METHODS

Weevil infestation and damage assessment. Seed of Cleopatra mandarin and trifoliolate orange 50-7 were obtained from registered seed source trees of the Florida Department of Agriculture and Consumer Services, Division of Plant Industry. Seed were sown in 150-cm³ containers (Stuewe & Sons Inc. Corvallis, OR) containing Metro Mix 500 (The Scotts Co., Marysville, OH) and seedlings were fertilized weekly with Peter's 20-10-20 Peat Lite Special (The Scotts Co.). Nine-month-old seedlings of each rootstock were transplanted in Candler fine sand (Typic quartzipsammets, pH 6.8, and 1% organic matter) in 150-cm³ containers and 180 of each rootstock were selected for uniform size and vigor for each experiment.

Neonate larvae of *D. abbreviatus* (approximately 48 h old) were obtained from eggs laid by adult females collected from the field and confined to screen cages in a greenhouse at 27 ± 2°C. The larvae were counted in sets of two and five larvae into Eppendorf tubes. The soil in each container was moistened with water, then two or five larvae were scattered on the soil surface. A no-larvae treatment was included in the experiment, and the zero-, two-, or five-larvae treatments each were replicated 60 times for each rootstock. Approximately 6

weeks later, all seedlings were harvested and visually rated for larval feeding damage using the Horsfall and Baratt (H-B) system on a scale of 1 to 11 (10). Each rating corresponded to an incremental change in percentage of injury to the root system, where 1 = 0, 2 = 0 to 3, 3 = 3 to 6, 4 = 6 to 12, 5 = 12 to 25, 6 = 25 to 50, 7 = 50 to 75, 8 = 75 to 87, 9 = 87 to 94, 10 = 94 to 97, and 11 = 97 to 100%. Injury consisted of larval feeding on the fibrous roots to expose the cortical tissues and vascular cylinder. As larvae developed to later N-star stages (3 weeks post infestation), feeding on the taproot removed the bark to expose the cambium.

Root-soil leachate assay. Leachates were extracted from rhizosphere soil in containers of seedlings of each rootstock with and without larval injury. About 35 seedlings were harvested from each larval infestation level (two and five larvae) to represent the range of larval injury ratings (2 to 11), and 20 seedlings with no root injury (rating = 1) were harvested from the noninfested treatment. The seedlings in containers were watered to field capacity the day before harvest. Twenty-four hours later, the soil was separated gently from the roots to minimize root breakage and loss. Any larvae (live or dead) were separated from the soil sample, counted, and weighed. The soil was oven dried at 60°C overnight and placed in plastic bags. Soil samples were kept frozen (-5°C) until the exudates were extracted. A sample of 100 g of soil was mixed with 15 ml of sterile distilled water and held at 4°C for 2 h to leach soluble sugars from the soil. The soil water was recovered by centrifugation at 1,500 × g for 10 min and the extracted solution filtered through two layers of #41 filter paper to remove debris. The volume of the filtrate was recorded and the filtrate was frozen (-5°C) until analysis. Total reducing sugars were measured for 1 ml of extract using the arsenomolybdate test (15). Fibrous roots (<2 mm in diameter) were removed from the taproot and dried at 70°C for 48 h. The reducing sugar in root-soil leachate was expressed as micrograms of fructose-equivalent sugar per milligram of fibrous root.

Phytophthora-Diaprepes interaction. *P. nicotianae* (Pn 117) isolated from citrus roots in Ona, FL, and *P. palmivora* (Pp101) isolated from citrus fruit in LaBelle, FL, were maintained on clarified V8 juice agar (7). Chlamydospores of each isolate were

