Pathogenicity and Relative Virulence of *Phytophthora* spp. from Walnut and Other Plants to Rootstocks of English Walnut Trees

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Accepted for publication 26 March 1985 (submitted for electronic processing).

ABSTRACT

Matheron, M. E., and Mircetich, S. M. 1985. Pathogenicity and relative virulence of *Phytophthora* spp. from walnut and other plants to rootstocks of English walnut trees. Phytopathology 75: 977-981.

Phytophthora cryptogea, *P. drechsleri*, *P. parasitica*, and two unidentified *Phytophthora* spp. were isolated from declining English walnut (*Juglans regia*) trees affected by root and crown rot in California orchards. All five *Phytophthora* spp. were pathogenic to Northern California black walnut (*J. hindsii*) seedlings grown in artificially infested potting mix in greenhouse tests. *J. hindsii* and Paradox (*J. hindsii* × *J. regia*), standard rootstocks of English walnut, were highly susceptible to *P. cryptogea*, whereas Paradox was significantly more resistant than *J. hindsii* to the two unidentified *Phytophthora* spp. A total of thirty-one different isolates from among *P. cactorum*, *P. cinnamomi*, *P. citricola*, and *P. cryptogea* isolated from walnut and numerous trees, shrubs, and other hosts were pathogenic to seedlings of *J. hindsii* grown in artificially infested potting mix. This is the first report directly implicating *P. cryptogea*, *P. parasitica*, and the two unidentified *Phytophthora* spp. (isolates W489R and 2833) in decline and death of English walnut trees in California's commercial walnut orchards.

Additional key words: decline of walnuts, Persian walnut, soilborne diseases.

Phytophthora cactorum (Leb. & Cohn) Schroet., *P. citricola* Sawada, *P. cinnamomi* Rands, *P. citrophthora* (R. E. Smith & E. H. Smith) Leonian, *P. megasperma* Drechsler, *P. cryptogea* Pethyb. & Laff., and four different, but unidentified, *Phytophthora* spp. were repeatedly isolated from decayed roots or trunks of dead and dying English walnut trees in California (12). Furthermore, *P. cactorum*, *P. citricola*, *P. cinnamomi*, *P. citrophthora*, *P. megasperma*, and one unidentified *Phytophthora* sp. (isolate 1029) have been shown experimentally to cause root rot or crown rot in seedlings of *Juglans hindsii* (Jeps.) Jeps. and Paradox (*J. hindsii* × *J. regia* L.) (12). Paradox rootstock was also significantly more resistant than *J. hindsii* to *P. cactorum*, *P. citrophthora*, *P. megasperma*, and *Phytophthora* sp. isolate 1029 under experimental conditions favorable for disease development (12). Subsequent isolations from walnut trees in orchards of California with typical root and/or crown rot symptoms revealed the presence of other *Phytophthora* spp. than those reported previously from similar orchards (12).

Furthermore, *P. cactorum*, *P. cinnamomi*, *P. citricola*, and *P. cryptogea* have been repeatedly isolated from dead or dying almond [*Prunus dulcis* (Mill.) D. A. Webb], apricot (*P. armeniaca* L.), sweet cherry (*P. avium* L.), peach [*P. persica* (L.) Batsch.], apple (*Malus sylvestris* Mill.), and many ornamental plants in California (8–13,17,22,23). There is a possibility that *Phytophthora* spp. associated with these hosts could spread and present a threat to English walnut trees in California orchards.

The present study was undertaken to further identify *Phytophthora* spp. associated with walnuts and to determine their likely role in decline and death of walnut trees in commercial California orchards. The pathogenicity of isolates of *P. cactorum*, *P. cinnamomi*, *P. citricola*, and *P. cryptogea* from walnut and other plant species to seedlings of *J. hindsii* was also determined.

