Phytophthora Root and Crown Rot of Walnut Trees

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ABSTRACT

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Phytophthora cactorum, P. citricola, P. cinnamomi, P. citrophthora, P. megasperma, P. cryptogea, and four different, but unidentified, *Phytophthora* spp. were isolated repeatedly from decayed roots or trunk cankers of dead and dying English walnut trees (*Juglans regia*) affected by root and crown rot in California commercial orchards. In artificially infested soil, *P. cactorum, P. citricola, P. cinnamomi, P. citrophthora*, and one unidentified *Phytophthora* sp. (isolate 1029) induced root rot and/or crown rot, whereas *P. megasperma* caused feeder root necrosis only in seedlings of Northern California black walnut (*Juglans hindsii*) and Paradox (*J. hindsii* × *J. regia*) which are the standard rootstocks of *J. regia* in California commercial orchards. Symptoms developed on seedlings of rootstocks of *J. regia* in artificially infested soil were the same as those observed in the rootstock portion of naturally infected orchard trees of *J. regia*. *P. citricola, P. cactorum, P. cinnamomi*, and *P. citrophthora* were more virulent than *P. megasperma* or *Phytophthora* sp. (1029) to seedlings of *J. hindsii* used as rootstocks. In artificially infested soil, seedlings of Paradox rootstock were significantly more resistant than those of *J. hindsii* to *P. cactorum, P. citrophthora, Phytophthora* sp. (1029), and *P. megasperma*, whereas seedlings of *J. regia* used as a rootstock was as highly susceptible as was *J. hindsii* to *P. cactorum, P. cinnamomi, P. megasperma*, and *P. citricola*. This is the first report implicating *P. cinnamomi, P. citricola, P. citrophthora, P. megasperma*, and *Phytophthora* sp. (1029) directly in root and/or crown rot and decline and/or death of *J. regia* trees in California commercial orchards.

Additional key words: Persian walnut, resistance of walnut rootstocks, soilborne diseases, "wet feet".

Root and crown rot resulting in decline and death of English walnut trees (*Juglans regia*) has increased during the last 15 yr in numerous California commercial orchards and presently is epidemic (Fig. 1A). Where *Armillaria mellea* (13,14,17) was not involved, tree decline and death was usually attributed to "wet feet" (14,17). The highest incidence of root and crown rot in walnut trees usually occurs on poorly drained sites subject to periodic flooding and prolonged soil saturation from excessive rainfall or irrigation.

Our surveys of commercial walnut orchards in California revealed that the highest incidence of root and crown rot usually, but not always, occurs in orchards where free water periodically stood around the lower trunk of the trees. We also observed that affected trees in certain orchards had only root rot whereas trees in other orchards had only crown rot and bark canker, the latter often extending into the trunk and occasionally into lower scaffold branches ⩾2 above ground level. We also observed that in certain orchards trees of *J. regia* propagated on Paradox (Northern California black walnut, *J. hindsii* × *J. regia*) rootstock were free of crown rot while trees propagated on rootstock of *J. hindsii* (Jeps.) Jeps. in the same orchard were severely damaged by crown rot. In other orchards, however, we noted an equally high incidence of declining and dead trees propagated on either Paradox or *J. hindsii* due to root and/or crown rot. Disease symptoms suggested a pathogenic cause. The sporadic and inconsistent association of *A. mellea* with affected walnut trees, the atypical symptoms, and the varying incidence of affected trees propagated on Paradox and *J. hindsii* in different orchards suggested that *Phytophthora* spp., rather than *A. mellea*, may be implicated in the decline and death of walnut trees in California commercial orchards. We repeatedly isolated several *Phytophthora* spp. from decayed roots and bark cankers. The same *Phytophthora* spp. were also readily recovered from soil in affected walnut orchards.

Although several reports of *Phytophthora* spp. isolated from other than *J. hindsii* or Paradox rootstocks are available (3,5,6–8,22), only *P. cactorum* has been experimentally implicated in crown rot of *J. regia* propagated on *J. hindsii* and also on rootstocks of Southern California black walnut (*J. californica*) in commercial orchards (2,16). *P. citricola* has been experimentally implicated in crown rot of *J. nigra* in nursery trees (8), but it is not a recognized problem in natural stands (7).

The present studies were undertaken to identify *Phytophthora* spp. on declining and dead walnut trees and to determine their role in root and crown rot of walnut trees in California commercial orchards. A short account of this work was reported (12).

MATERIALS AND METHODS

Isolation and identification of *Phytophthora* spp. from infected trees and from soils. Species of *Phytophthora* were isolated from decayed rootlets and fragments of decayed bark from the trunk cankers of diseased walnut trees plated on pimaricin-vancomycin (PVP) selective medium as described previously (11). Segments of decayed rootlets ~2 cm long were dipped in 70% ethyl alcohol, dried on a paper towel, and pressed into the agar surface in plates of selective medium. Small pieces (~2×2 mm) of bark collected from the margins of advancing cankers on the trunk or larger roots were similarly surface-sterilized and plated. Twenty to 40 root and/or bark pieces were plated from each tree. The plates were incubated at 18 C in darkness and examined daily for 10 days for growth of *Phytophthora* spp. from the plated tissue.

Isolation of *Phytophthora* spp. from soil was accomplished by using ripe, green, unblemished Bartlett pear fruits as bait (11).

Phytophthora spp. developing on PVP plates were transferred to and maintained on V-8 juice agar (V8A). Cardinal temperatures for vegetative growth and colony type of various isolates were determined on cornmeal agar (CMA). Features of reproductive structures were studied as previously described (11). The walnut

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isolates of *Phytophthora* spp. were identified from descriptions of Frezzi (6), Tucker (19), and Waterhouse (20,21).