produced by the method of Tsao (22) for use as inoculum. Mycelium and chlamydospores were comminuted in a blender for 30 s and then added to several liters of pasteurized Candler fine sand. The soil was mixed manually to produce an inoculum concentrate. The inoculum was incubated at room temperature (25 ± 2°C) for 2 days and then assayed on pimarcin-ampicillin-rifampicin-pentachloronitrobenzene-hymexazol (PARPH) semiselective agar medium to determine *Phytophthora* propagule density as previously described (3). The inoculum concentrate for each fungus was added to pasteurized Candler fine sand and mixed in a cement mixer to achieve 10 to 20 propagules/cm³ of soil. At least six seedlings from each larval damage rating (2 to 11) were transplanted into soil infested with *P. nicotianae* or *P. palmivora* in 150-cm³ containers. An additional 20 noninjured seedlings (rating = 1) were included: 10 inoculated with *P. nicotianae* or *P. palmivora* and 10 noninoculated.

Each replicate seedling was placed randomly on the greenhouse bench. Seedlings were moved to a new position on the bench each week to minimize location effects of temperature (25 to 35°C diurnal cycle) and relative humidity (60 to 100%). Seedlings were watered daily and fertilized weekly with Peters 20-20-20 liquid fertilizer.

Approximately 6 weeks after inoculation with *Phytophthora* spp., seedlings were harvested. Roots were washed and visually rated for root rot on the same H-B scale from 1 to 11 used to estimate larval damage. After rating the root system, 20 root tips (1-cm segments) were clipped at random from each root system and stabbed into the surface of PARPH medium. If fewer than 20 root tips were present on a seedling, all available root tips were plated. After 4 days, the percentage of root tips positive for *P. nicotianae* of the total assayed was calculated as incidence of infection. Fibrous roots were separated from taproots and each tissue was dried and weighed (70°C for 48 h). Soil was assayed for populations of each *Phytophthora* sp. on PARPH medium and expressed as propagules/cm³ of soil.

Statistical analysis. The experimental design was a factorial with main effects of rootstock (R), *Phytophthora* sp. inoculation (P), larval damage class (L), and first and second order interactions. The analysis was performed with SAS PROC GLM (version 8.1; SAS Institute, Cary, NC). Data from the different years were pooled for the analyses after it was determined that there was no significant year-treatment interaction. Regression analysis was performed to obtain models that best described the relationship between initial larval damage and subsequent interactions of rootstocks with estimates of *Phytophthora* root rot damage. The root-soil leachate and larval interaction experiments

Table 1. Recovery of *Diaprepes abbreviatus* larvae from trifoliolate orange and 'Cleopatra' mandarin 6 weeks after infestation of seedlings with 2 or 5 larvae^z

Rootstock	Larvae (no./seedling)		Total larval weight (mg/seedling)	
	2 larvae	5 larvae	2 larvae	5 larvae
Trifoliolate orange	1.4 a	3.3 b	99 a	136 c
Cleopatra mandarin	1.3 a	2.9 c	84 b	116 d

^z Significant difference between larval infestation levels and rootstocks at *P* < 0.05 (*t* test) is indicated by unlike letters in each row or column.

were repeated in the same greenhouse location in 1997 and 1998.

RESULTS

Recovery of larvae, damage assessment, and root-soil leachates from rootstock seedlings. The number and weight of larvae recovered per seedling increased with level of infestation from two to five neonate larvae per seedling (Table 1). The recovery and weight of larvae per plant was slightly higher on trifoliolate orange rootstock than on Cleopatra mandarin. The weight of larvae per plant decreased at the higher infestation level of neonates.

Larval damage and loss of fibrous root and taproot dry weight per seedling were similar for trifoliolate orange and Cleopatra mandarin (Fig. 1A and B). Reducing sugars in root-soil leachates increased sharply as root ratings increased above 8 ($\geq 75\%$ of the root system damaged; Fig. 1C and D), and as fibrous root dry weight decreased below approximately 0.15 g per seedling of each rootstock (Fig. 1A and B). Taproot dry weight decreased slightly above a root rating of 8 (Fig. 1A and B).