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MATERIALS AND METHODS

Isolation and identification of Phytophthora spp. *Phytophthora* spp. were isolated from decayed root and crown tissue and from soil surrounding affected walnut trees by using previously described procedures (11,12). Colony type, cardinal temperatures for vegetative growth and production, type and size of sporangia, chlamydospores, and oospores were determined by methods reported earlier (11). Isolates of *Phytophthora* were identified from descriptions of Waterhouse (19,20), Tucker (18), and Frezzi (4).

Pathogenicity and relative virulence tests. Pathogenicity and virulence of walnut isolates of *P. cactorum*, *P. cinnamomi*, *P. citricola*, *P. cryptogea*, *P. drechsleri* Tucker, *P. parasitica* Dast., and two unidentified *Phytophthora* spp. (isolates W489R and 2833) to seedlings of Northern California black walnut (*J. hindsii*) and Paradox (*J. hindsii* × *J. regia*) were determined under greenhouse conditions. For studies on host specificity, *P. cactorum* isolated from almond, apricot, apple, strawberry (*Fragaria* L.), coast live oak (*Quercus agrifolia* Nee), and toyon (*Photinia* Lindl.); *P. cinnamomi* isolated from apricot, blueberry (*Vaccinum* L.), avocado (*Persea americana* C. F. Gaertn.), camellia (*Camellia japonica* L.), and cork oak (*Quercus suber* L.); *P. citricola* isolated from almond, apricot, hops (*Humulus lupulus* L.), rhododendron, and coast live oak; and *P. cryptogea* from sweet cherry were all tested for pathogenicity and virulence to *J. hindsii* in the greenhouse. Inocula consisted of 4- to 6-wk-old cultures of an individual isolate of *Phytophthora* grown in 0.5-L canning jars on a mixture of 250 cc of vermiculite and 20 cc of whole oat seeds moistened with 175 ml of V-8 juice broth (11). The colonized medium was rinsed with tap water to remove excess nutrients and then mixed with steam-pasteurized U.C. potting mix (50% fine sand, 50% peat moss, plus 3.4 kg of dolomite, 1.4 kg of superphosphate, 1.4 kg of gypsum, 114 g of KNO_3, and 114 g of K_2SO_4 per cubic meter) (1) at the rate of 10 cm^3 of inoculum per 1,000 cm^3 of U.C. mix. The controls received only rinsed uninfested vermiculite mixture. Two-month-old *J. hindsii* and Paradox seedlings were grown in pasteurized U.C. potting mix in 7.6 × 7.6-cm Jiffy pots (E. C. Geiger, Box 285, Harleysville, PA), transplanted individually into 14-cm-diameter × 12.7-cm-deep plastic pots or 1.9-L ceramic crocks with infested potting mix and

