Influence of Soil Water Matric Potential on the Development of Phytophthora Root and Crown Rots of Mahaleb Cherry

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ABSTRACT

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Mahaleb cherry seedlings were grown for 3 mo in UC mix (UCM) artificially infested with *Phytophthora cryptogea, P. cambivora, P. megasperma,* or *P. drechsleri* and subjected to various levels of soil moisture. When the soil water matric potential (ψ_m) was maintained at −10 millibars (mb), −25 mb, or −25 mb with 4-hr flooding ($\psi_m = 0$) interruptions once every 2 wk, *P. cryptogea, P. megasperma*, and *P. drechsleri* caused no crown rot, negligible root rot, and usually insignificant ($P = 0.05$) shoot and root growth reductions. In contrast, *P. cambivora* caused a 20–60% incidence of crown rot, moderate root rot, and moderate reductions in shoot and root growth at these same ψ_m values. When ψ_m was normally maintained at −25 mb but the soil was flooded ($\psi_m = 0$) for a 48-hr period once every 2 wk, *P. cryptogea* and *P. cambivora* caused 80 and 60% incidences of crown rot, respectively, and all four *Phytophthora* spp. caused severe root rot and significant ($P = 0.05$) growth reductions on Mahaleb seedlings. The same soil water regimes similarly influenced disease severity when seedlings were grown in a clay loam infested with *P. cryptogea*, while *P. cambivora* caused less root rot in clay loam than in the coarser UCM. When colonized leaf disks were buried for 3 days in UCM held at −25 mb ψ_m, *P. cryptogea* formed numerous sporangia, whereas *P. cambivora, P. drechsleri,* and *P. megasperma* formed few or no sporangia. One hour after the UCM was subsequently flooded, sporangia of *P. cryptogea* began releasing zoospores, and sporangium production by the other three *Phytophthora* spp. was initiated. These sporangia completed development and began discharging zoospores within 3–6 hr. Thus, soil water conditions that were optimum for disease development were also optimum for sporangium production and/or zoospore discharge.

Additional key words: *Prunus avium, Prunus mahaleb,* soilborne diseases, sweet cherry, wet feet.

Root and crown rots caused by several *Phytophthora* spp. are serious and widespread diseases of sweet cherry trees in California (16,25). Although disease is typically most severe on plants growing in wet, poorly drained soils (5,16), relatively little is known about the precise effects of soil water status on the development of the Phytophthora root and crown rots on sweet cherry or other deciduous fruit trees. However, small changes in the matric component of soil water potential (ψ_m) have been shown to strongly influence the development of Phytophthora root rots of other perennial plants. For instance, Sterne et al (20,21) reported that 50–100% root rot developed on *Persea indica* seedlings grown in a sandy loam infested with *Phytophthora cinnamomi* when ψ_m was maintained at 0, −50 millibars (mb), or −100 mb, but only 4–8% root rot developed with $\psi_m = -250$ mb. Similarly, Kuan and Erwin (13) found that the incidence of alfalfa seedlings killed by *P. megasperma* f. sp. *medicaginis* was two and five times as great when soil ψ_m was held at 0 as when ψ_m was maintained at −10 and −50 mb, respectively. Mircetich et al (17) likewise reported that *P. megasperma* and *P. cambivora* caused higher incidences of crown rot and much more severe root rot on Mahaleb and Mazzard cherry seedlings when infested potting mix was flooded for a 48-hr period every 2 wk than when plants were irrigated in a manner that avoided prolonged saturation of the soil. Stolzy et al (22) also presented data suggesting that the severity of root rot caused in *Citrus sinensis* by *P. parasitica* and *P. citrophthora* increased when soil was saturated or nearly saturated with water.

Such reports that small changes in soil ψ_m values can markedly influence the development of Phytophthora root rots are coincident with a growing body of literature detailing the pronounced effects of ψ_m on the biology of various *Phytophthora* spp., including some that attack cherry (e.g., 8,9,14,23). These relationships between soil water status, pathogen biology, and disease development are of great practical interest, as soil ψ_m is an environmental parameter over which an orchard manager maintains a degree of control through drainage and irrigation practices.

The objective of the investigations reported here was to more precisely determine the role that soil ψ_m plays in the development of Phytophthora root and crown rots of sweet cherry. A brief account of a portion of this work has been published (24).

MATERIALS AND METHODS

***Phytophthora* species.** Isolates of four *Phytophthora* spp. recovered from diseased cherry trees in California were used in these studies: *P. cryptogea* Pethyb. and Laff. (isolate P1349), *P. cambivora* (Petri) Buisman (isolate P543), *P. megasperma* Drechsler (isolate CH275 C-1), and *P. drechsleri* Tucker (isolate P527).