Phytophthora infection of rootstocks with larval damage. The main effects and interaction of rootstocks and larval damage were highly significant for root infection and rhizosphere populations of *P. palmivora* and *P. nicotianae* (Table 2). Incidence

of root infection and rhizosphere soil populations of *P. palmivora* were higher ($P < 0.05$) than those of *P. nicotianae* (47 versus 13.7% and 252 versus 47 propagules/cm³, respectively). *P. palmivora* had higher ($P <$

0.05) incidence of root infection and soil populations on trifoliolate orange than on Cleopatra mandarin (70 versus 28% and 346 versus 160 propagules/cm³, respectively). Conversely, incidence and rhizo-

Table 2. Main effects and interactions of rootstocks (trifoliolate orange and Cleopatra mandarin) and larval damage by *Diaprepes abbreviatus* for root infection and rhizosphere soil populations after inoculation of seedlings with *Phytophthora nicotianae* or *P. palmivora*

Source	df	Probability > F			
		Root infection incidence		Rhizosphere populations	
		<i>P. nicotianae</i>	<i>P. palmivora</i>	<i>P. nicotianae</i>	<i>P. palmivora</i>
Rootstock (R)	1	<0.0001	<0.0001	<0.0001	<0.0001
Larval damage rating (L)	10	0.069	<0.0001	0.040	<0.0001
R × L	10	0.0002	<0.0001	<0.0001	<0.0001

Table 3. Main effects and interactions of rootstocks (trifoliolate orange and Cleopatra mandarin) and larval damage by *Diaprepes abbreviatus* and inoculation with *Phytophthora nicotianae* or *P. palmivora* on root rot rating and fibrous root dry weight

Source	df	Probability > F			
		Root rot rating		Fibrous root dry weight	
		<i>P. nicotianae</i>	<i>P. palmivora</i>	<i>P. nicotianae</i>	<i>P. palmivora</i>
Rootstock (R)	1	<0.0001	<0.0001	0.01	<0.0001
Larval damage rating (L)	10	<0.0001	<0.0001	<0.0001	<0.0001
<i>Phytophthora</i> inoculation (P)	1	0.0003	<0.0001	<0.0001	<0.0001
R × L	10	0.0008	<0.0001	0.05	0.017
R × P	1	0.55	<0.0001	0.22	0.0007
P × L	10	0.11	0.017	0.96	0.41
R × L × P	10	0.35	0.32	0.86	0.71