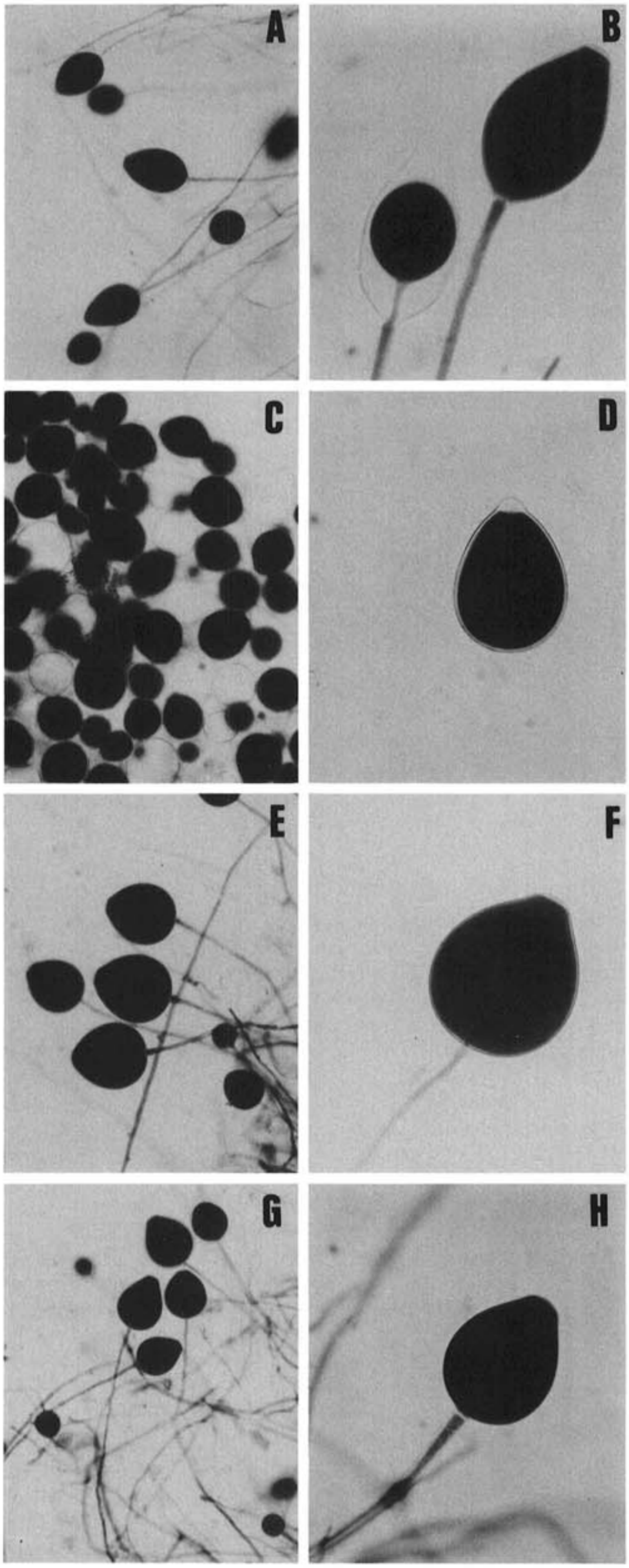

Fig. 1. Sporangia of *Phytophthora* spp. that cause root and crown rot of English walnut trees in California. Sporangia developed on disks of V8 agar medium flooded with 1.5% soil extract at 24 C. (**A and B**) *Phytophthora drechsleri*: **A,** Sporangia developing after 10 hr (×150); **B,** Typical sporangium (×375). (**C and D**) *P. parasitica*; **C,** Sporangia developing after 18 hr (×150); **D,** Typical sporangium (×375). (**E and F**) *Phytophthora* sp. (W489R): **E,** Sporangia developing after 10 hr (×150); **F,** Typical sporangium (×375). (**G and H**) *Phytophthora* sp. (2833); **G,** Sporangia developing after 9 hr. (×150); **H,** Typical sporangium (×375).

maintained for 3 mo in the greenhouse. During the entire experimental period, the potting mix temperature ranged from 17 to 23 C. Plants were fertilized weekly with an aqueous mixture of $Ca(NO_3)_2$, iron chelate, and Nutri-min minor element concentrate (E. C. Geiger).

To enhance disease development, each seedling was flooded once every 2 wk for 48 hr by placing the plastic pot in a 16.5-cm-diameter × 13-cm-deep container filled with water so that approximately 1 cm of water stood on the surface of the potting mix. When crocks were used, the drain-hole was plugged and water was added to a depth of 1 cm above the potting mix surface for 48 hr once every 2 wk. Between flooding treatments, the seedlings were watered as needed and the potting mix was allowed to drain freely. After 3 mo, the experiments were terminated and disease severity was evaluated. Trunk canker severity was rated by using a trunk-girdling index (10) in which: 0 = no crown rot; 1 = up to 25% of the trunk circumference cankered; 2 = up to 50% of the trunk circumference cankered; 3 = up to 75% of the trunk circumference cankered; and 4 = completely girdled trunk, plant dead. Each experiment was repeated at least twice and, as each repeated experiment yielded comparable results, data from individual representative experiments are presented in the results section. Root and crown rot were confirmed as resulting from infection by the appropriate *Phytophthora* spp. by reisolating the pathogens from test walnut seedlings (11).