Pathogenicity tests. Pathogenicity of walnut isolates of *P. citricola* Sawada, *P. cactorum* (Leb. & Cohn) Schroet., *P. cinnamomi* Rands, *P. megasperma* Drechsler, *P. citrophthora* (R. E. Smith & E. H. Smith) Leonian, and an unidentified *Phytophthora* sp. (isolate 1029) to seedlings of *J. hindsii* Paradox (*J. hindsii* × *J. regia*) and *J. regia* L. 'Eureka' was determined under greenhouse conditions. *J. hindsii* and Paradox seedlings are standard walnut rootstocks in California commercial orchards (14). Paradox is a first-generation hybrid from seed of *J. hindsii* that was naturally pollinated by *J. regia*. Inocula for pathogenicity

Fig. 1. Orchard English walnut (*Juglans regia*) trees naturally affected by Phytophthora root and crown rot. **A,** Twenty-five-year-old *J. regia* 'Eureka' on *J. hindsii* rootstock in a commercial orchard with a high incidence of dead trees due to Phytophthora root and crown rot. **(B to D)** Twenty-year-old orchard *J. regia* trees. **B,** Healthy tree, showing dense foliage and vigorous terminal shoots. **C,** Declining tree infected with *Phytophthora cactorum*; note small, chlorotic, drooping leaves, sparse foliage, and lack of growth in terminal shoots; **Inset,** Lower trunk of the tree in C with typical crown rot symptoms; note dead bark and upper margin of the canker (arrow) near the ground level. **D,** Tree collapsed due to infection by *Phytophthora citricola*, which caused rapid development of extensive crown rot and trunk canker. **Inset,** Trunk of the tree in D showing typical trunk canker with the upper margin (arrow) near the scaffold branches.

tests were isolates of *Phytophthora* grown for 4–6 wk on vermiculite moistened with V-8 juice broth (11), then mixed with steam-pasteurized U.C. mix (1) at the rate of 12.5 to 25 cc of infested vermiculite/1,000 cc of the U.C. mix. The controls received vermiculite with V-8 juice broth, but no *Phytophthora*. Three- to 4-mo-old seedlings of *J. hindsii*, Paradox, and *J. regia* growing in steam-pasteurized U.C. mix in 7.6×7.6-cm Jiffy pots (E. C. Geiger, Harleysville, PA 19438) were transplanted into 1.9-L crocks with artificially infested U.C. mix and grown for 3 mo in the greenhouse. Ambient temperature in the greenhouse was alternated and maintained at 16 ± 3 C during night and at 21 ± 3 C during the day. Soil temperature in the crocks ranged from 18 to 22 C during the entire experimental period. The plants were fertilized weekly with 20-20-20 (N-P-K) water-soluble general purpose fertilizer and Nutra-min minor element concentrate (E. C. Geiger) throughout the experimental period. To simulate periodic excesses of soil moisture that occur during irrigation in poorly drained commercial walnut orchards, the pots were water-saturated periodically by flood-irrigation. Each container was flooded every 2 wk and free water was allowed to stand on the soil surface and around the lower trunks of the seedlings for 48 hr. Between floodings, the seedlings were watered as needed. Root and crown rot were confirmed to result from *Phytophthora* spp. by reisolation of the pathogens from test walnut seedlings. Each treatment consisted of five replicates. Each experiment was repeated at least twice; but, since the data are similar, only those from one of the experiments are presented in the results section.

RESULTS

***Phytophthora* spp. associated with walnut trees and field symptoms of the disease.** Ten apparently different *Phytophthora* spp. were repeatedly isolated from soil collected in walnut orchards affected by crown and root rot. The same species were also isolated consistently from decayed rootlets and trunk cankers of walnut trees. More than one *Phytophthora* species often was recovered from an orchard and occasionally from the same tree. Isolation success was best from late fall through early spring and was sporadic and difficult from May through September. *Phytophthora* spp. were recovered from declining and dead trees ranging in age from 1 to >60 yr.

The specific symptoms of infected walnut trees in orchards, such as the presence of crown rot (Fig. 1C), trunk canker (Fig. 1D), or root rot, differed with the particular *Phytophthora* sp., but generally aboveground symptoms were usually common in all declining trees (Fig. 1A, C, and D) irrespective of the *Phytophthora* spp. involved. The first observable aboveground symptoms of infected trees are lack of growth in terminal shoots with small and chlorotic leaves (Fig. 1B and C). Trees with early symptoms show decay of feeder roots and some smaller secondary roots or they may have trunks partially girdled by crown rot (Fig. 1C inset) and/or trunk cankers (Fig. 1D inset). As the disease progresses, the trees exhibit drooping and severely chlorotic leaves, partial defoliation and dieback of terminal shoots, and general defoliation followed by death of entire trees (Fig. 1D). The trees usually die shortly after the root system was decayed or after the trunk is girdled by crown rot or trunk cankers. The time interval between infection and death depended on the relative virulence of the *Phytophthora* sp. involved. Generally younger, smaller, and vigorously growing trees declined faster and died sooner than older, larger, and less vigorous trees. Trees affected with crown rot or trunk canker declined more rapidly than did trees affected with root rot only.

