Etiology

Pathogenicity and Relative Virulence of Nine *Phytophthora* spp. from Kiwifruit

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ABSTRACT

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Nine species of *Phytophthora,* including *P. cactorum, P. citrophthora, P. cryptogea, P. drechsleri, P. megasperma,* and four unidentified *Phytophthora* spp., were isolated from kiwifruit vines (*Actinidia deliciosa*) affected with root and crown rot in California commercial orchards. *P. citrophthora, P. cryptogea,* and *P. megasperma* were the most commonly recovered *Phytophthora* spp., whereas the remaining species were recovered sporadically. Kiwifruit vines infected by *Phytophthora* spp. exhibited poor terminal growth, stunted, chlorotic, and drooping leaves, and various degrees of dieback, including complete vine death. The highest incidence of diseased kiwifruit vines usually occurred on sites subjected to prolonged and repeated soil saturation due to poor drainage, flooding, or over-irrigation. In greenhouse experiments with artificially infested U.C. mix, seedlings of kiwifruit cultivars Hayward, Bruno, and Abbott developed various degrees of root rot and/or crown rot within 3 mo when periodically flooded for 48-h intervals every 2 wk. *P. cryptogea* and two of the unidentified *Phytophthora* spp. (3 and 4) caused severe root rot (90–100% of root mass rotted) and crown rot (58–100% of seedlings affected), regardless of the kiwifruit cultivar. Isolates of *P. citrophthora* caused moderate to severe root rot (50–93%) on all cultivars, but varied greatly in their ability to cause crown rot (0–100%). *P. megasperma* caused moderate to severe disease on seedlings of the cultivars Bruno and Abbott, inducing 61–88% and 79–89% root rot, and 8–50% and 75–100% crown rot, respectively. However, *P. megasperma* was less virulent to seedlings of the cultivar Hayward, causing 26–30% root rot and no crown rot. *P. drechsleri* and unidentified *Phytophthora* sp. 1 were weakly to moderately virulent on all three kiwifruit cultivars, causing 26–57% and 28–48% root rot, and 0–17% and 0–8% crown rot, respectively. *P. cactorum* and unidentified *Phytophthora* sp. 2 were avirulent and caused no measurable disease in any of the three kiwifruit cultivars.

Kiwifruit, *Actinidia deliciosa* (Chevalier) Liang et Ferguson (syn. *A. chinensis* Planchon var. *hispida* Liang) commonly is grown in California in the San Joaquin and Sacramento valleys and in regions extending to the coast. Approximately 9,000 acres are planted to kiwifruit in California.

With increased cultivation of kiwifruit, disorders and diseases have become more apparent and widespread, particularly root and crown rots. Researchers in Spain reported 6-mo-old cultivar Abbott seedlings to be markedly intolerant of flooding (29), whereas researchers in New Zealand concluded that kiwifruit can tolerate *Phytophthora* but not 'wet feet' (26). Additionally, a number of pathogens have been reported to cause root and crown rot infections of kiwifruit (6,11,12,22,24,25,27,30,37). In New Zealand, *P. cactorum* (Lebert & Cohn) Schröeter, *P. cinnamomi* Rands, *P. citricola, P. lateralis,* and *P. megasperma* Drechsler previously have been associated with root and crown rot of kiwifruit (7,26,27).

Since the early 1970s, much work has been done in California on the occurrence, pathogenicity, and relative virulence of a large number of *Phytophthora* spp. that induce root, crown, or collar rots of deciduous fruit and nut trees (15–21). Many species of *Phytophthora* occur in many soil types and geographic locations in agricultural areas of the state, but it was not known which species are most important as causes of root and crown rot of kiwifruit. Our objectives of this research were to identify the

species of *Phytophthora* associated with symptomatic kiwifruit vines in California and to determine their pathogenicity and relative virulence to kiwifruit vines. A preliminary report has been published (5).