Soils. A steam-pasteurized UC mix potting medium (UCM) (2) was used in most experiments. The particular formulation employed consisted primarily of equal volumes of sand and peat, and had a pH of 6.3. In experiments designed to examine the influence of soil texture on disease development, an air-dried, sieved (1.0-mm mesh) Wyman clay loam (WCL) with a pH of 6.9 was substituted for UCM. This is the dominant soil type in the Stockton-Lodi cherry growing district of California, where Phytophthora root and crown rots have been particularly severe (16). The water release characteristics of UCM, sieved and reconstituted WCL, and of an undisturbed core of WCL from an orchard near Stockton, CA, are shown in Fig. 1.

Control of ψ_m. Soil ψ_m was controlled in all experiments by using finely porous fritted glass tension plates in 9-cm-diameter Büchner funnels, as detailed by Duniway (8).

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Influence of ψ_m on sporangium production and germination. The influence of ψ_m on the production and germination of sporangia of *P. cryptogea, P. cambivora, P. megasperma*, and *P. drechsleri* was investigated by using colonized Mahaleb cherry (*Prunus mahaleb* L.) leaf disks (23). Disks cut with a 5-mm-diameter cork borer from freshly excised, surface disinfested leaves were placed at the edge of a colony of *Phytophthora* sp. growing on V-8 juice agar. After 24–48 hr of incubation at 24 C, colonized leaf disks were removed from the agar and placed on top of a 5-mm layer of UCM that had been packed against the glass tension plate in a Büchner funnel. The disks were then covered with an additional 10-mm layer of UCM. Tap water was added to the soil until it was saturated, and the water column was immediately adjusted to provide drainage to −25 mb ψ_m at the level of the leaf disks. After 3 days at −25 mb ψ_m, the soil was flooded so that 3–5 mm of water stood on the soil surface ($\psi_m = 0$). Disks were removed from the soil at various times thereafter, fixed and stained with acid fuchsin in lactophenol, and the numbers of full and empty sporangia along the disk margins were counted at ×125 magnification. Empty sporangia were presumed to have germinated indirectly. The soil temperatures were maintained at 21 C for *P. cryptogea, P. drechsleri* and *P. cambivora* and at 15 C for *P. megasperma* because it has lower temperature optima for sporangium formation and zoospore discharge (23; and *unpublished*). There were two funnels for each *Phytophthora* sp. and the experiment was conducted twice; hence, each reported value represents an average of four replicated counts per treatment.

Influence of ψ_m and soil texture on disease incidence and severity. Mahaleb seedlings with small rootballs and lignified hypocotyls were produced 6–8 wk after stratified seed were planted in 30-ml cups of uninfested UCM. These seedlings were then transplanted into Büchner funnels containing either: UCM artificially infested with *P. cryptogea* or *P. cambivora*, UCM artificially infested with *P. megasperma* or *P. drechsleri*, or WCL artificially infested with *P. cryptogea* or *P. cambivora*, in different experiments. Seedlings were also transplanted into uninfested soil in each experiment to serve as controls.

To ensure that all treatments and replicates received equal doses of inoculum, bulk preparations of infested soil were formulated for each experiment and repeatedly mixed throughout the transplanting operation. First, inoculum grown on vermiculite soaked with dilute vegetable juice broth (16) was mixed with soil at 20 cc of infested vermiculite (or sterile vermiculite for uninfested control treatments) per 1,000 cc of soil. To add nutrients and