RESULTS

***Phytophthora* spp. associated with declining walnut orchard trees.** In addition to the *Phytophthora* spp. reported earlier (12), *P. drechsleri, P. parasitica*, and two different but unidentified *Phytophthora* spp. (isolates W489R and 2833) were isolated from decayed rootlets and trunk cankers of walnut trees and from the surrounding soil. The cardinal temperatures, morphology of sporangia, and general morphology of isolates of *P. drechsleri* and *P. parasitica* from walnut trees (Fig. 1A to D) were similar to or within the limits previously reported for these species (11,14,18–20). The isolate of *P. drechsleri* formed no sexual reproductive organs in single culture on clarified V-8 juice agar amended with β-sitosterol (V8β) (11), but it formed oospores when paired with known A2 compatibility types of *P. cryptogea* or *P. drechsleri*. The isolate of *P. parasitica* formed oospores when paired with the A1 compatibility types of *P. cryptogea* or *P. cambivora* (Petri) Buisman.

The two unidentified *Phytophthora* spp. (isolates W489R and 2833) have nonpapillate, broadly ovate sporangia which, upon discharge of zoospores, proliferate internally on single undifferentiated sporangiophores (Fig. 1E to H). The sporangia of isolate W489R were 40–65 μm long × 35–58 μm wide (average of 50 sporangia, 53 × 45 μm) with an average length/width ratio of 1.2 when formed at 21 C. Minimum, optimum, and maximum temperatures for growth on corn meal agar (CMA) were 6, 21–27, and 33 C, respectively. The sporangia of isolate 2833 were 35–54 μm long × 29–44 μm wide (average of 50 sporangia, 45 × 36 μm) with an average length/width ratio of 1.2 when formed at 21 C. Minimum, optimum, and maximum temperatures for growth of this species were 12, 30–36, and 39 C, respectively. Neither one of these *Phytophthora* spp. formed sexual structures in single culture on V8β, but both produced oospores within oogonia with amphigynous antheridia when paired with known A2 isolates of *P. cryptogea* and *P. drechsleri*.

In summary, isolates W489R and 2833 are both heterothallic, produce amphigynous antheridia, and form nonpapillate sporangia that proliferate internally, which are the characteristics that place these *Phytophthora* spp. in group VI of Waterhouse (19). However, other morphological characters of these isolates do not appear to conform to any described species within this taxonomic group. Further extensive collection, examination, and evaluation of isolates resembling these pathogens will be necessary to determine their taxonomic status. Cardinal growth temperatures and size of sporangia distinquish isolate W489R from isolate 2833. Perhaps these two isolates are variants of one species of *Phytophthora*.

Pathogenicity and relative virulence tests. In initial experiments, we examined the pathogenicity and compared the relative virulence of isolates of *P. cryptogea, P. drechsleri*, and *P. parasitica* from walnut, as well as an isolate of *P. cryptogea* from cherry, to seedlings of walnut rootstock *J. hindsii* in artificially infested potting mix. The results of one of these experiments are summarized in Table 1 and Fig. 2. All four fungi were pathogenic and highly virulent to 2-mo-old seedlings of *J. hindsii* and caused total destruction of roots and crown and death of seedlings.

TABLE 1. Virulence of single isolates of three *Phytophthora* spp. to *Juglans hindsii* (Northern California black walnut) seedlings grown in artificially infested potting mix

Potting mix artificially infested with	Plant growth and disease severity[y]		
	Fresh wt. of roots (g)	Root rot[z] (%)	Plants with crown rot
Control (uninfested)	56 a	12 a	0 a
P. cryptogea (walnut isolate)	5 c	100 b	5 b
P. cryptogea (cherry isolate)	4 c	100 b	5 b
P. drechsleri (walnut isolate)	12 b	100 b	5 b
P. parasitica (walnut isolate)	9 bc	91 b	5 b

[y] Average of five replicate plants per treatment. Numbers in each column with the same letter do not differ according to Duncan's multiple range test, $P = 0.05$.
[z] Percent of root system rotted as estimated by visual observation 3 mo after inoculation. Plants were 2 mo old when planted in artificially infested potting mix. *Phytophthora* was reisolated from rotted roots of all plants grown in infested potting mix, but not from those grown in uninfested potting mix.