MATERIALS AND METHODS

Isolation of *Phytophthora* spp. from infected vines and from soils. Kiwifruit orchards in California were surveyed for the occurrence of symptomatic vines between 1985 and 1988. Roots and crowns of three to six dead or dying vines were collected from each orchard, and approximately 3 L of soil was collected from near the crown of each vine. Roots and crowns were washed under running tap water to remove adhering soil particles. Discolored rootlets 1 cm long, or discolored cortical tissue (1 cm^2) from larger roots and crowns, were excised with a sterile scalpel. Forty decayed root and/or crown tissue pieces from each vine were placed on modified PARP selective medium (16) containing the following ingredients per liter of distilled water: cornmeal agar (Difco Laboratories, Detroit, MI), 17 g; pimaricin, 5 mg; sodium ampicillin, 250 mg; rifampicin, 10 mg; and PCNB, 25 mg. Dishes were incubated in the dark at 18 C and examined daily over 10 days for growth of *Phytophthora* spp. Recovery of *Phytophthora* spp. from soil was accomplished by the green pear baiting method (17). The advancing margins of brown lesions, which developed on the pears, were excised, placed on modified PARP medium, and observed for the development of *Phytophthora* spp. Emerging hyphae of *Phytophthora* spp. were subcultured on modified PARP media and then maintained on slants of cornmeal agar (CMA) or V8 juice agar (V8A) (4) for later taxonomic study. Additionally, a number of kiwifruit isolates (P343, P345, P1619, P2227, and P2437) previously recovered by S. M. Mircetich were included in these studies.

Identification of *Phytophthora* spp. Colony morphology of 5-day-old isolates, which had been grown at 24 C in the dark on CMA and V8A, was compared. Cardinal temperatures were determined by transferring a 4-mm-diameter mycelial plug of each isolate to CMA (20 ml per dish) and incubating three replicate dishes per isolate per temperature at 3 C increments from 6 to 39 C. Mycelial characteristics of CMA cultures grown at 24 C in the dark were compared. Production, morphology, and size of sporangia were compared by incubating isolates on V8A (5 ml/65-mm-diameter petri dish) for 2–3 days at 23 ± 1 C and then transferring 4-mm-diameter disks from the advancing margin of the colony to 5 ml of 1.5% soil extract per 65-mm-diameter petri dish. Soil extract was prepared by suspending 15 g of soil in 1 L of tap water, stirring for 24 h, and clearing by repeatedly filtering through Whatman No. 2 filter paper (17). Five disks from each V8A dish were incubated upside down in each soil extract dish at 21 C in the dark. Sporangia typically formed in 12–36 h under these conditions. At approximately 5% zoospore release, the mycelial disks with sporangia were removed, placed on microscope slides, and stained with lactophenol in acid fuchsin. Isolates that produced few or no sporangia under these conditions, or produced sporangia of distorted and irregular shapes, were subjected to further incubation in soil extract at a range of temperatures from 15 to 30 C at 3 C increments in the dark. Additionally, many isolates producing few or no sporangia under these conditions produced substantial numbers of sporangia when isolates were incubated in soil extract as described, except that the mycelial plugs were removed every 2–4 h, washed with distilled water, and the soil extract was replaced with fresh soil extract. At least 40 sporangia were measured per isolate, and the mean length/breadth ratio of sporangia was calculated for each isolate.

Production and morphology of sexual reproductive structures and mating type of the kiwifruit isolates were studied on modified clarified V8 juice agar (CV8A) (4). Petri dishes (65 mm diameter) were poured to a uniform volume of 5 ml. Dishes were incubated at 21 C in the dark for 4–6 wk. At first, all isolates were incubated in single culture. Those that failed to produce sex organs then were paired with known A1 and A2 compatibility type isolates of *P. cryptogea* Pethyb. & Laff. (P913 and P915), *P. drechsleri* Tucker (P445 and P447), and *P. cinnamomi* (P433 and P214) from the Department of Plant Pathology Culture Collection, University of California, Davis. Production of oospores in single or dual culture was noted, as was compatibility type and attachment of antheridia.

Pathogenicity tests. Pathogenicity of kiwifruit isolates of *P. citrophthora* (R. E. Sm. & E. H. Sm.) Leonian, *P. cryptogea, P. drechsleri, P. megasperma, P. cactorum,* and four unidentified, yet distinct, species of *Phytophthora* was tested on three cultivars of kiwifruit under greenhouse conditions. Pathogenicity tests with the three cultivars, Hayward, Bruno, and Abbott, were carried out separately because of space limitations and difficulties in obtaining seed.