Isolates recovered from walnut trees were identified as *P. citricola* Sawada, *P. cactorum* (Leb. & Cohn) Schroet., *P. citrophthora* (R. E. Smith & E. H. Smith) Leonian, *P. cinnamomi* Rands, *P. megasperma* Drechsler, and *P. cryptogea* Pethyb. & Laff. The general morphology of cultures, morphology of sporangia and oospores, as well as cardinal temperature of the walnut isolates of *P. megasperma*, were similar to those reported for cherry isolates of *P. megasperma* (11). The taxonomic characters of the isolates of *P. cactorum* from walnut trees (Fig. 2A and B), *P. citricola* (Fig. 2C and D), *P. cinnamomi* (Fig. 2E), *P. citrophthora* (Fig. 2F), and *P. cryptogea* were either similar or within the limits reported previously for these species (6,19–22). In addition to the above species, we recovered four apparently different, but as yet unidentified, *Phytophthora* spp. The unidentified *Phytophthora* spp. have nonpapillate, ovate-to-ellipsoidal sporangia (Fig. 1G). They differ from each other in colony type, hyphal morphology, cardinal temperatures, and in morphology and size of sporangia. They formed no sexual reproductive organs in single culture, but formed oospores when paired with known A^2 compatibility types of *P. cinnamomi* or *P. drechsleri* Tucker. None of the tested walnut isolates of the unidentified *Phytophthora* spp. produced sex organs in paired cultures with known A^1 compatibility types of the above species.

P. citricola, P. cactorum, and *P. citrophthora* were repeatedly recovered in orchards with a large number of walnut trees rapidly declining and dying due primarily to crown rot (Fig. 1C and inset) and/or trunk canker (Fig. 1D and inset). *P. citricola* and *P. cactorum* were recovered from numerous California commercial orchards in many walnut producing areas as far north as Tehama County and as far south as Tulare County. Often both of these species were present in the same orchards. However, *P. citrophthora* was recovered from only three different walnut orchards that had 7, 9, and 13% of the trees, respectively, affected with crown rot and/or trunk canker. In orchards with trees propagated on *J. hindsii* and Paradox rootstocks and infected with *P. cactorum* we observed decline and death of numerous walnut trees on *J. hindsii* due to an extensive crown rot in the rootstock while adjacent trees on Paradox rootstock were unaffected (Fig. 3A). The dying or dead trees of *J. regia* on *J. hindsii* exhibited extensive crown rot that often girdled the rootstock, whereas the symptomless trees on Paradox rootstock in the same orchard had crown rot only on a few trees that had very limited and very slowly advancing cankers in the Paradox rootstock. We isolated *P. cactorum* from crown rot of both *J. hindsii* and Paradox rootstocks. However, when a narrow and upward advancing canker caused by *P. cactorum* in Paradox rootstock reached the graft union, it invaded the English walnut scion, resulting in rapid and extensive canker development that girdled the trunk and caused quick decline of the tree. These observations indicated that under field conditions *J. hindsii* and scion of *J. regia* are significantly more susceptible than Paradox walnut rootstocks to *P. cactorum*. However, in several orchards infested with *P. citricola* alone, extensive crown rot and decline was observed in trees of *J. regia* on both *J. hindsii* and Paradox rootstocks.

P. cinnamomi was recovered from six different orchards with large numbers of declining and dead trees displaying primarily a severe root rot, although crown rot was observed in an occasional declining tree in the upper San Joaquin Valley. Orchard walnut trees on rootstock of both *J. hindsii* and Paradox were usually severely affected with this pathogen under field conditions.

P. megasperma was recovered from orchard walnut trees exhibiting stunted growth of terminal shoots, small chlorotic leaves and very slow decline due to necrosis of feeder and small secondary roots. This pathogen is distributed throughout California's walnut growing regions. Walnut orchard trees were more severely affected by this pathogen when propagated on *J. hindsii* rather than on Paradox rootstock. *P. cryptogea* causing extensive root rot was recovered from only a few orchards with a large number of declining walnut trees on rootstocks of both *J. hindsii* and Paradox.

Four unidentified *Phytophthora* spp. were recovered occasionally from orchard walnut trees that were declining due primarily to root rot. All of these *Phytophthora* species were less common on declining walnut trees than the six identified species. Unidentified *Phytophthora* spp. (1029) (Fig. 2G) appears to be more common than the other three. In two commercial orchards infested only with *Phytophthora* sp. (1029), we observed many declining trees on rootstocks of *J. hindsii* that exhibited both root and crown rot, whereas adjacent trees on Paradox rootstock appeared healthy.

Pathogenicity tests. In two different experiments we compared the relative virulence of walnut isolates of *P. cinnamomi, P. cactorum, P. megasperma*, and an unidentified *Phytophthora* sp.

(1029) to *J. hindsii* and Paradox walnut rootstock seedlings in artificially infested soil. The results from one of these duplicate experiments are summarized in Table 1 and Fig. 4. *P. cinnamomi* was highly virulent to 6-mo-old seedlings of *J. hindsii* and Paradox; it completely destroyed root systems, rotted crowns, and killed both walnut rootstocks (Table 1, Fig. 4Ac, Bc, Cc, and Dc). *P. cactorum* was highly virulent to *J. hindsii*; it caused severe crown rot and killed all seedlings (Table 1, Fig. 4Ab and Bb; Fig 5Ab). In contrast, Paradox seedlings in soil infested with this pathogen were comparable to controls (Fig. 4Cab and Dab). *P. cactorum* caused only a negligible canker in one of five and killed no Paradox seedling (Table 1, Fig. 5Bb). Similarly, *Phytophthora* sp. (1029) was more virulent to *J. hindsii* than to Paradox (Table 1, Fig. 4Ad, Bd, Cd, and Dd; Fig. 5Bc). *P. megasperma* was least virulent of the four *Phytophthora* spp.; it caused only feeder root necrosis and no crown rot or death in either *J. hindsii* or Paradox (Table 1), although seedlings of *J. hindsii* were more stunted and more affected with this pathogen than were Paradox seedlings (Fig. 4Ae, Be, Ce, and De). Apparently, all four *Phytophthora* spp. used in these experiments are pathogenic to rootstocks *J. hindsii* and Paradox. However, these results also showed that *P. cinnamomi* and *P. cactorum* are more virulent to *J. hindsii* than are *Phytophthora* sp. (1029) and *P. megasperma*, and that Paradox is significantly more resistant than *J. hindsii* to *P. cactorum*, *Phytophthora* sp. (1029) and *P. megasperma* (Table 1, Figs. 2, 4, and 5).