Previous findings, that Paradox is significantly more resistant than *J. hindsii* to *P. cactorum, P. citrophthora*, and *P. megasperma*, led to experiments to compare the relative virulence of walnut isolates of *P. citricola, P. cryptogea*, and isolates W489R

TABLE 2. Growth and disease development in *Juglans hindsii* and cultivar Paradox walnut rootstock seedlings grown with walnut isolates of four *Phytophthora* spp. in artificially infested potting mix

Potting mix artificially infested with	Seedlings	Plant growth and disease severity[x]			
		Fresh wt. of root (g)	Root rot[y] (%)	Plants with crown rot	Girdling index[z]
Control (uninfested)	*J. hindsii*	43 a	8 a	0 a	0 a
	Paradox	29 b	6 a	0 a	0 a
P. citricola	*J. hindsii*	3 c	100 d	10 c	4.0 d
	Paradox	10 c	86 cd	10 c	4.0 d
P. cryptogea	*J. hindsii*	9 c	98 d	10 c	3.8 d
	Paradox	11 c	67 b	8 c	2.4 c
Phytophthora sp. (isolate 2833)	*J. hindsii*	10 c	80 bc	10 c	3.6 d
	Paradox	32 b	9 a	9 c	1.6 b
Phytophthora sp. (isolate W489R)	*J. hindsii*	26 b	18 a	4 b	0.7 a
	Paradox	29 b	10 a	1 a	0.1 a

[x] Average of ten replicate plants per treatment. Numbers in each column with the same letter do not differ according to Duncan's multiple range test, $P = 0.05$.
[y] Percent of root system rotted as estimated by visual observation 3 mo after inoculation. Plants were 2 mo old when planted in artificially infested potting mix. *Phytophthora* spp. were reisolated from rotted roots of all plants grown in infested potting mix, but not from those grown in uninfested potting mix.
[z] 0 = no crown rot; 4 = canker completely girdled seedling trunk. See text for details.