Inoculum for pathogenicity tests was prepared by growing the isolates in 0.5-L screw-top jars containing 250 cm^3 of vermiculite and 20 cm^3 of whole oat kernels thoroughly wetted with 175 ml of V8 juice broth (commercial V8 juice, 200 ml; $CaCO_3$, 2 g; distilled water, 800 ml) (17). The medium was autoclaved for 60 min twice before infesting with the fungal isolates. After 4–5 wk of growth at 21 ± 2 C, inoculum was rinsed repeatedly in tap water to remove excess nutrients and then mixed with steam-pasteurized U.C. mix (1) and sand (2:1, v/v) at a rate of 20 cm^3 of inoculum per liter of mixture. Controls received equal volumes of uninfested V8-vermiculite medium.

Six- to 9-mo-old kiwifruit seedlings growing in steam-pasteurized U.C. mix in 102-mm-diameter × 102-mm-tall plastic pots were transplanted into 1.9-L crocks or 2-L plastic pots containing the artificially infested U.C. mix:sand mixture (2:1, v/v). Glass wool was placed in the bottom of the pots before transplanting to reduce soil loss from the pots. After transplanting, seedlings were given a 2-wk establishment period before exposure to flooding treatments. To simulate periodic exposure to flood irrigation, seedlings were flooded for 48 h every 2 wk for 3 mo by plugging the hole in the crock pots with a rubber stopper or, alternatively, by immersing the plastic pots in water to a depth of 1 cm above the soil line. All three cultivars were tested once between April and October and again between November and March. Soil temperatures over the course of the experiments ranged from 20 to 27 C for experiments conducted from April to October and from 15 to 22 C for experiments conducted from November to March. Lighting was supplemented to provide a 15-h photoperiod in all experiments. The seedlings were fertilized biweekly with a half-strength Hoagland's solution and were watered as needed between flooding episodes.

The experimental design was a randomized complete block design. Each treatment consisted of six replicate plants, and each experiment was conducted twice. Pathogenicity ratings of isolates were based on final shoot and root fresh weights, a visual estimation of the percent root mass rotted, and the incidences of crown rot and seedling mortality. Log transformations of shoot and root fresh weights and an angular transformation of percent root rot data were made to normalize data. Analysis of variance was applied to the transformed data, and, where appropriate, Duncan's multiple range test was used to separate means (13). Reisolation of individual isolates from symptomatic seedlings confirmed Koch's postulates.

RESULTS

Incidence and field symptoms. Symptomatic kiwifruit vines were observed between 1985 and 1988 in 36 orchards in 14 counties representing the major kiwifruit growing regions in California. *Phytophthora* spp. were isolated from 30 of 36 kiwifruit orchards. Nine different *Phytophthora* spp. were isolated from the roots, crown, or soil surrounding symptomatic vines. The incidence of root and crown rot varied from a few vines in poorly drained areas in some kiwifruit orchards to almost 100% of vines in poorly managed orchards. Vines with root and/or crown rot usually occurred in orchards with poor drainage due to nonleveled sites. Root and crown rot was more prevalent in orchards where there was over-irrigation, where weed control around vines was poor, or where drip or sprinkler emitters kept the crowns of vines

saturated with water.

Irrespective of the *Phytophthora* spp. present, affected kiwifruit vines generally exhibited similar foliar symptoms. Early symptoms were lack of terminal growth and stunted, chlorotic leaves. As disease progressed, vines exhibited partial defoliation, drooping of leaves, and various degrees of dieback. Poor vine growth often resulted in an open canopy leading to sunburned fruit, canes, and cordons. Leaves of young vines (2–4 yr old) often failed to emerge in spring, or, alternatively, they would emerge and grow vigorously until fruit set in June and the first hot days of summer occurred. These vines then would collapse in a few weeks. Older vines (5–12 yr old) generally underwent a gradual decline over a few seasons. Initial root symptoms were a decay of feeder roots and small secondary roots, and, as disease progressed, primary roots decayed and the cortex sloughed off. Root cankers often progressed into the crown and eventually girdled the vines. Conversely, when crown rot occurred first, the pathogen slowly girdled the vine but left the majority of the root system healthy and intact. By repeatedly visiting some orchards, we observed that the interval of time between infection and death depended on the virulence of the *Phytophthora* sp. present, the age and size of the vine, the presence or absence of crown rot, and edaphic and environmental conditions. In general, younger, smaller, vigorously growing vines declined faster than less vigorous vines, whereas vines affected with crown rot declined faster than vines affected with root rot only.