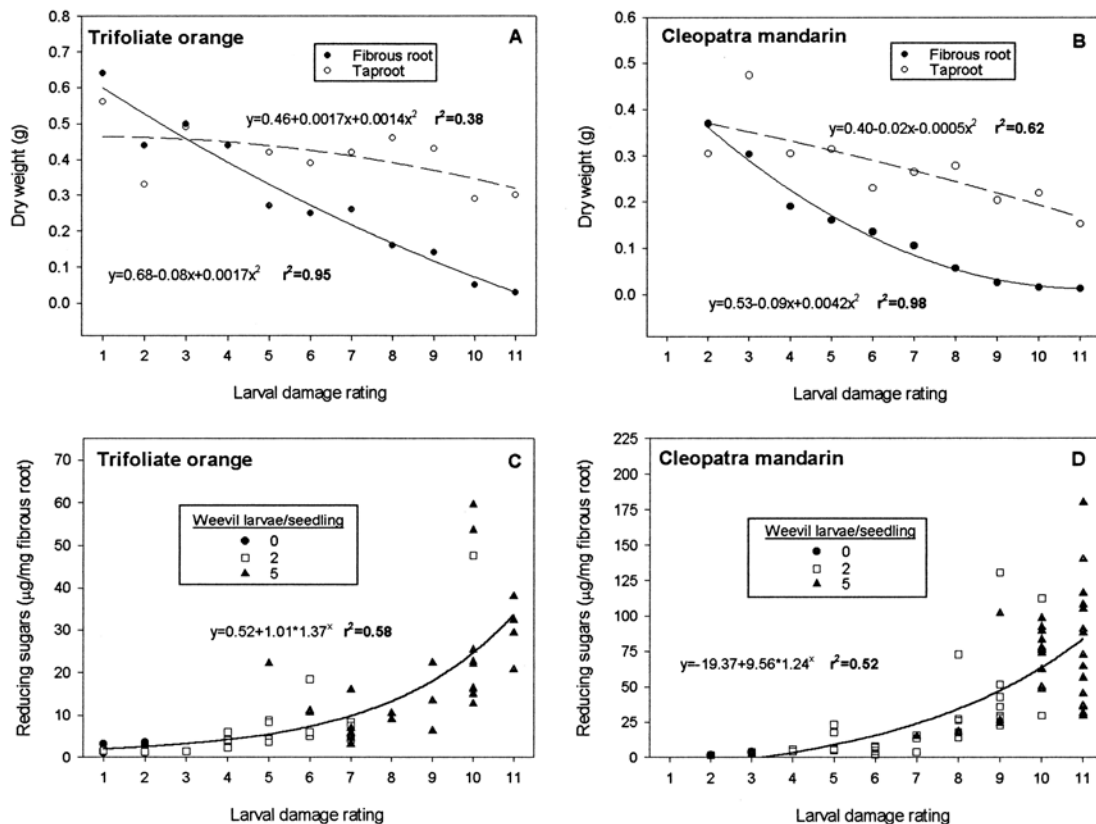


Fig. 1. Regressions of A and B, the relationships between fibrous root and taproot loss or C and D, concentration of reducing sugars in root-soil leachates after a range of damage feeding by *Diaprepes abbreviatus* larvae was established on seedlings of trifoliolate orange and 'Cleopatra' mandarin. Larval damage ratings are based on the Horsfall-Baratt (H-B) system, where 1 = 0, 2 = 0 to 3, 3 = 3 to 6, 4 = 6 to 12, 5 = 12 to 25, 6 = 25 to 50, 7 = 50 to 75, 8 = 75 to 87, 9 = 87 to 94, 10 = 94 to 97, and 11 = 97 to 100% injury of roots. Regressions are significant at $P < 0.0001$.

sphere soil populations of *P. nicotianae* were higher ($P < 0.05$) on Cleopatra mandarin than on trifoliolate orange (27 versus 1.5% and 92 versus 3 propagules/cm³, respectively).

Phytophthora root rot of rootstocks with larval damage. Rootstock, larval damage, and inoculation with *Phytophthora* spp. affected root rot rating and fibrous root dry weight as measures of root loss (Table 3). The rootstock-larval damage interaction was highly significant. As previously reported (3), seedlings of trifoliolate orange regenerated fibrous roots more slowly than Cleopatra mandarin during 6 weeks of recovery from loss after larval feeding as measured by root rot rating or fibrous root dry weight (see responses of noninoculated rootstocks in Figs. 2 and 3).

P. palmivora was more damaging to trifoliolate orange roots than the other *Phytophthora* spp.-rootstock combinations (Table 3). *P. palmivora* interacted with larval damage based on root rot rating but not on fibrous root dry weight. *P. nicotianae* did not interact with rootstocks or larval damage based on measures of root loss.

The relationship between larval damage and Phytophthora root rot was modeled. Inclusion of larval ratings from 1 to 11 resulted in polynomial curves for inocu-

lated and noninoculated seedlings that converged at ratings ≥ 8 (analysis not shown). This interaction was noted in our previous study (17) as an inability to measure Phytophthora root rot when the quantity of fibrous roots was severely limited by larval feeding. Linear regressions of larval damage ratings from 1 to 7 provided the best fit for the relationships of larval damage with root rot rating and fibrous root loss (0.10 $\leq r^2 \leq 0.97$; Figs. 2 and 3).

After inoculation of trifoliolate orange and Cleopatra mandarin seedlings with *P. nicotianae*, the slope and intercepts of the linear regressions for root rating and fibrous root loss with larval damage rating did not differ from those for noninoculated seedlings (Fig. 2A to D). The 95% confidence intervals for the linear regressions of root ratings and fibrous root loss due to *P. nicotianae* overlapped considerably with the noninoculated response for both rootstocks.