The previous reports that *J. regia* is more resistant than *J. hindsii* to *P. cactorum* (2,9,18) and to *P. cinnamomi* (9) and that seedlings of *J. regia* are highly resistant to and could be used for control of Phytophthora crown rot (9,14,16), prompted a series of

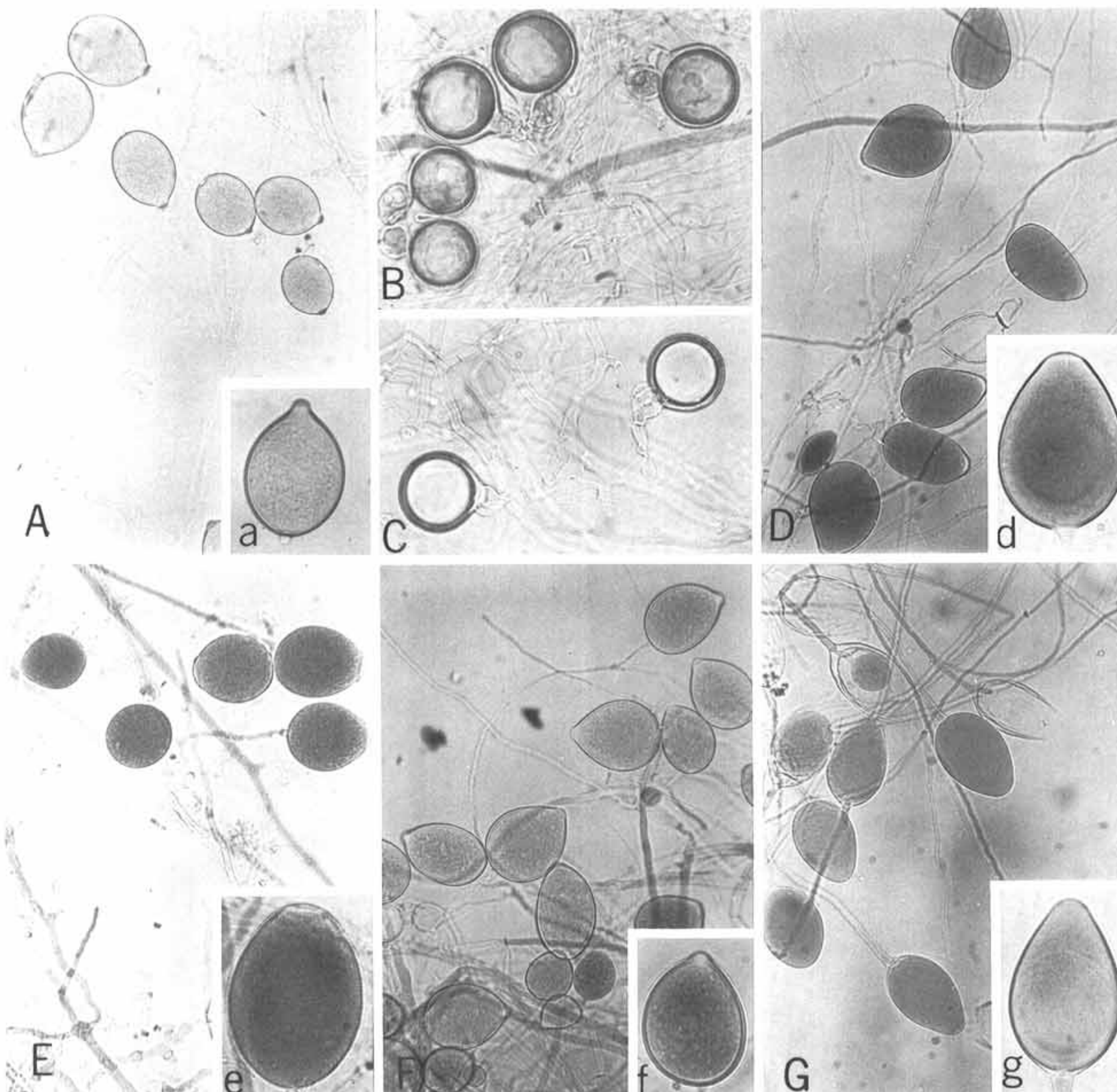

Fig. 2. Characteristic sporangia and oospores of *Phytophthora* spp. that cause crown and root rot of English walnut (*Juglans regia*) trees. **(A and B)** *Phytophthora cactorum*. **A,** Sporangia that developed on disks of V8 agar medium (V8A) flooded with 1.5% soil extract after 41 hr at 23 C (×300). **Inset,** Typical sporangium (×480). **B,** Typical oogonia and oospores with paragynous antheridia (×480). **(C and D)** *P. citricola*. **C,** Typical oogonia and oospores with paragynous antheridia (×480). **D,** Sporangia that developed on disks of V8A flooded with 1.5% soil extract after 23 hr at 23 C (×300). **Inset,** Typical sporangium (×480). **E,** *P. cinnamomi*, sporangia that developed on disks of V8A flooded with 1.5% soil extract after 49 hr at 23 C (×300). **Inset,** Typical sporangium (×480). **F,** *P. citrophthora* sporangia that developed on disks of V8A flooded with 1.5% soil extract after 22 hr at 23 C (×300). **Inset,** Typical sporangium (×480). **G,** *Phytophthora* sp. (isolate 1029) sporangia that developed on disks of V8A flooded with 1.5% soil extract after 22 hr at 23 C (×300). **Inset,** Typical sporangium (×480).