Identification of *Phytophthora* spp. Isolates recovered were identified as *P. cactorum* (one orchard), *P. citrophthora* (eight orchards), *P. cryptogea* (seven orchards), *P. drechsleri* (three orchards), and *P. megasperma* (five orchards). The general morphology of colonies, sporangia, and oospores, as well as sporangial dimensions and cardinal temperatures, were within the limits previously reported for these species (8,10,23,31–33). Isolates of *P. citrophthora, P. cryptogea,* and *P. drechsleri* were of the A1 compatibility type as determined by matings with known A1 and A2 compatibility type isolates of *P. cinnamomi, P. cryptogea,* and *P. drechsleri.* Additionally, four different but unidentified *Phytophthora* spp. were isolated from four different orchards. Descriptions of the four unidentified species are given in detail.

Unidentified *Phytophthora* sp. 1. Two isolates (designated 4B and P1619) of this species were recovered and studied. Colonies were uniform to slightly radiate, with sparse aerial hyphae on CMA after 4 days at 24 C; on V8A, colonies were uniform with abundant aerial hyphae. On CMA, hyphae branched primarily at right angles, although sparsely. Growth on CMA after 4 days at 6 C was minimal; growth increased at temperatures from 6 to 24 C, was optimal at 27 C (14.8 and 18.9 mm/day for isolates 4B and P1619, respectively), and no growth occurred at 36 C. Both isolates died after 4 days at 39 C. Sporangia formed within 24 h when V8A disks were placed in 1.5% soil extract. Sporangia, borne terminally, were nonpapillate, broadly ovoid, rounded at the base, and proliferated internally by short extension from simple undifferentiated sporangiophores. Sporangia measured 37–66 × 32–52 μm (mean 51 × 41 μm), with a mean length:breadth ratio of 1.24. Sex organs were produced on CV8A only when each isolate was paired with a known A2 compatibility type isolate of *P. cryptogea* or *P. drechsleri.* In all cases, antheridia were amphigynous. Isolates 4B and P1619 are similar to an unidentified *Phytophthora* sp. isolated from cherry (35) and walnut (14) in California and raspberry (34) in New York.

Unidentified *Phytophthora* sp. 2. One isolate (5A) of this species was recovered. The colony was slightly stellate, with sparse aerial hyphae on CMA after 4 days at 24 C; on V8A, the colony was uniform with moderate aerial hyphae. Primary hyphae branched mainly at acute angles, whereas secondary and tertiary hyphae tended to branch at right angles. The isolate's growth increased at temperatures from 6 to 21 C and was optimal at 24 C (11.9 mm/day), with no growth occurring at 36 C. Sporangia formed within 12–24 h when V8A disks were placed in 1.5% soil extract and rinsed repeatedly every 2 h until sporangia began to form. Sporangia, borne terminally on simple undifferentiated sporangiophores that often widened to meet the base of the sporangium, were nonpapillate and rounded at the base. Sporangia were ovoid to ellipsoid and proliferated internally by short extension. Sporangia measured 37–48 × 26–35 μm (mean 43 × 31 μm), with a mean length:breadth ratio of 1.39. Sex organs with amphigynous antheridia were produced on CV8A only when the isolate was paired with known A2 compatibility type isolates of *P. cryptogea* and *P. drechsleri.* Cardinal temperatures and size and shape of sporangia differentiate *Phytophthora* sp. 2 from *Phytophthora* sp. 1.