By contrast, *P. palmivora* interacted with larval damage (Fig. 3A to D). The increase in the root rot rating with larval damage rating was steeper for inoculated than for noninoculated seedlings (Fig. 3A and B). Little or no overlap in the 95% confidence intervals occurred for the regressions of root ratings for trifoliolate orange and Cleopatra mandarin (Fig. 3A). Fibrous root loss of trifoliolate orange inoculated with *P.*

palmivora was greater than for the noninoculated seedlings but did not increase with level of larval damage (Fig. 3C and D). Fibrous roots of Cleopatra mandarin were much less affected by *P. palmivora* than were those of trifoliolate orange.

Feeding on the structural roots of the seedlings predisposed each rootstock to infection of the taproot by *P. palmivora* (Fig. 4). Taproot infection was not observed after inoculation with *P. nicotianae*. Damage to the taproot by *P. palmivora* was not detected by measurement of fibrous roots. Taproot infection stimulated adventitious root growth (Fig. 4) that may have confounded assessment of fibrous root loss due to root rot by *P. palmivora*.

DISCUSSION

As previously reported (18), fibrous root and taproot damage of trifoliolate orange and Cleopatra mandarin was severe 6 weeks after infestation of seedlings with neonate larvae. After larval feeding damage, trifoliolate orange regenerated roots more slowly because this rootstock is slower growing and less vigorous than Cleopatra mandarin (3). Differential response to the *Phytophthora-Diaprepes* complex was not based on unique resistance of the rootstocks to larval feeding. Nevertheless, larval-damaged roots of trifoliolate orange