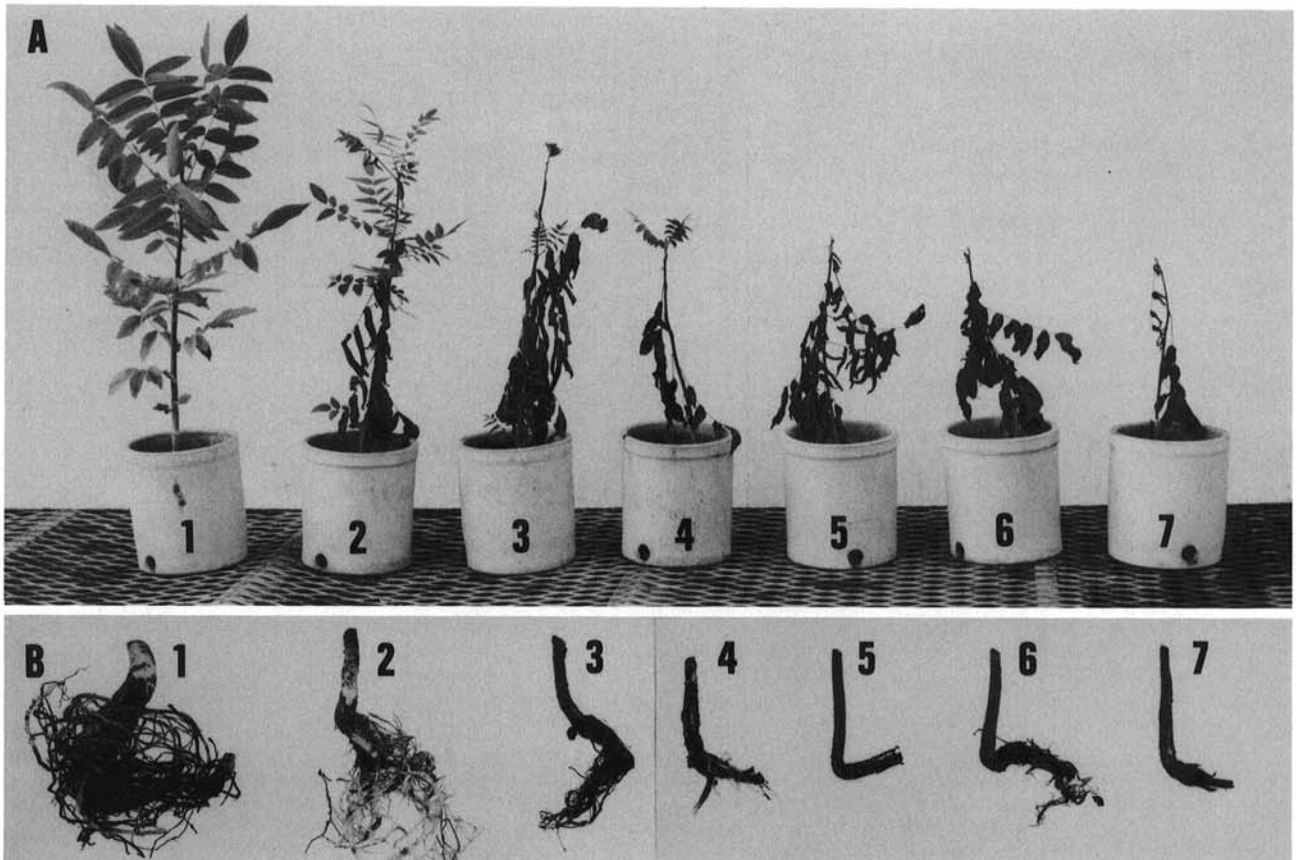

Fig. 2. A, Tops and **B,** roots of 5-mo-old seedlings of *Juglans hindsii* (Northern California black walnut) grown for 3 mo in **1,** noninfested soil or in soil artificially infested with **2,** *Phytophthora* sp. (W489R); **3,** *P. drechsleri*; **4,** *P. parasitica*; **5,** *P. citricola*; **6,** *Phytophthora* sp. (2833); or **7,** *P. cryptogea*.

and 2833 to these rootstocks. Results from one of these experiments are summarized in Table 2. *P. citricola* and *P. cryptogea* were highly virulent and caused severe root and crown rot on seedlings of both *J. hindsii* and Paradox (Table 2). Isolate 2833 also was highly virulent to *J. hindsii*, but it was less virulent to Paradox, causing only moderate crown rot and, relative to controls, no significant root rot or reduction in root fresh weight (Table 2). Isolate W489R was least virulent among all *Phytophthora* spp. that were tested. It caused moderate root and crown rot on J. hindsii but few symptoms on Paradox seedlings (Table 2). Thus, while all four *Phytophthora* spp. were pathogenic to *J. hindsii* and Paradox and were consistently recovered from roots of seedlings 3 mo after planting in artificially infested potting mix, by at least one measure of disease, Paradox was significantly more resistant than *J. hindsii* to the two unidentified isolates.

The pathogenicity of isolates of *P. cactorum, P. cinnamomi*, and *P. citricola* from walnuts and other hosts to seedlings of *J. hindsii* is shown in Tables 3 to 5. Differences are evident in the severity of disease caused by various isolates of each *Phytophthora* sp. (Tables 3 to 5). Although these results suggest variations in the relative virulence to *J. hindsii* between isolates of *P. cactorum, P. cinnamomi*, and *P. citricola*, we found that all isolates were still pathogenic to seedlings of *J. hindsii* and that all were reisolated from rotted roots of all plants grown in infested potting mix. Apparently, *P. cactorum, P. cinnamomi*, and *P. citricola* associated with hosts other than walnuts can infect and cause root and crown rot in the seedlings of walnut rootstock *J. hindsii*.