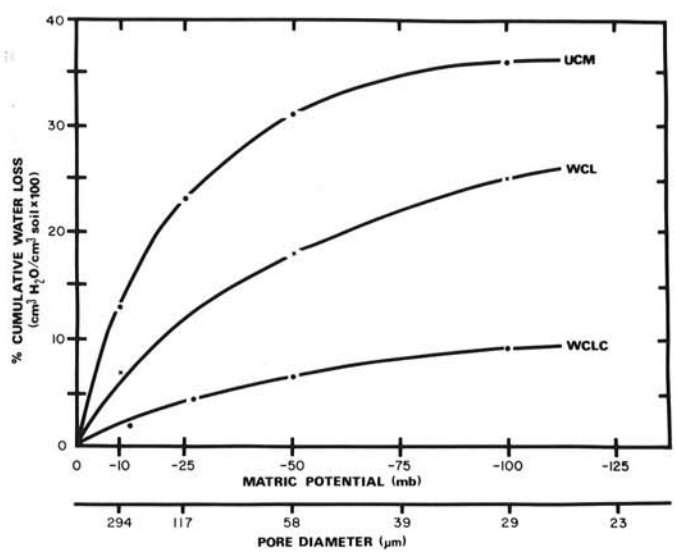

Fig. 1. The cumulative water loss from UC mix (UCM), bulk density = 1.10 g/cm^3; from reconstituted Wyman clay loam (WCL), bulk density = 1.25 g/cm^3; and from an undisturbed core of Wyman clay loam (WCLC), taken from an orchard at a depth of 30–36 cm, bulk density = 1.58 g/cm^3. Cumulative water loss is given as the percentage of the total soil volume that drained water when the matric potential decreased from 0 to the values shown. The pore size distribution among soil types can be compared by matching the volume of water lost at a given matric potential against the bottom axis, which gives the maximum pore diameter that is expected to retain water as the matric potential is lowered from 0 to the indicated values (5).

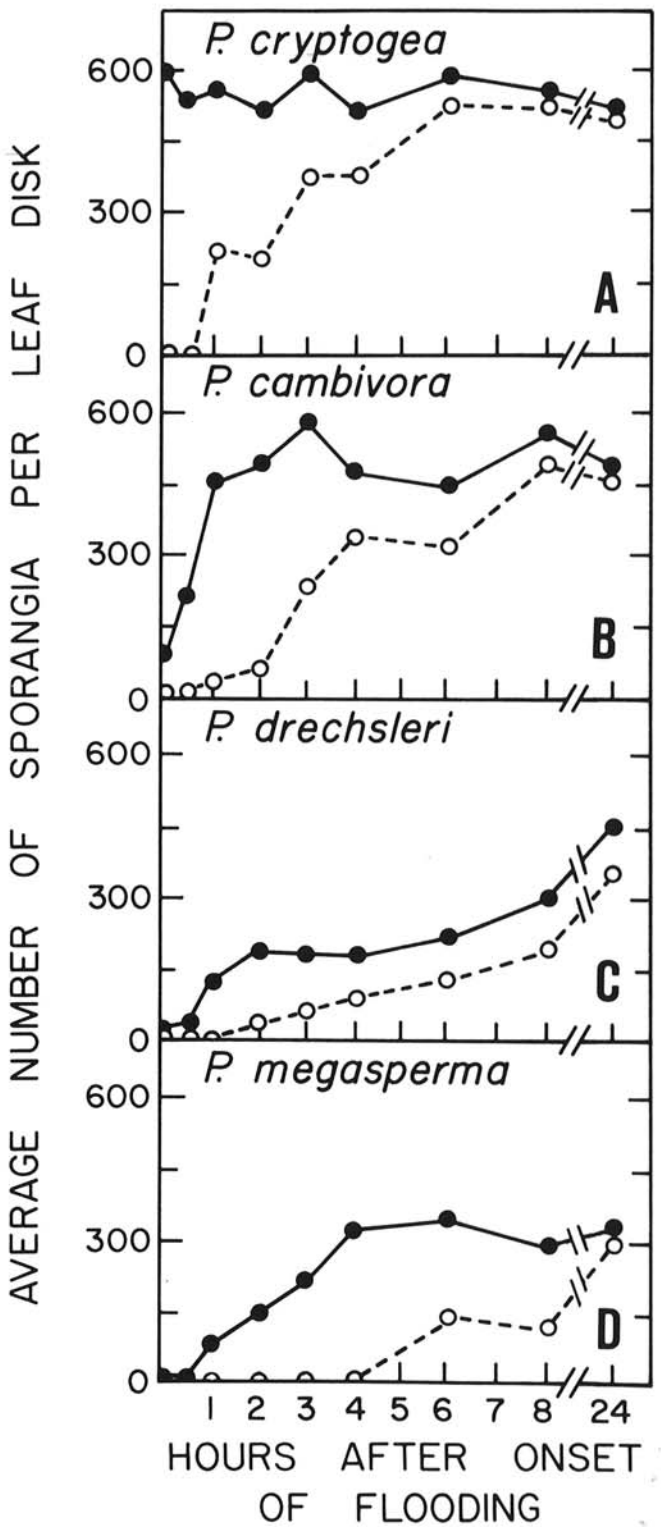

Fig. 2. A–D. The effects of flooding on the production and indirect germination of sporangia by four *Phytophthora* spp. Data points represent the average numbers of all sporangia (•——•) and empty sporangia (o——o) on the perimeter of four Mahaleb leaf disks at various times after the onset of flooding. Disks were buried in UC mix at $\psi_m = -25$ mb for 3 days prior to flooding. Empty sporangia are assumed to have germinated indirectly.