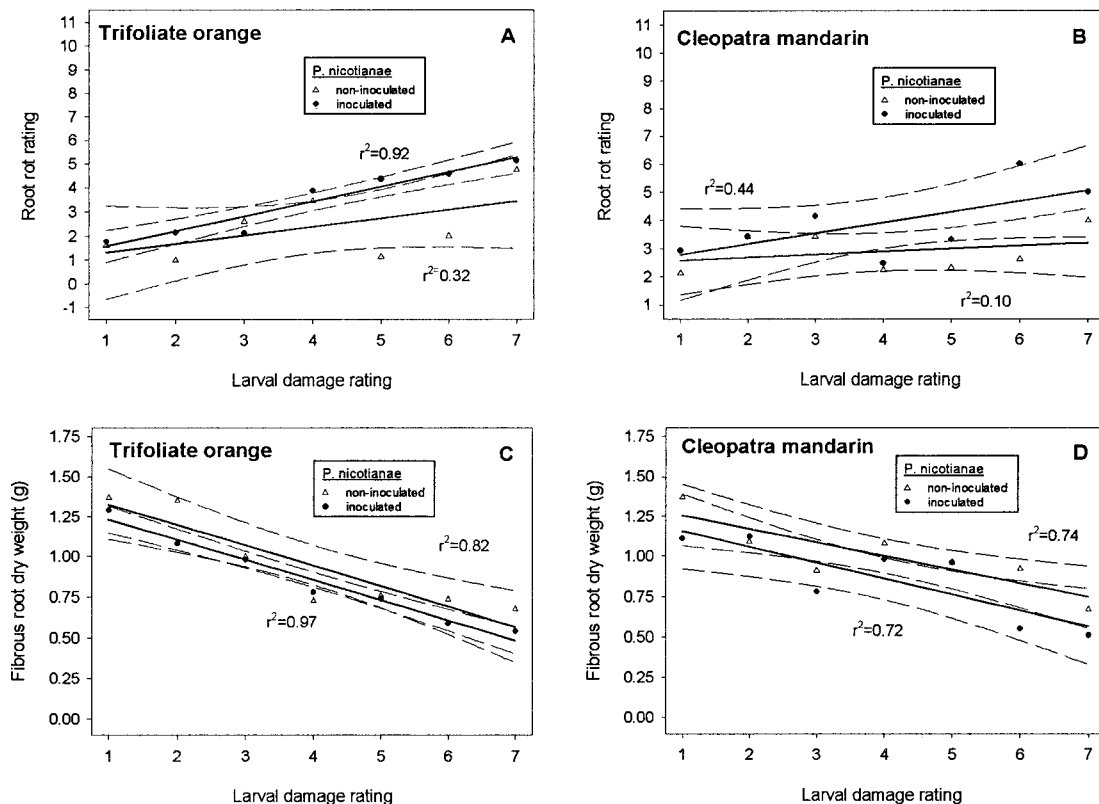


Fig. 2. Linear regressions of **A** and **B**, root rot rating and **C** and **D**, fibrous root weight on larval damage rating of seedlings of trifoliolate orange and 'Cleopatra' mandarin after feeding damage by larvae of *Diaprepes abbreviatus* and inoculation with *Phytophthora nicotianae*. Root rot and larval damage ratings are based on the Horsfall-Baratt (H-B) scale, where 1 = 0, 2 = 0 to 3, 3 = 3 to 6, 4 = 6 to 12, 5 = 12 to 25, 6 = 25 to 50, 7 = 50 to 75, 8 = 75 to 87, 9 = 87 to 94, 10 = 94 to 97, and 11 = 97 to 100% injury of roots. Regressions are significant at $P < 0.05$, except the root rot rating curves for trifoliolate orange and 'Cleopatra' mandarin in the noninoculated treatments (**A** and **B**) significant at $P < 0.20$. Dashed lines are the 95% confidence intervals for the predicted values.

inoculated with *P. nicotianae* were resistant to infection and reproduction by this pathogen; whereas, susceptible Cleopatra mandarin roots were more severely infected and rhizosphere populations higher compared with noninjured roots. Here and

in a previous study (17), root loss from *P. nicotianae* did not increase measurably with larval damage. This lack of response to root infection may be due to the limited exposure (6 weeks) of the roots to *P. nicotianae* before the root assessments.

Root infection and rot of the two rootstocks were more severe when weevil-injured roots were challenged by *P. palmivora*. The greater severity of the complex of *D. abbreviatus* with *P. palmivora* than with *P. nicotianae* is further evidence that