experiments on the relative resistance of rootstocks *J. regia*, *J. hindsii*, and Paradox to *P. citricola*, *P. cactorum*, *P. megasperma*, and *P. cinnamomi*. The results from one of two experiments are summarized in Table 2. Seedlings of all three walnut rootstocks (*J. regia*, *J. hindsii*, and Paradox) were highly susceptible to *P. citricola* (Table 2). Likewise, the three walnut rootstocks were also highly susceptible to *P. cinnamomi* (Table 2) which causes primarily severe root rot in walnut orchard trees in California. Seedlings of *J. regia* and *J. hindsii* appeared equally and highly susceptible to *P. cactorum*, whereas Paradox seedlings were significantly more resistant (Table 2). *P. megasperma* was less virulent to rootstocks *J. hindsii* and *J. regia* than the above-mentioned three *Phytophthora* spp., but was equally virulent to both.

In these investigations, we recovered *P. citrophthora* from declining orchard trees of *J. regia* propagated on rootstocks *J. hindsii* and Paradox that were affected with crown rot and/or trunk canker. Our pathogenicity tests showed that the walnut isolate of *P. citrophthora* is pathogenic to seedlings of both *J. hindsii* and Paradox and it had similar virulence to that of *P. cactorum* to these walnut rootstocks (Table 3). Furthermore, Paradox was similarly and significantly more resistant than rootstock *J. hindsii* to both *P. citrophthora* and *P. cactorum* (Table 3).

DISCUSSION

Our investigation showed that *P. cactorum*, *P. cinnamomi*, *P. cryptogea*, *P. citricola*, *P. citrophthora*, *P. megasperma*, and four different unidentified *Phytophthora* spp. are associated with declining and dead orchard trees of *J. regia* affected with root and/or crown rot and trunk cankers.

Our survey and isolation of *Phytophthora* from California's

TABLE 1. Relative virulence of four *Phytophthora* spp. to Northern California black walnut (*Juglans hindsii*) and Paradox hybrid (*J. hindsii* × *J. regia*) walnut rootstock seedlings in artificially infested soil

Soil artificially infested with	Rootstock	Avg.[x] growth and disease severity				
		Fresh wt. (g)		Root rot[y] (%)	Ratio[z] of plants:	
		Tops	Roots		crown rotted	dead
P. cinnamomi	*J. hindsii*	6 efg	3 g	100 a	5/5 e	5/5 e
	Paradox	2 g	5 g	98 a	4/5 e	4/5 ef
P. cactorum	*J. hindsii*	5 g	5 g	88 ab	5/5 e	5/5 f
	Paradox	37 c	100 e	31 ef	1/5 f	0/5 g
Phytophthora sp. (1029)	*J. hindsii*	16 defg	30 fg	33 ef	4/5 ef	1/5 f
	Paradox	29 cd	97 e	30 ef	1/5 f	0/5 g
P. megasperma	*J. hindsii*	26 cd	69 e	43 ef	0/5 g	0/5 g
	Paradox	24 cde	83 ef	31 ef	0/5 g	0/5 g
Control	*J. hindsii*	27 cd	67 ef	5 g	0/5 g	0/5 g
	Paradox	23 cdef	91 e	6 g	0/5 g	0/5 g

[x] Average of five replicates per treatment. Numbers with the same letter do not differ from each other ($P = 0.05$) according to Duncan's multiple range test.
[y] Percent of root system rotted as estimated by visual observations 3 mo after inoculation.
[z] Number of plants with crown rot or dead per number of plants in the treatment within 3 mo. Plants were 3 mo old when planted in artificially infested soil.