facilitate subsequent wetting, half-strength Hoagland's solution 2 was also mixed with UCM at this time until it became nearly saturated, or with WCL at the rate of 1 L of dilute solution per 12 L of soil. A single seedling was then placed on a 2-cm layer of soil that had been firmly packed against the glass tension plate within each Büchner funnel. Additional increments of soil were added and packed around the plant's root system until a total volume of 500 cc was attained. Final bulk densities were approximately 1.10 g/cm^3 for UCM and 1.25 g/cm^3 for WCL. After the final packing, soils were saturated with half-strength Hoagland's solution 2, and the height of the water column beneath each tension plate was immediately adjusted to allow drainage to an average ψ_m of −10 or −25 mb. (Since the soil cylinder was 7 cm high, ψ_m values actually ranged from −6.5 to −13.5 mb and from −21.5 to −28.5 mb, respectively). To prevent the growth of algae, aluminum foil was then wrapped around all funnels and the 1-L reservoirs used to support individual water columns. Finally, the funnels and seedlings were covered loosely with wire-supported plastic bags to retard evapotranspiration. Distilled water was regularly added to the reservoirs to maintain water columns at the proper height throughout the experiment.

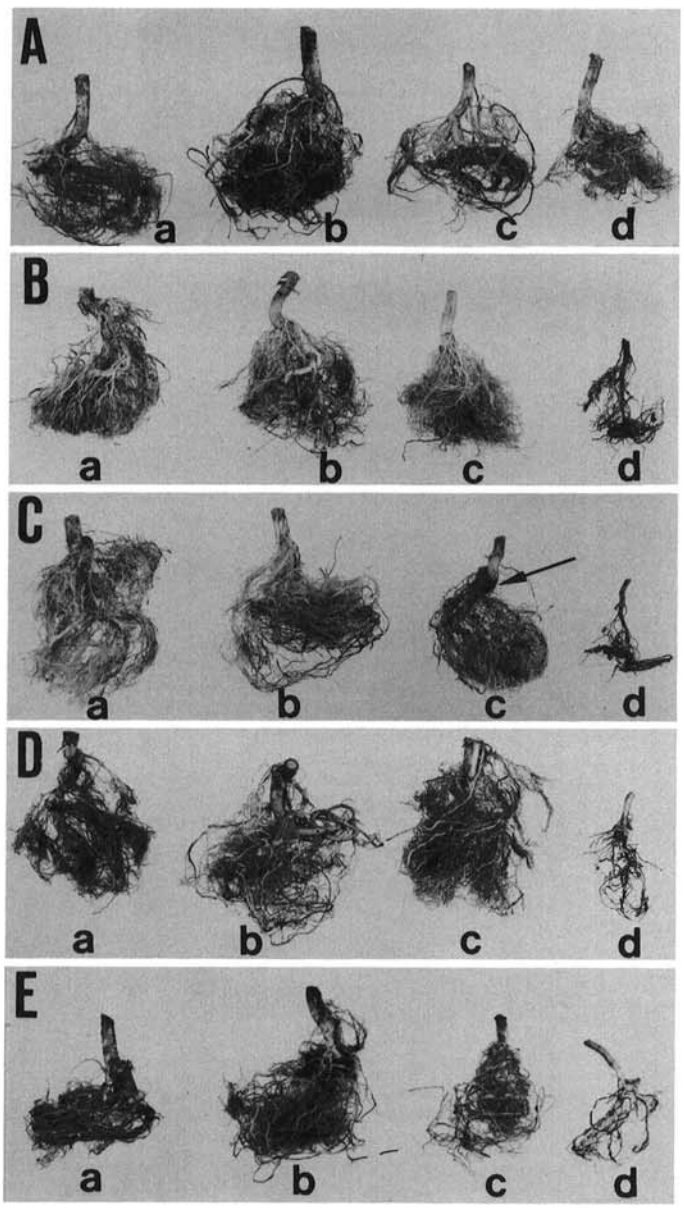

Fig. 3. Roots of Mahaleb seedlings grown for 3 mo in UC mix which was either: **A,** uninfested, or artificially infested with **B,** *Phytophthora cryptogea*; **C,** *P. cambivora*; **D,** *P. megasperma*; or **E,** *P. drechsleri*. The soil ψm was maintained at: **a,** −25 mb constantly; **b,** −10 mb constantly; **c,** −25 mb, interrupted by a 4-hr flooding (ψm = 0) period every 2 wk; or **d,** −25 mb, interrupted by a 48-hr flooding period every 2 wk. Note developing crown rot lesion in **C** (arrow) unaccompanied by massive root rot. **A, D,** and **E** show representative plants from the experiment summarized in Table 2; **B** and **C** show representative plants from the experiment summarized in Table 1.