Unidentified *Phytophthora* sp. 3. One isolate (43D) of this species was recovered. The colony was stellate, with moderate aerial hyphae on CMA after 4 days at 24 C; on V8A, the colony was slightly rosette with profuse aerial hyphae. Hyphae were coralloid with many small hyphal swellings. Primary hyphae branched at acute angles, whereas secondary and tertiary hyphae branched at both acute and right angles. Spherical and irregularly rounded chlamydospores formed on CMA and V8A after approximately 10 days. No hyphal growth occurred at 6 or 9 C; growth increased from 12 C to a maximum at 27 C (19 mm/day). Slight growth occurred at 33 C after 4 days, whereas the isolate died after 4 days at 36 C. Sporangia formed within 36 h when V8A disks were placed in 1.5% soil extract. Sporangia were borne terminally on simple undifferentiated sporangiophores, occasionally in clusters of three or four sporangiophores. Sporangia were ovoid to ellipsoid, nonpapillate, with a wide apical thickening, and occasionally tapered at the base to meet a widened sporangiophore. The isolate exhibited nested internal proliferation in addition to elongation of the sporangiophore from just below the base of the sporangium. Sporangia measured 49–74 × 37–54 μm (mean 67 × 48 μm), with a mean length:breadth ratio of 1.40. Sex organs were produced on CV8A when the isolate was paired with known A1 compatibility type isolates of *P. cinnamomi, P. cryptogea,* and *P. drechsleri.* In all cases, antheridia were amphigynous.

Unidentified *Phytophthora* sp. 4. Two isolates (P343 and P345) of this species were recovered, but only one (P343) was included in pathogenicity tests. Colonies were radiate to stellate on CMA after 4 days at 24 C; on V8A, colonies were uniform to stellate, with profuse aerial hyphae. On CMA, primary hyphae branched at acute and right angles, whereas secondary and tertiary hyphae branched at acute angles. Slight growth occurred at 6 C on CMA after 4 days; growth increased at temperatures from 6 to 24 C, was optimal at 27 C (14.5 and 16.8 mm/day for isolates P343 and P345, respectively), and decreased to 36 C where growth still was moderate (9 mm/day). Neither isolate grew at 39 C and both were dead after 4 days at this temperature. Abundant small hyphal swellings were observed on CMA after 21 days. Sporangia formed within 12 h when V8A disks were flooded with 1.5% soil extract. Sporangia, borne terminally on undifferentiated sporangiophores of uniform width, were nonpapillate, ovoid to ellipsoid, frequently much elongated and tapered at the base, and proliferated internally by short extension of the sporangiophore. Sporangia measured 46–68 × 28–38 μm (mean 57 × 34 μm), with a mean length:breadth ratio of 1.68. Sex organs were produced on CV8A when each isolate was paired with a known A2 compatibility type isolate of *P. drechsleri.* Antheridia were amphigynous.

Pathogenicity tests. Error variances of the repeated experiments for each of the three kiwifruit cultivars tested were homogeneous; therefore, combined data of the experiments for each cultivar are presented (Tables 1–3).

With the exception of *P. cactorum* and *Phytophthora* sp. 2, all *Phytophthora* spp. isolated from symptomatic kiwifruit vines were pathogenic to at least one of the three kiwifruit cultivars, but they differed in their relative virulence. *P. cactorum* (Table 2) and *Phytophthora* sp. 2 (Tables 1 and 3) caused no significant reductions in shoot or root fresh weights, or increases in percent root rot when compared with the flooded, uninfested controls. All other *Phytophthora* spp. tested caused considerable disease. *P. cryptogea* (Tables 1–3), *Phytophthora* sp. 3 (Tables 1 and 2), and *Phytophthora* sp. 4 (Tables 1–3) all were highly virulent, causing significant reductions in shoot and root fresh weights

and 90–100% root rot. All three species caused severe crown rot (58–100% of inoculated seedlings), which often was followed by death of the seedlings for *P. cryptogea* and *Phytophthora* sp. 4 (67–100% and 50–100% mortality, respectively), but not as often for *Phytophthora* sp. 3 (17 and 25% dead seedlings).