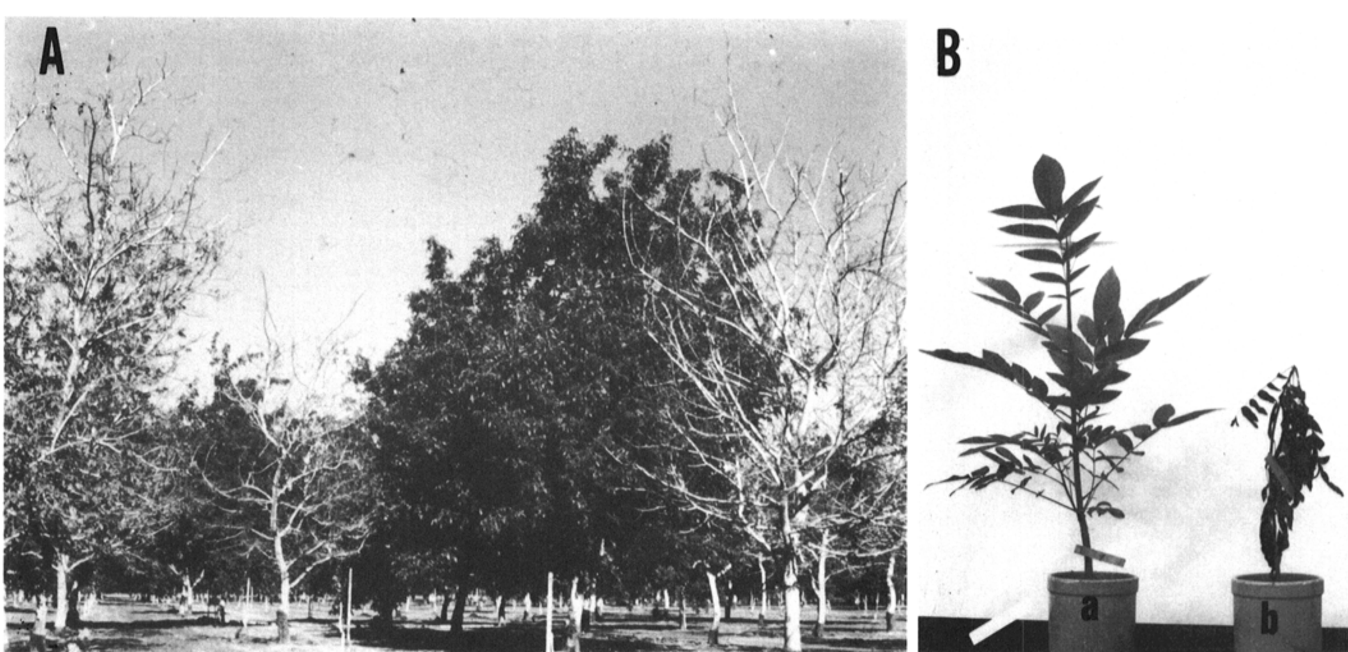

Fig. 3. Differential susceptibility of Northern California black walnut (*Juglans hindsii*) and Paradox (*J. hindsii* × English walnut [*J. regia*]) rootstocks to crown rot caused by *Phytophthora cactorum*. **A,** Nineteen-year-old dead or dying trees of *J. regia* top worked on *J. hindsii* surrounding a vigorous, unaffected tree of *J. regia* top worked on Paradox in a commercial orchard naturally infested with *P. cactorum*. **B,** Seven-month-old Paradox seedling (inset a) and *J. hindsii* seedling (inset b) grown for 3 mo in soil artificially infested with an isolate of *P. cactorum* recovered from the orchard shown in A.

commercial orchards during the last 9 yr strongly indicate that *P. citricola, P. cactorum,* and *P. megasperma* have a wide geographical distribution and are more prevalent in walnut orchards than are *P. cinnamomi, P. cryptogea, P. citrophthora,* and the four unidentified *Phytophthora* spp. Furthermore, our field observation on the severity and incidence of declining trees and our pathogenicity tests also suggests that among the 10 *Phytophthora* spp. studied, *P. citricola* and *P. cinnamomi* are the most destructive to walnut trees and are potentially the most serious threat to the walnut industry in California. *P. cactorum* has been previously shown to cause crown rot of trees of *J. regia* propagated on *J. californica, J. hindsii,* and *J. californica* × *J. regia* rootstocks in California (2,16). *P. cinnamomi* has been reported to cause root rot in nursery stock of Eastern black walnut (*J. nigra*) and seedlings of *J. regia* (3,4,22), while *P. citricola* was shown to be the causal agent of crown rot of *J. nigra* (7,8) in forest nurseries in the Eastern part of the United States. The present work is believed to be the first to establish by pathogenicity tests the role of *P. cinnamomi, P. citricola, P. citrophthora, P. megasperma,* and an unidentified *Phytophthora* sp. (1029) as pathogens of *J. hindsii* and