Two weeks after transplanting, when all seedlings had resumed active growth, periodic flooding of the soil was initiated in some funnels previously adjusted to provide a ψ_m of −25 mb. The rubber tubing that connected each funnel stem to its reservoir was first clamped shut, and distilled water was slowly added until the soil became flooded to a depth of 5–10 mm. The tubes were then unclamped either 4 or 48 hr later, depending upon the treatment, to allow the soil to quickly redrain to an average ψ_m of −25 mb. The flooding process was repeated at 2-wk intervals until experiments were terminated 10–13 wk after transplanting. Thus, in each experiment plants were exposed to one of four different soil moisture regimes: ψ_m = −25 mb constantly, ψ_m = −10 mb constantly, ψ_m = −25 mb, interrupted by a 4-hr flooding (ψ_m = 0) period once every 2 wk, or ψ_m = −25 mb, interrupted by a 48-hr flooding (ψ_m = 0) period once every 2 wk.

All experiments were conducted in a growth chamber, with each plant equidistant from the overhead light source (5,380 lux, provided by a combination of fluorescent and incandescent bulbs). In experiments involving *P. cryptogea* and *P. cambivora*, the soil temperature was 23 C during the 16-hr light period and 19 C during the 8-hr dark period; in those involving *P. megasperma* and *P. drechsleri*, the soil temperature was 21 and 17 C during the same respective periods. There were five replicate plants for each treatment, and each experiment was conducted twice. Differences among treatments in root rot severity (visually estimated) and in the fresh weights of shoots and roots were evaluated using Duncan's multiple range test. *Phytophthora* spp. were confirmed to be the cause of root and crown rots in infested soils by plating symptomatic tissue on a modified PVP medium (16). Since results were consistent among repetitions of a given experiment, data are presented only for single representative experiments.

RESULTS

Influence of ψ_m on sporangium production and germination. The influence of ψ_m on the production and germination of sporangia of *P. cryptogea*, *P. cambivora*, *P. drechsleri*, and *P. megasperma* is summarized in Fig. 2. Prior to flooding (ψ_m = 0), *P. cryptogea* formed numerous sporangia within 3 days at ψ_m = −25 mb, but none germinated. After flooding was initiated, many of these sporangia began to germinate indirectly within 1 hr, and nearly all had germinated within 6 hr (Fig. 2A). In contrast, *P. cambivora*, *P. drechsleri*, and *P. megasperma* formed few or no sporangia after 3 days at ψ_m = −25 mb, but numerous sporangial initials formed within 30–60 min when colonized leaf disks were subsequently flooded (Fig. 2B–D). These initials developed into mature sporangia and released zoospores within 3–6 hr after the onset of flooding (Fig. 2B–D). The response pattern reported for each *Phytophthora* sp. was consistently followed on all four replicate leaf disks examined.

In a separate experiment leaf disks colonized by *P. cambivora* were buried for 3 days in UCM with ψ_m = −25 mb and then flooded, as described above. After 30 min of flooding, the UCM in half of the funnels was redrained to −25 mb ψ_m, while in the other funnels it remained flooded. Again, numerous sporangial initials formed within 30 min after the onset of flooding. These initials continued to develop into mature sporangia regardless of whether the UCM was subsequently redrained to −25 mb ψ_m, or whether it remained flooded; however, the sporangia proceeded to release zoospores only in UCM that remained flooded.

Influence of ψ_m on disease incidence and severity. The influence of ψ_m on disease development was basically the same whether Mahaleb seedlings were grown in UCM infested with *P. cryptogea*, *P. megasperma*, or *P. drechsleri* (Tables 1 and 2). When plants were grown in infested soil and ψ_m was maintained constantly at −10 or

−25 mb, or when an otherwise constant ψ_m of −25 mb was interrupted by 4-hr flooding ($\psi_m = 0$) episodes every 2 wk, neither shoot nor root fresh weights were significantly ($P = 0.05$) reduced relative to plants grown in uninfested soil. Similarly, symptoms of root rot were negligible and no crown rot occurred under these same conditions (Tables 1 and 2; Fig. 3B, D, and E). However, when soil normally maintained at $\psi_m = -25$ mb was flooded for 48 hr once every 2 wk, *P. cryptogea* and *P. megasperma* both caused nearly complete root rot and significant ($P = 0.05$) reductions in shoot and root fresh weights, and *P. cryptogea* caused a high incidence of crown rot and seedling mortality as well (Tables 1 and 2; Fig. 3B and D). Under this same soil moisture regime, *P. drechsleri* also caused significant ($P = 0.05$) reductions in shoot and root fresh weights relative to control plants and rotted nearly half of each seedling's root system (Table 2).