Isolates of *P. citrophthora* caused moderate to severe root rot (50–93%) and varied greatly in their ability to cause crown rot (0–100% of seedlings) (Tables 1–3). All isolates of *P. citrophthora* caused significant reductions in shoot and root fresh weights relative to the flooded control in each experiment (Tables 1–3). *P. megasperma* caused only slight reductions in root fresh weights and no significant reductions in shoot fresh weights or increases in percent root rot or crown rot in experiments with seedlings of the cultivar Hayward (Table 1). However, *P. megasperma* was moderately to highly virulent on seedlings of the cultivars Bruno and Abbott, causing significant reductions in shoot and root fresh weights and increases in percent rot rot, which ranged from 61 to 88% for Bruno (Table 2) and 79 to 89% for Abbott (Table 3). Crown rot, caused by *P. megasperma,* varied greatly, ranging from 8 to 50% in affected Bruno seedlings (Table 2) and 75 to 100% in affected Abbott seedlings (Table 3).

P. drechsleri and *Phytophthora* sp. 1 were less virulent than the other species, often not causing significant reductions in shoot and root fresh weights or significant increases in percent root rot when compared with flooded controls (Tables 1–3). For these two species, crown rot was sporadic; incidence ranged from 0 to 17% of inoculated seedlings, and no seedling death occurred.

In all cases, the flooded control seedlings had reduced shoot and root fresh weights when compared with the nonflooded control seedlings (Tables 1–3), and these reductions were

TABLE 1. Relative virulence of eight *Phytophthora* spp. to *Actinidia deliciosa* 'Hayward' seedlings grown for 3 mo in artificially infested U.C. mix

Treatment[v]	Fresh weight (g)[w] Shoots	Roots	Root rot[w,x]	Crown rot[y] (%)	Dead[y] (%)
Uninfested soil					
Nonflooded	57.7 a	40.6 a	5 g	0	0
Flooded	38.6 b	29.0 b	11 fg	0	0
Artificially infested soil					
P. megasperma (41A)	34.7 bc	19.8 cd	30 d–f	0	0
P. megasperma (P2437)[z]	32.3 b–d	19.3 cd	26 e–g	0	0
Phytophthora sp. 2 (5A)	29.9 b–d	23.7 bc	22 e–g	0	0
Phytophthora sp. 1 (4B)	24.5 c–e	22.9 bc	30 d–f	0	0
P. drechsleri (10A)	24.0 de	16.9 c–e	40 c–e	0	0
Phytophthora sp. 1 (P1619)[z]	23.9 de	17.1 c–e	35 de	0	0
P. citrophthora (14A)	22.1 ef	15.7 d–f	50 cd	0	0
P. drechsleri (P2227)[z]	20.4 e–g	14.5 ef	57 c	8	0
P. citrophthora (16A)	14.8 f–h	10.5 fg	74 b	67	67
P. citrophthora (17B)	14.2 g–i	15.5 d–f	74 b	75	58
Phytophthora sp. 3 (43D)	11.0 h–j	7.8 g–h	92 a	67	17
P. cryptogea (19A)	9.8 ij	5.8 h	98 a	92	67
Phytophthora sp. 4 (P343)[z]	8.8 j	6.2 h	98 a	100	50

[v] Inoculum was added at the rate of 20 cm^3 of colonized vermiculite per 1,000 cm^3 of U.C. mix.
[w] Average of 12 observations (six replicates per experiment × two experiments) per isolate. Values in each column with letters in common do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.
[x] Percent of root system rotted as estimated by visual observation. The *Phytophthora* sp. introduced by soil infestation was reisolated from rotted roots of all plants, but not from those grown in uninfested U.C. mix.
[y] Percentage of plants with crown rot or dead.
[z] Isolate provided by S. M. Mircetich, Department of Plant Pathology, University of Califoria, Davis.