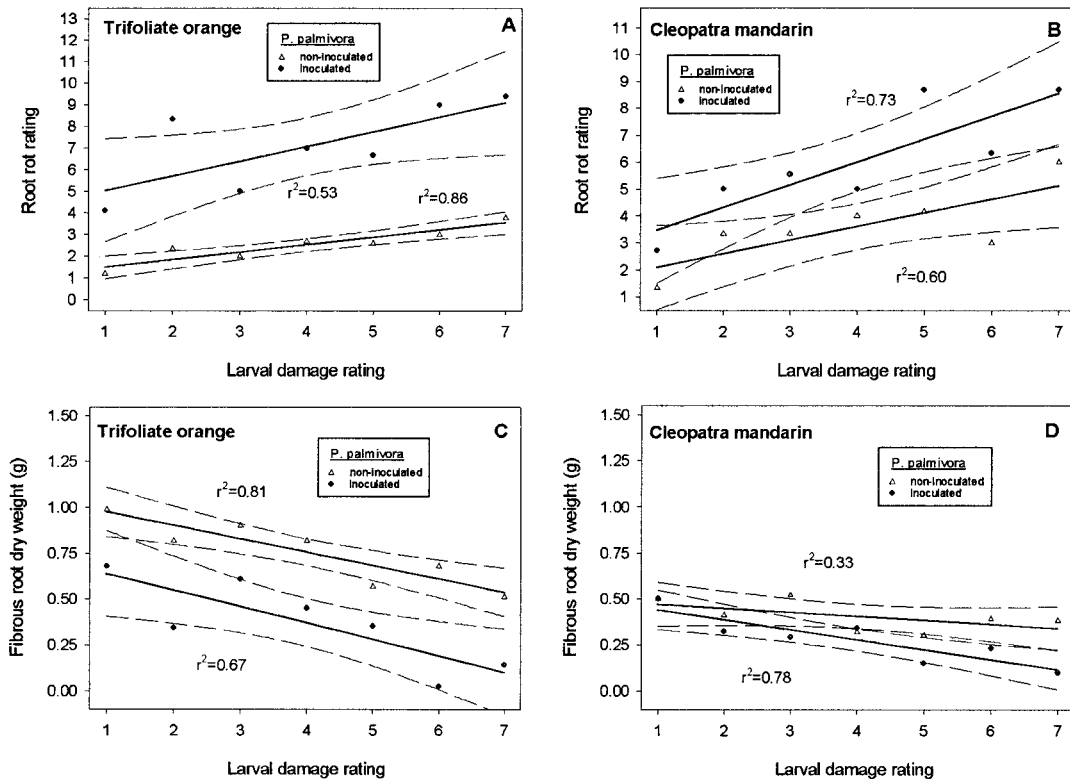


Fig. 3. Linear regressions of **A** and **B**, root rot rating and **C** and **D**, fibrous root weight on larval damage rating of seedlings of trifoliate orange and 'Cleopatra' mandarin after feeding damage by larvae of *Diaprepes abbreviatus* and inoculation with *Phytophthora palmivora*. Root rot and larval damage ratings are based on the Horsfall-Baratt (H-B) scale, where 1 = 0, 2 = 0 to 3, 3 = 3 to 6, 4 = 6 to 12, 5 = 12 to 25, 6 = 25 to 50, 7 = 50 to 75, 8 = 75 to 87, 9 = 87 to 94, 10 = 94 to 97, and 11 = 97 to 100% injury of roots. Regressions are significant at $P < 0.05$. Dashed lines are the 95% confidence intervals for the predicted values.

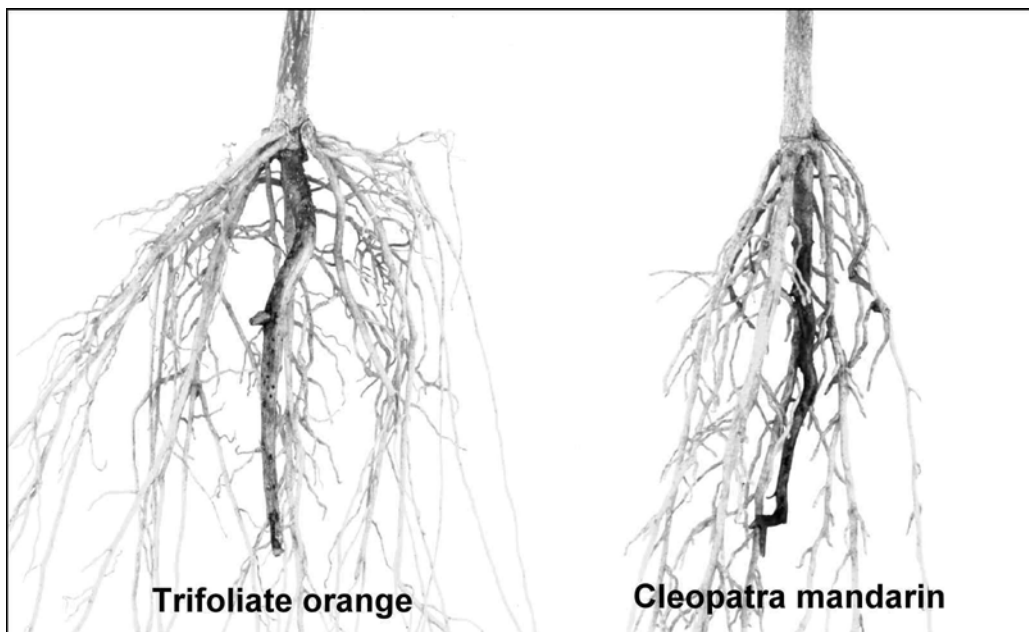


Fig. 4. Taproot infection and adventitious root growth on seedlings of trifoliate orange and 'Cleopatra' mandarin after feeding damage by larvae of *Diaprepes abbreviatus* and inoculation with *Phytophthora palmivora*.