P. cambivora likewise caused the most root rot, the greatest reductions in root and shoot fresh weights, and the highest incidences of crown rot and seedling mortality when UCM was periodically flooded for 48 hr (Table 1). However, in contrast with the other *Phytophthora* spp., *P. cambivora* also caused some crown rot and seedling death when UCM was periodically flooded for only 4 hr, or when ψ_m was constantly maintained at −25 or −10 mb (Table 1). In fact, *P. cambivora* often caused crown rot on plants that were relatively free of root rot in these three treatments (Fig. 3C).

Influence of soil texture on disease incidence and severity. Soil texture did not appear to influence the effect of ψ_m on the incidence or severity of disease caused by *P. cryptogea*; differences among soil moisture regimes were comparable whether seedlings were grown in WCL (Table 3) or in the much coarser UCM (Table 1). In contrast, *P. cambivora* caused considerably less root rot and growth reduction on seedlings in WCL than on those in UCM when both soils were subjected to the periodic 48-hr flooding treatment (Tables 1 and 3).

TABLE 1. Incidence and severity of root and crown rots of Mahaleb cherry seedlings grown for 13 wk in UC mix artificially infested with *Phytophthora cryptogea* or *P. cambivora* at different soil water matric potentials (ψ_m)

Inoculum[x]	ψ_m (−mb) and flooding duration	Plant fresh weight (g)[w]		Root rot[w,y] (%)	Fraction of plants[w]	
		Shoots	Roots		With crown rot	Dead
Control (uninoculated)	10	14.8 a	15.0 a	8 bc	0/5	0/5
	25	13.8 a	11.6 ab	9 bc	0/5	0/5
	25 + 4 hr[z]	13.2 a	10.6 ab	3 c	0/5	0/5
	25 + 48 hr[z]	12.8 a	10.0 ab	6 bc	0/5	0/5
P. cryptogea	10	15.4 a	10.6 ab	13 bc	0/5	0/5
	25	12.2 a	10.8 ab	13 bc	0/5	0/5
	25 + 4 hr[z]	12.4 a	9.6 b	16 bc	0/5	0/5
	25 + 48 hr[z]	3.0 b	2.4 c	99 a	4/5	4/5
P. cambivora	10	9.2 a	8.0 a	31 b	2/5	1/5
	25	11.8 a	9.2 a	31 b	1/5	1/5
	25 + 4 hr[z]	10.0 a	8.6 a	19 bc	2/5	0/5
	25 + 48 hr[z]	3.2 b	2.6 b	88 a	3/5	3/5

[w] There were five replicate plants per treatment. Values followed by the same letter within a column do not differ significantly from each other ($P = 0.05$) according to Duncan's multiple range test.
[x] Inoculum added at 20 cc of colonized vermiculite per 1,000 cc of soil. Uninoculated controls received sterile vermiculite.
[y] Percent of the root system rotted, based upon visual estimation. The appropriate *Phytophthora* sp. was reisolated from rotted roots of all plants grown in infested soil, but not from those grown in uninfested soil.
[z] Soil ψ_m was maintained at −25 mb except for flooding ($\psi_m = 0$) interruptions of 4 or 48 hr every 2 wk.

TABLE 2. Incidence and severity of root and crown rots of Mahaleb cherry seedlings grown for 10 wk in UC mix artificially infested with *Phytophthora megasperma* or *P. drechsleri* at different soil water matric potentials (ψ_m)

Inoculum[x]	ψ_m (−mb) and flooding duration	Plant fresh weight (g)[w]		Root rot[w,y] (%)	Fraction of plants[w]	
		Shoots	Roots		With crown rot	Dead
Control	10	23.0 a	9.5 a	4 d	0/5	0/5
	25	12.5 bcd	7.0 c	5 d	0/5	0/5
	25 + 4 hr[z]	12.1 cd	7.0 c	5 d	0/5	0/5
	25 + 48 hr[z]	13.9 bcd	7.6 bc	5 d	0/5	0/5
P. megasperma	10	18.2 ab	9.1 a	6 cd	0/5	0/5
	25	12.0 cd	7.4 bc	7 cd	0/5	0/5
	25 + 4 hr[z]	9.4 ce	6.9 c	9 c	0/5	0/5
	25 + 48 hr[z]	1.7 f	1.0 e	96 a	1/5	1/5
P. drechsleri	10	17.4 bc	8.7 ab	6 cd	0/5	0/5
	25	10.0 d	7.0 c	6 cd	0/5	0/5
	25 + 4 hr[z]	10.3 d	7.0 c	6 cd	0/5	0/5
	25 + 48 hr[z]	4.1 ef	2.6 d	48 b	0/5	0/5