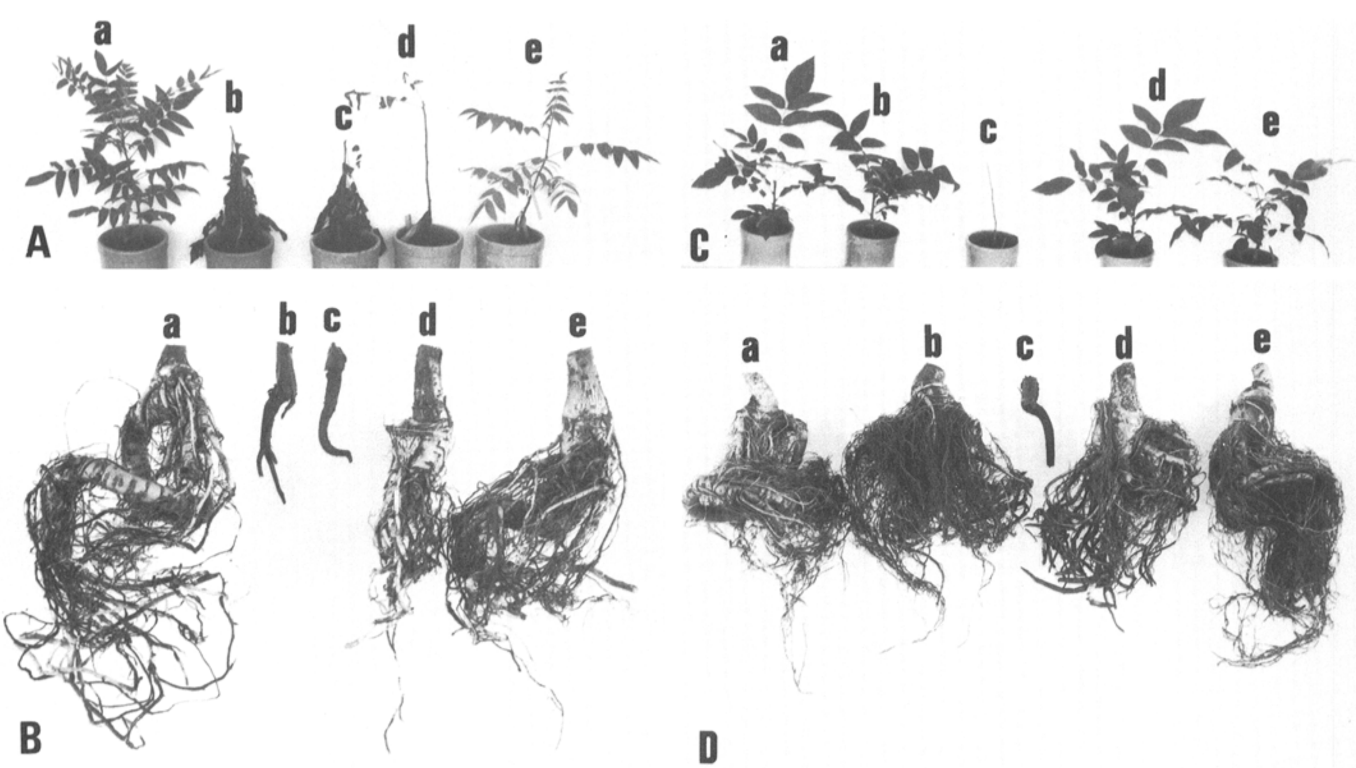

Fig. 4. Tops and roots of 6-mo-old seedlings of Northern California black walnut (*Juglans hindsii*) **(A and B)** and Paradox (*J. hindsii* × English walnut [*J. regia*]) **(C and D)** grown for 3 mo in noninfested soil (a) and artificially infested soil with *Phytophthora cactorum* (b), *P. cinnamomi* (c), *Phytophthora* sp. (isolate 1029) (d), and *P. megasperma* (e). Note that all four *Phytophthora* spp. (b, c, d, and e) caused visible damage to *J. hindsii* **(A and B)** whereas only *P. cinnamomi* (c) severely affected Paradox seedlings **(C and D)**.

TABLE 2. Relative growth and disease development of *Juglans regia, J. hindsii,* and Paradox hybrid (*J. hindsii* × *J. regia*) walnut rootstock seedlings when planted in soil artificially infested with three *Phytophthora* species

Soil artificially infested with	Rootstock	Avg.[x] growth and disease severity: Fresh wt. (g) Tops	Fresh wt. (g) Roots	Root rot[y] (%)	Ratio[z] of plants: crown rotted	Ratio[z] of plants: dead
P. citricola	*J. regia*	1 d	1 d	100 a	5/5 a	5/5 a
	J. hindsii	5 d	1 d	100 a	5/5 a	5/5 a
	Paradox	2 d	2 d	100 a	5/5 a	5/5 a
P. cactorum	*J. regia*	14 bcd	27 d	82 a	4/5 a	4/5 a
	J. hindsii	15 bcd	26 d	73 a	4/5 a	4/5 a
	Paradox	51 a	138 a	5 b	1/5 b	0/5 c
P. cinnamomi	*J. regia*	2 d	2 d	100 a	5/5 a	5/5 a
	J. hindsii	5 d	2 d	100 a	5/5 a	5/5 a
	Paradox	9 bcd	11 d	85 a	5/5 a	2/5 b
Control	*J. regia*	22 bc	78 bc	5 b	0/5 b	0/5 c
	J. hindsii	53 a	106 ab	4 b	0/5 b	0/5 c
	Paradox	43 a	116 ab	3 b	0/5 b	0/5 c

[x] Based on five replications per treatment. Numbers with the same letter do not differ from each other ($P = 0.05$) according to Duncan's multiple range test.
[y] Percent of root system rotted as estimated by visual observations 3 mo after inoculation.
[z] Number of plants with crown rot or dead per number of plants in the treatment within 3 mo. Plants were 4 mo old when planted in artificially infested soil.

TABLE 3. Comparative growth and disease development of *Juglans hindsii* and Paradox hybrid (*J. hindsii* × *J. regia*) walnut rootstock seedlings in soil artificially infested with *Phytophthora citrophthora* and *P. cactorum*

Soil artificially infested with	Rootstock	Avg.[x] growth and disease severity				
		Fresh wt. (g)		Root rot[y] (%)	Ratio[z] of plants:	
		Tops	Roots		crown rotted	dead
P. cactorum	*J. hindsii*	10 b	25 b	83 a	5/5 a	4/5 a
	Paradox	36 ab	74 a	42 b	2/5 ab	0/5 b
P. citrophthora	*J. hindsii*	8 b	25 b	96 a	5/5 a	4/5 a
	Paradox	11 b	57 ab	40 b	2/5 ab	1/5 b
Control	*J. hindsii*	15 ab	65 ab	10 c	0/5 b	0/5 b
	Paradox	11 b	77 a	11 c	0/5 b	0/5 b

[x]Based on five replicates per treatment. Numbers with the same letter do not differ from each other ($P = 0.05$) according to Duncan's multiple range test.
[y]Percent of root system rotted as estimated by visual observation 3 mo after inoculation.
[z]Number of plants with crown rot or dead per number of plants in the treatment within 3 mo. Plants were 4 mo old when planted in artificially infested soil.

Paradox walnut rootstocks and to directly implicate these pathogens as a major primary factor in root and crown rot and decline and death of trees of *J. regia* in commercial orchards in California.

Our survey of commercial deciduous fruit and nut tree orchards affected with crown and root rot revealed that *P. citricola*, *P. cryptogea*, *P. cactorum*, *P. megasperma*, and *Phytophthora* sp. (1029) are widely distributed in California and often are associated, in addition to walnuts, with crown and root rot of: peach (*Prunus persica* (L.) Batsch.), apricot (*P. armeniaca* L.), almond (*P. amygdalus* Batsch.), European plum (*P. domestica* L.), sweet cherry (*P. avium* L.), and apple (*Malus sylvestris* Mill.). Furthermore, *P. cinnamomi* and *P. citrophthora* are widely distributed and are known to be associated with many plant species in California (15,22). We often recovered several and occasionally six different *Phytophthora* spp. in the same orchard, regardless of the fruit or nut tree species. This situation suggests that *Phytophthora* spp. are disseminated among orchards.