TABLE 2. Relative virulence of eight *Phytophthora* spp. to *Actinidia deliciosa* 'Bruno' seedlings grown for 3 mo in artificially infested U.C. mix

Treatment[v]	Fresh weight (g)[w] Shoots	Roots	Root rot[w,x]	Crown rot[y] (%)	Dead[y] (%)
Uninfested soil					
Nonflooded	54.4 a	31.1 a	8 g	0	0
Flooded	47.6 ab	23.7 ab	12 fg	0	0
Artificially infested soil					
P. cactorum (45)	40.8 a–c	23.7 ab	24 ef	0	0
Phytophthora sp. 1 (P1619)[z]	38.4 a–c	20.2 a–c	28 e	0	0
P. drechsleri (10A)	37.5 b–d	17.4 b–d	26 ef	0	0
P. drechsleri (P2227)[z]	37.0 b–d	20.8 a–c	34 e	0	0
P. citrophthora (17B)	32.2 c–e	13.5 c–e	65 d	17	8
P. megasperma (P2437)[z]	29.1 d–f	11.8 de	61 d	8	17
P. citrophthora (16A)	28.0 ef	11.8 de	66 d	50	33
P. citrophthora (46A)	27.6 ef	11.6 de	77 c	42	42
Phytophthora sp. 3 (43D)	23.0 f	9.0 e	90 b	58	25
P. megasperma (41A)	16.4 g	4.8 f	88 b	50	33
P. cryptogea (15C)	9.2 h	2.8 g	100 a	100	100
Phytophthora sp. 4 (P343)[z]	8.3 h	3.0 g	100 a	100	100
P. cryptogea (19A)	7.6 h	2.5 g	100 a	100	92

[v] Inoculum was added at the rate of 20 cm^3 of colonized vermiculite per 1,000 cm^3 of U.C. mix.
[w] Average of 12 observations (six replicates per experiment × two experiments) per isolate. Values in each column with letters in common do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.
[x] Percent of root system rotted as estimated by visual observation. The *Phytophthora* sp. introduced by soil infestation was reisolated from rotted roots of all plants, but not from those grown in uninfested U.C. mix.
[y] Percentage of plants with crown rot or dead.
[z] Isolate provided by S. M. Mircetich, Department of Plant Pathology, University of Califoria, Davis.

TABLE 3. Relative virulence of eight *Phytophthora* spp. to *Actinidia deliciosa* 'Abbott' seedlings grown for 3 mo in artificially infested U.C. mix

Treatment[v]	Fresh weight (g)[w] Shoots	Fresh weight (g)[w] Roots	Root rot[w,x]	Crown rot[y] (%)	Dead[y] (%)
Uninfested soil					
Nonflooded	23.4 a	44.4 a	5 g	0	0
Flooded	19.4 ab	27.1 ab	28 ef	0	0
Artificially infested soil					
Phytophthora sp. 2 (5A)	19.1 a–c	24.0 bc	28 ef	0	0
P. drechsleri (P2227)[z]	18.5 b–d	22.3 b–e	55 d	17	0
Phytophthora sp. 1 (4B)	17.1 b–e	23.5 bc	35 ef	0	0
Phytophthora sp. 1 (P1619)[z]	16.2 b–e	18.2 c–e	48 de	8	0
P. drechsleri (10A)	13.7 c–e	17.1 c–f	42 d–f	17	0
P. citrophthora (14A)	13.0 d–f	13.7 d–g	50 d	25	0
P. megasperma (41A)	12.3 ef	13.6 d–g	89 bc	100	17
P. megasperma (P2437)[z]	9.8 fg	10.1 gh	79 c	75	25
P. citrophthora (16A)	9.6 fg	11.7 f–h	92 ab	100	58
Phytophthora sp. 4 (P343)[z]	8.8 g	10.1 gh	98 a	100	67
P. citrophthora (17B)	8.7 g	9.8 gh	93 ab	100	67
P. cryptogea (19A)	8.3 g	8.8 h	99 a	100	75

[v] Inoculum was added at the rate of 20 cm^3 of colonized vermiculite per 1,000 cm^3 of U.C. mix.
[w] Average of 12 observations (six replicates per experiment × two experiments) per isolate. Values in each column with letters in common do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.
[x] Percent of root system rotted as estimated by visual observation. The *Phytophthora* sp. introduced by soil infestation was reisolated from rotted roots of all plants, but not from those grown in uninfested U.C. mix.
[y] Percentage of plants with crown rot or dead.
[z] Isolate provided by S. M. Mircetich, Department of Plant Pathology, University of Califoria, Davis.

significant in one instance (Table 1). Percent root rot also was greater for the flooded control seedlings than the nonflooded control seedlings, and this difference was significant in one case (Table 3). No crown rot or death of seedlings occurred in any of the control treatments.