[w] There were five replicate plants per treatment. Values followed by the same letter within a column do not differ significantly from each other ($P = 0.05$) according to Duncan's multiple range test.
[x] Inoculum was added at 20 cc of colonized vermiculite per 1,000 cc of soil. Uninoculated controls received sterile vermiculite.
[y] Percent of the root system rotted, based upon visual estimation. The appropriate *Phytophthora* sp. was reisolated from rotted roots of all plants grown in infested soil, but not from those grown in uninfested soil.
[z] Soil ψ_m was maintained at −25 mb except for flooding ($\psi_m = 0$) interruptions of 4 or 48 hr every 2 wk.

DISCUSSION

The large number of sporangia formed by *P. cryptogea* on colonized leaf disks at $\psi_m = -25$ mb (Fig. 2A), and the dramatic increase in the production of sporangia by *P. cambivora, P. megasperma*, and *P. drechsleri* when ψ_m was raised from −25 mb to 0 (Fig. 2B–D), are consistent with previously reported results (6,15,18,23) concerning the influence of ψ_m on the formation of sporangia by these *Phytophthora* spp. However, our experiments with *P. cambivora* indicate that saturated soil ($\psi_m = 0$) merely stimulates this species to initiate sporangium formation, but has no influence on the subsequent completion of sporangium development. This observation raises questions as to the nature of the stimulus involved, and suggests the possibility that a similar mechanism might also underlie the increased production of sporangia by *P. megasperma* and *P. drechsleri* under saturated conditions (18, 23; and Fig. 2C and D).

The speed with which previously formed sporangia of *P. cryptogea* and *P. cambivora* released zoospores in response to soil flooding (Fig. 2A and B) was very similar to that reported by other workers for *P. cryptogea* (14), *P. megasperma* (14), and *P. megasperma* f. sp. *glycinea* (4). Likewise, those sporangia which *P. cambivora, P. drechsleri*, and *P. megasperma* initiated in response to soil flooding required just a few additional hours at $\psi_m = 0$ to complete development before releasing zoospores at approximately the same rate (Fig. 2B–D).

Disease severity on plants grown in soils infested with *P. cryptogea, P. megasperma,* or *P. drechsleri* was profoundly influenced by the different soil moisture regimes in a manner that parallels the influence of ψ_m on zoospore discharge and motility. For instance, the negligible levels of disease that developed when ψ_m was held at −25 or −10 mb (Tables 1–3) may have been due to the low frequency of sporangium production or the failure of sporangia to discharge zoospores at these ψ_m values (Fig. 2; 13,14,18,23). Furthermore, even if discharged, zoospores are significantly hindered from moving through soils maintained at such ψ_m levels (8).

Although the evidence is correlative in nature, the severe disease caused by all four *Phytophthora* spp. when soils were regularly flooded for 48-hr periods (Tables 1–3; Fig. 3 B–E) indicates that soil water conditions which were optimum for zoospore discharge and dispersal (Fig. 2; 6,8,14,18,23) were also most conducive to disease development. This relationship suggests that zoospores may be the most important propagules of infection for the Phytophthora diseases examined in the present study. However, the generally insignificant effects of biweekly 4-hr floodings (Tables 1–3; Fig. 3 B–E), which should have been sufficient to induce zoospore discharge (14; Fig. 2), suggest that the liberation of large numbers of zoospores into the soil is not sufficient in itself to produce high levels of disease on Mahaleb cherry. While longer periods of flooding might increase disease severity by extending the period of zoospore motility, prolonged flooding also produces numerous root environment changes (19) that may influence pathogen behavior and increase host susceptibility to infection (3,12).

The high incidences of crown rot which were caused by *P. cambivora* under unsaturated soil conditions (Tables 1 and 3) indicate that this species can readily colonize Mahaleb crowns under conditions suboptimal for zoospore release. Furthermore, the attendant lack of root rot on many of these plants (Fig. 3C) suggests that *P. cambivora* may spread throughout regions of susceptible crown tissue from a limited number of infection sites.