P. palmivora is a more aggressive and damaging root and fruit pathogen of citrus (7,24). In this study, infection and rot of the taproot of each rootstock by *P. palmivora* after larval feeding reproduced the rapid and extensive invasion of structural roots by *P. palmivora* in orchards (5).

Differential response of rootstocks to the *P. nicotianae*-*Diaprepes* sp. complex apparently was based on maintenance of tissue resistance to infection by this pathogen after larvae attack. Larval feeding injured fibrous root and taproot tissues, increasing leakage of reducing sugars and probably other nutritional compounds from damaged root cells. These compounds serve as attractants and a food source for *Phytophthora* spp. (2,9). Substantial increase in leakage of compounds was detected only after root injury exceeded 75% and the response was similar for trifoliolate orange and Cleopatra mandarin. Above this threshold, leachates probably stimulated the activity of *P. nicotianae* or *P. palmivora*, but seedling roots were severely reduced by larval feeding and provided limited substrate for *Phytophthora* infection. At lower levels of root injury, greater resistance of trifoliolate orange to *P. nicotianae* and Cleopatra mandarin to *P. palmivora* was maintained despite the wounding. Fungal resistance compounds in roots have been postulated to reduce the rate of ingress of *Phytophthora* spp. into cortical and vascular tissues, allowing roots to heal and regenerate (3,23). In trifoliolate orange, resistance compounds apparently were not as effective against *P. palmivora*, because roots were infected and damaged at a higher rate by this pathogen than by *P. nicotianae* (23). The greater susceptibility of trifoliolate orange to *P. palmivora* was confirmed by a survey of orchards on Florida's east coast where soil populations of this pathogen were higher on trifoliolate orange hybrids, Swingle citrumelo, and Carrizo citrange than on Cleopatra mandarin and sour orange (1,4).

The significance of these findings in orchard management of the *Phytophthora*-*Diaprepes* complex depends on which *Phytophthora* sp. is present and whether the soil and water conditions are conducive to the fungus or to rootstock stress. In most situations, *P. nicotianae* is the predominant pathogen and populations of *P. palmivora*, although present, remain low due to soil conditions unfavorable for its activity as a root rot pathogen (7). Swingle citrumelo appears to perform acceptably as a replant in weevil-infested groves, provided soil conditions are suited for this rootstock (e.g., sandy soil texture, well-drained, favorable pH, calcium carbonate status, and so on). *P. palmivora* is damaging to citrus

roots in fine-textured, poorly drained soils, high in clay, pH, and calcium carbonate. In these soils, Swingle citrumelo is rendered susceptible to the *Phytophthora*-*Diaprepes* complex and may decline rapidly (1,4). Thus, tolerance of Swingle citrumelo to the complex is restricted to certain locations and better soils. Under adverse soil conditions in Florida, new rootstocks of parentage other than trifoliolate orange should be sought for resistance to *P. palmivora* and greater tolerance of the complex.

In this study, larvae were removed from roots before inoculation with *Phytophthora* spp. to demonstrate that increase in root rot resulted from feeding injury and not from larvae spreading infections to the roots through the soil. Other experiments involving interaction of soilborne pathogens with root insects have been performed as coinoculations of the insect with the pathogen (11,12). Although the importance of vectoring of the pathogen cannot be estimated, this interaction is likely secondary to the predisposition of roots by feeding damage. Our results here and previously (17) showed that greater infection resulted from root and bark injury, so it is likely that other citrus root and bark-feeding insects, such as subterranean termites (*Reticulitermes flavipes*) or fire ants (*Solenopsis invicta*), also predispose the roots and trunk to *Phytophthora* rots (20,21).

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