Our results disagree with previous contentions that seedlings of rootstock *J. regia* are more resistant to *P. cactorum* and *P. cinnamomi* than rootstocks *J. hindsii* and Paradox (2,9,16). The results of our studies show *J. regia* to be as susceptible as *J. hindsii* to *P. cactorum*, *P. cinnamomi*, *P. megasperma*, and *P. citricola*, whereas Paradox rootstock is significantly more resistant than *J. hindsii* to *P. cactorum*, *P. citrophthora*, *P. megasperma*, and *Phytophthora* sp. (isolate 1029). Paradox exhibited a high degree of resistance to those *Phytophthora* spp., even though we purposely simulated favorable conditions for the disease (eg, periodic soil flooding) in our experiments. Under the same experimental conditions, *P. cinnamomi* and *P. citricola* caused severe root and/or crown rot in rootstock Paradox within the 3-mo experimental period. However, we observed that all seedlings of *J. hindsii* in infested soil usually collapsed within 1 mo, while Paradox seedlings declined more slowly and usually began to die after 2 mo. Likewise, we also observed that orchard walnut trees on poorly drained soil, when infected with *P. cinnamomi* or *P. citricola*, declined slower if on Paradox rootstock than those on rootstock *J. hindsii*. In orchards infested with *P. cinnamomi* or *P. citricola*, located on well drained soil, and under a proper soil-water management, the incidence of declining trees and the rate of decline were notably less in trees on Paradox than in those on rootstock *J. hindsii*. Furthermore, 2-mo-old seedlings of *J. hindsii* and *Paradox* grown in soil artificially infested with *P. citricola* and subjected to flooding by irrigation for periods of 0, 6, 12, 24, and 48 hr every 2 wk resulted in death of all plants of *J. hindsii* within 3 mo, regardless of the irrigation regime. In contrast, within 3 mo, none of the Paradox died at 0 and 6 hr flooding treatment and 20, 40, and 100% of Paradox plants died when subjected to the biweekly flooding periods of 12, 24, and 48 hr, respectively (M. E. Matheron, *unpublished*). Therefore, improvement of internal and surface water drainage in orchards will minimize losses due to Phytophthora root and crown rot. Careful soil-water management in walnut orchards to avoid prolonged and periodic soil saturation or standing water around the base of walnut trees should also help control Phytophthora root and crown rot.

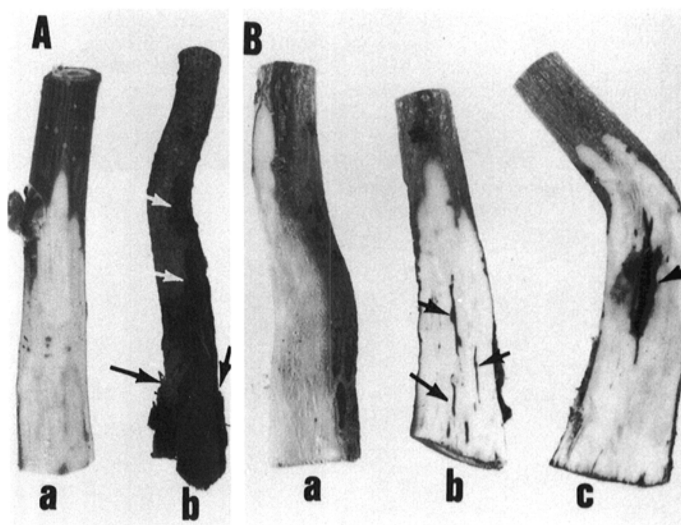

Fig. 5. Lower trunks of 6-mo-old seedlings of Northern California black walnut (*Juglans hindsii*) **A**, and Paradox (*J. hindsii* × English walnut [*J. regia*]) **B**, grown for 3 mo in noninfested soil (a) and soil artificially infested with *Phytophthora cactorum* (b) and *Phytophthora* sp. (isolate 1029) (c). Note severe and extensive canker (arrows) in *J. hindsii* (**A**, b) and very limited infection and canker (arrows) in Paradox (**B**, b and c), and the absence of infection and canker in controls (**A**, a; **B**, a).

Chinese wingnut (*Pterocarya stenoptera* DC) is used widely in China and to a limited extent in California as a walnut rootstock (14). Seedlings of *P. stenoptera* were reported to be highly resistant to *P. cinnamomi* when grown in soil artificially infested with a mixture of isolates of *P. cinnamomi* recovered from five different host plants other than walnut (10). Likewise, seedlings of *P. stenoptera* grown for 3 mo in soil artificially infested with the walnut isolates of *P. citricola* and subjected to biweekly flooding with water for 48 hr developed no crown rot and had a very limited infection of feeder roots and the plants in infested soil were as vigorous as controls in uninfested soil (M. E. Matheron, *unpublished*). The use of *P. stenoptera* or Paradox instead of *P. regia* or *J. hindsii* as rootstock for English walnuts at sites subject to Phytophthora root and crown rot offers the possibility of minimizing tree losses due to *Phytophthora* spp.

Research on the relative resistance to *Phytophthora* spp. of different and potential walnut rootstocks such as various selections of Paradox, several different *Juglans* spp., and Chinese wingnut (*P. stenoptera*) is in progress. We are also conducting research on the effects of different levels of soil moisture on severity of Phytophthora root and crown rot in the rootstocks used with *J. regia*.

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