TABLE 3. Virulence of walnut and nonwalnut isolates of *Phytophthora cactorum* to *Juglans hindsii* walnut rootstock seedlings grown in artificially infested potting mix

	Plant growth and disease severity[x]			
Source of isolate	Fresh wt. of roots (g)	Root rot[y] (%)	Plants with crown rot	Girdling index[z]
Control	71	15	0	0
Walnut (911)	38	67	5	3.2
Walnut (1473)	14	97	5	3.6
Walnut (1927)	64	34	3	1.2
Walnut (2317)	37	65	5	3.6
Coast live oak (1129)	20	78	5	3.4
Toyon (1643)	30	58	5	2.8
Apricot (2947)	33	66	5	2.8
Almond (2743)	50	25	2	1.0
Apple (2837)	59	48	5	2.6
Strawberry (1735)	56	32	1	0.6

[x] Average of five replicate plants per treatment. Plants were 2 mo old when planted in artificially infested potting mix.
[y] Percent of root system rotted as estimated by visual observation 3 mo after inoculation. *Phytophthora cactorum* was reisolated from decayed roots of all plants grown in infested potting mix, but not from those grown in uninfested potting mix.
[z] 0 = no crown rot; 4 = canker completely girdled seedling trunk. See text for details.

DISCUSSION

Results of this study show that *P. drechsleri, P. parasitica*, and two different, but unidentified isolates of *Phytophthora* spp. (W489R and 2833), in addition to the *Phytophthora* spp. reported earlier (12), are associated with declining English walnut trees affected with root and/or crown rot in California. Furthermore, pathogenicity studies revealed that *P. cryptogea, P. drechsleri, P. parasitica*, and the two unidentified *Phytophthora* species cause root and crown rot, as well as seedling mortality, in rootstock *J. hindsii*. This report is believed to be the first to implicate these five species as pathogens of *J. hindsii*. *P. parasitica*, however, has been previously reported to cause root and collar rot of *J. regia* (English walnut) in Australia (2).

The severe root and crown rot caused by *P. cryptogea* on both *J. hindsii* and Paradox walnut rootstocks, which are the standard rootstocks in commercial walnut orchards in California (16), suggests that this species, as well as *P. citricola* and *P. cinnamomi* (12) are potentially the most devastating *Phytophthora* spp. that may attack walnuts in California. Additionally, the results suggest that Paradox is more resistant than *J. hindsii* to the two unidentified species. These results complement those of earlier work (12) which showed that Paradox has some resistance to *P. cactorum, P. citrophthora, P. megasperma*, and *Phytophthora* sp. isolate 1029.

Host specificity among isolates of *P. megasperma* and other *Phytophthora* spp. has been reported (5,7,14,15,19). The demonstrated pathogenicity of isolates of *P. cactorum, P. cinnamomi, P. citricola*, and *P. cryptogea* from hosts other than walnut to seedlings of *J. hindsii* suggests that these *Phytophthora* spp. are not host specific and that various hosts may serve as sources of inoculum in California's walnut orchards. For example, walnut trees infected with *P. cinnamomi* have been found adjacent to homesites, where runoff from rainfall or irrigation apparently carried inoculum from diseased ornamentals to susceptible orchard trees. Also, walnut orchards are often found adjoining fruit tree

TABLE 4. Virulence of walnut and nonwalnut isolates of *Phytophthora citricola* to *Juglans hindsii* walnut rootstock seedlings grown in artificially infested potting mix