DISCUSSION

This is the first report on the association of *P. cactorum, P. citrophthora, P. cryptogea, P. drechsleri,* and four unidentified species of *Phytophthora* with kiwifruit vines affected with root or crown rot in North American commercial plantings. *P. cactorum* (7,26,28) and *P. megasperma* (2) previously have been associated with root and crown rot of kiwifruit in New Zealand, in addition to *P. cinnamomi, P. citricola,* and *P. lateralis* (7,26–28), which were not isolated in this study. Kiwifruit is listed as a host of *P. megasperma* in North America (9,36).

P. citrophthora, P. cryptogea, and *P. megasperma* were most commonly associated with kiwifruit in California, whereas *P. cactorum, P. drechsleri,* and the four unidentified species of *Phytophthora* were of limited distribution. All four unidentified species of *Phytophthora* belong in Waterhouse's group VI (32) on the basis of their nonpapillate, internally proliferating sporangia and amphigynous antheridia. Disease symptoms on kiwifruit are similar to those exhibited by other deciduous fruit and nut trees. Symptomatic vines tended to occur in low or poorly drained areas of orchards, or where irrigation or rainfall led to free standing water (15–18,20,21). *P. cryptogea, Phytophthora* sp. 3, and *Phytophthora* sp. 4 consistently were most virulent on kiwifruit seedlings. *P. cryptogea* is highly virulent on a number of deciduous fruit and nut trees in California (14,18,35). It is unclear whether isolates resembling the two virulent unidentified species have been recovered from other hosts.

Isolates of *P. citrophthora* and *P. megasperma* also were highly virulent on kiwifruit, although the relative virulence varied with the particular isolate examined. Seedlings of cultivar Hayward appear to be more resistant to root and crown rot caused by *P. megasperma* than seedlings of cultivars Bruno or Abbott. Both *P. citrophthora* and *P. megasperma* have been reported on a number of deciduous fruit and nut crops in California (15,17,18,20).

P. drechsleri and *Phytophthora* sp. 1 were weakly to moderately virulent, depending on the particular kiwifruit cultivar tested, and it would be difficult to conclude that these two species should not be of concern to kiwifruit growers when so few isolates were examined. Both *P. drechsleri* and *Phytophthora* sp. 1 are reported to be weakly to moderately virulent on deciduous fruit and nut crops in California (14,17,35).

P. cactorum and *Phytophthora* sp. 2 were avirulent to kiwifruit vines. It is unclear whether isolates resembling *Phytophthora* sp. 2 have been recovered from tree and nut crops in California. However, *P. cactorum* commonly is isolated from perennial crops and virulence has varied greatly, depending on the host of origin (3,14,16,18). Only one isolate each of *P. cactorum* and *Phytophthora* sp. 2 were recovered during this study, and it is difficult to judge fully the virulence of either species to kiwifruit. However, because neither species was isolated commonly, we assume that neither is prevalent on kiwifruit. The three species most commonly recovered from kiwifruit in California, *P. citrophthora, P. cryptogea,* and *P. megasperma,* also were moderately to highly virulent on the three kiwifruit cultivars examined.

When kiwifruit seedlings of the three cultivars were flooded in the absence of a pathogen, reductions in shoot and root fresh weights and increases in percent root death occurred, although the differences were not always significant (Tables 1–3). It is clear that careful soil-water management is essential for the vigorous growth of vines and that saturated soil conditions inhibit vine growth. Proper irrigation and orchard management to avoid prolonged and repeated soil saturation should be helpful in preventing or minimizing root and crown rot caused by species of *Phytophthora.* However, we have clearly demonstrated the extreme damage that species of *Phytophthora* can cause to kiwifruit seedlings and to mature vines. Identification of a resistant rootstock is highly desirable and should be the focus of future research.

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