The reduced root rot caused by *P. cambivora* after 48-hr floodings in fine-textured WCL relative to that in coarse-textured UCM (Tables 1 and 3) might be attributed to differences in zoospore movement through the two substrates. For example, the water release curves shown in Fig. 1 indicate that only 9% of the total WCL volume, versus 20% of the UCM volume, consisted of pores >90 μm in diameter. This is the minimum pore size through which active movement of zoospores of *P. cinnamomi* is believed to occur (1). Similarly, only 18% versus 31% of the same substrate volumes consisted of pores greater than 60 μm in diameter, which appears to be the minimum pore size through which significant motility of zoospores of *P. cryptogea* occurs (8). The detrimental effect of fine-textured soils on zoospore movement has been shown by several workers (8,10,15,18), and the importance of zoospore movement in the development of different Phytophthora root rots has been demonstrated (10,11). Although soil texture had no effect on the severity of disease caused by *P. cryptogea* (Tables 1 and 3), it is possible that the textural restraints imposed do not inhibit the movement of zoospores of *P. cryptogea* to the extent that they do those of *P. cambivora*. For example, MacDonald and Duniway (17) found that zoospores of *P. cryptogea* are more motile than those of *P. megasperma* and suggested that this could affect the relative movement of these zoospores through the soil.

Sterne et al (20,21) reported that avocado root rot caused by *P. cinnamomi* was severe at ψ_m values much lower than those that limited disease severity in our experiments. Unlike the present study, they also found that severe root rot developed at even lower ψ_m levels in a fine-textured clay than in a coarser sandy loam (21). However, these differences may result partly from differences in the

TABLE 3. Incidence and severity of root and crown rots of Mahaleb cherry seedlings grown for 10 wk in Wyman clay loam artificially infested with *Phytophthora cryptogea* or *P. cambivora* at different soil water matric potentials (ψ_m)

Inoculum[x]	ψ_m (−mb) and flooding duration	Plant fresh weight (g)[w]		Root rot[w,y] (%)	Fraction of plants[w]	
		Shoots	Roots		With crown rot	Dead
Control	10	25.6 ab	28.0 a	5 d	0/5	0/5
	25	26.0 ab	28.4 a	6 d	0/5	0/5
	25 + 4 hr[z]	19.0 bcd	21.4 b	5 d	0/5	0/5
	25 + 48 hr[z]	18.2 cd	15.4 b	11 cd	0/5	0/5
P. cryptogea	10	24.8 bc	28.0 a	8 cd	0/5	0/5
	25	25.8 ab	26.4 a	8 cd	0/5	0/5
	25 + 4 hr[z]	21.6 abc	17.0 b	11 cd	0/5	0/5
	25 + 48 hr[z]	1.6 e	1.2 d	98 a	3/5	4/5
P. cambivora	10	22.8 abc	15.4 b	28 bc	2/5	1/5
	25	27.6 a	27.2 a	10 cd	1/5	0/5
	25 + 4 hr[z]	25.8 ab	14.4 bc	12 cd	3/5	0/5
	25 + 48 hr[z]	13.4 d	8.8 c	41 b	2/5	0/5

[w] There were five replicate plants per treatment. Values followed by the same letter within a column do not differ significantly from each other ($P = 0.05$) using Duncan's multiple range test.

[x] Inoculum added at 20 cc of colonized vermiculite per 1,000 cc of soil. Uninoculated controls received sterile vermiculite.

[y] Percent of the root system rotted, based upon visual estimation. The appropriate *Phytophthora* sp. was reisolated from rotted roots of all plants grown in infested soil, but not from those grown in uninfested soil.

[z] Soil ψ_m was maintained at −25 mb except for flooding ($\psi_m = 0$) interruptions of 4 or 48 hr every 2 wk.

biology of the *Phytophthora* spp. involved. For instance, soil texture and ψ_m appear to influence the development of avocado root rot primarily through their effects on the availability of nutrients stimulatory to mycelial growth, chlamydospore germination, and germ tube development by *P. cinnamomi* (21). In contrast, ψ_m and soil texture appear to influence the development of cherry root rot through their effects on sporangium formation, zoospore discharge, and zoospore movement by *P. cryptogea, P. megasperma, P. drechsleri,* and *P. cambivora*.

The use of small seedlings in a growth chamber, and differences in porosity between our experimental soils and an undisturbed orchard soil (Fig. 1), collectively suggest caution in directly extrapolating these results to an orchard situation. Nonetheless, our findings indicate a strong potential for minimizing these diseases by preventing prolonged periods of soil saturation in infested orchards. This might involve improving the surface or internal drainage of problem soils, and it should certainly include adoption of an irrigation system compatible with this goal. For instance, prolonged "flood" irrigations, as simulated by our periodic 48-hr flooding treatment, should be avoided in orchards infested with *Phytophthora* spp. On the other hand, irrigation practices that cause the soil to remain saturated for only a relatively short period before redraining, such as simulated by our periodic 4-hr flooding treatment, may help minimize losses in cherry orchards resulting from Phytophthora root and crown rots.

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