	Plant growth and disease severity[x]			
Source of isolate	Fresh wt. of roots (g)	Root rot[y] (%)	Plants with crown rot	Girdling index[z]
Control	71	15	0	0
Walnut (521)	4	100	5	4.0
Walnut (2121)	9	100	5	4.0
Walnut (2517)	17	98	5	4.0
Walnut (2823)	3	100	5	4.0
Walnut (W455C)	12	88	5	4.0
Apricot (1329)	21	79	5	3.0
Almond (2811)	22	80	5	3.4
Coast live oak (1125)	27	66	5	3.0
Rhododendron (117)	61	28	2	0.6
Hops (1337)	63	34	0	0

[x] Average of five replicate plants per treatment. Plants were 2 mo old when planted in artificially infested potting mix.
[y] Percent of root system rotted as estimated by visual observation 3 mo after inoculation. *Phytophthora citricola* was reisolated from decayed roots of all plants grown in infested potting mix, but not from those grown in uninfested potting mix.
[z] 0 = no crown rot; 4 = canker completely girdled seedling trunk. See text for details.

TABLE 5. Virulence of walnut and nonwalnut isolates of *Phytophthora cinnamomi* to *Juglans hindsii* walnut rootstock seedlings grown in artificially infested potting mix

	Plant growth and disease severity[w]			
Source of isolate[x]	Fresh wt. of roots (g)	Root rot[y] (%)	Plants with crown rot	Girdling index[z]
Control	71	15	0	0
Walnut (947)	21	73	3	1.8
Walnut (1011)	11	95	5	3.8
Walnut (2141)	10	95	5	3.8
Walnut (2835)	6	97	5	3.4
Apricot (217)	5	99	5	4.0
Blueberry (2721)	4	100	5	3.8
Camellia (433)	14	78	5	2.2
Cork oak (1135)	12	89	5	3.2
Avocado (215)	52	31	1	0.6

[w] Average of five replicate plants per treatment. Plants were 2 mo old when planted in artificially infested potting mix.
[x] All isolates are A2 mating type except camellia, which is A1 mating type.
[y] Percent of root system rotted as estimated by visual observation 3 mo after inoculation. *Phytophthora cinnamomi* was reisolated from decayed roots of all plants grown in infested potting mix, but not from those grown in uninfested potting mix.
[z] 0 = no crown rot; 4 = canker completely girdled seedling trunk. See text for details.

orchards infested with *P. cactorum, P. cinnamomi, P. citricola*, and *P. cryptogea*, and these pathogens could be spread between orchards. In fact, all four of these *Phytophthora* spp. are widely distributed in California and occur in orchards as well as in ornamental plantings (8–13,17,22,23). Their pathogenicity to *J. hindsii* indicates that extreme care should be exercised to avoid the spread of *Phytophthora* spp., regardless of host, from infested areas to walnut orchards by runoff water, contaminated soil, or farm machinery.

Variability in virulence to *J. hindsii* was noted among isolates of all *Phytophthora* spp. from walnut and from other hosts. In general, this variability has been encountered most often with isolates of *P. cactorum* and *P. drechsleri* in our tests with rootstock *J. hindsii*. Results of our studies support reports on variation in virulence among isolates of *P. cinnamomi* (3,6,21,23) and point out the importance of considering possible variability when evaluating rootstocks for resistance to certain *Phytophthora* spp.

The results show the importance of identifying *Phytophthora* spp. when considering strategies for disease control in affected walnut orchards. For example, the use of Paradox rootstock would be beneficial at walnut orchard sites infested with *P. cactorum, P. citrophthora, P. megasperma*, or the two unidentified *Phytophthora* spp. However, Paradox would not offer significant resistance to *P. cinnamomi, P. citricola*, or *P. cryptogea*, particularly in orchard sites subject to periodic or prolonged soil saturation. The high susceptibility of rootstock *J. hindsii* and Paradox to these three *Phytophthora* spp. with intermittent periods of soil saturation suggests a need for further research on the effects of soil water and specific saturation periods on disease severity. Also, the search for potential new walnut rootstocks and their evaluation for relative resistance to these *Phytophthora* spp. should be given a high priority.

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