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Effects of Flooding Duration on the Development of Phytophthora Root and Crown Rots of Cherry

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ABSTRACT

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Mahaleb and Mazzard cherry seedlings were grown for 3 mo in UC mix artificially infested with *Phytophthora cryptogea* or *P. megasperma* and flooded for periods of 0, 8, 12, 24, or 48 hr at 2-wk intervals. For each host/pathogen combination, disease severity progressed from mild (2–7% of the root system rotted) in treatments that were not flooded to extreme (81–99% of the root system rotted) with 48-hr flooding periods. Similarly, *P. cryptogea* caused crown rot only after 48-hr flooding periods, whereas *P. megasperma* caused no crown rot. When seedlings were grown in uninfested UC mix, and a single 48-hr flooding period was partitioned to provide various flooding intervals before and after inoculation with zoospores of *P. cryptogea*, disease severity was proportional to the length of the postinoculation flooding interval. In contrast, preinoculation flooding periods (regardless of their length) had no apparent effect on disease development. Furthermore, a postinoculation treatment consisting of 6 hr of flooding followed by 42 hr at 0.5% soil O_2 resulted in a disease rating comparable to that which occurred with 48 hr of continuous flooding. These data indicate that the severe Phytophthora root and crown rots that develop on cherry after prolonged flooding periods result in part from phenomena that occur in flooded soil after zoospore discharge. In addition, these data suggest that the susceptibility of Mahaleb root and crown tissues to colonization by *Phytophthora* spp. may increase during periods of reduced oxygen availability which develop during persistent flooding.

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

Phytophthora root and crown rots of sweet cherry trees occur most frequently in orchards with poorly drained or periodically flooded soils (14). Prolonged flooding periods can also dramatically increase the incidence and severity of these diseases on cherry seedlings grown under controlled conditions (15,22). For example, when Mahaleb cherry (*Prunus mahaleb* L.) seedlings were grown in UC mix artificially infested with *Phytophthora cryptogea* Pethyb. and Laff. or *P. megasperma* Drechsler, negligible disease developed if the soil water matric potential (ψ_m) was held at −25 millibars (mb) either constantly, or with a 4-hr flooding ($\psi_m = 0$) interruption once every 2 wk (22). However, if biweekly flooding periods were extended to 48 hr, both pathogens caused crown rot and massive root rot (22).

Flooding appears to increase disease severity by promoting the discharge (10,22) and dispersal (6) of zoospores of *P. cryptogea* and *P. megasperma*. However, inoculum availability may not be the only factor involved. In the study (22) mentioned above, disease incidence was minimal on plants subjected to the periodic 4-hr flooding treatment, even though both pathogens release numerous zoospores under such conditions (10,22). These results suggest that longer periods of flooding might also increase disease severity by increasing the susceptibility of Mahaleb cherry to infection or subsequent disease development. For example, alfalfa (9) and rhododendron (3) are apparently predisposed to infection by *P.*

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megasperma Drechs. f. sp. *medicaginis* Kuan and Erwin and *P. cinnamomi* Rands, respectively, when the root zones of these hosts are saturated for prolonged periods prior to inoculation. Oxygen deficits that develop in the plant roots under waterlogged soil conditions have been suggested as a possible cause of the predisposition (3,9). Furthermore, temporary oxygen deficits imposed after inoculation can markedly increase the development of root diseases caused by nonpythiaceous fungi (5,13) and are suggested as a reason that such diseases are more pronounced following periods of irrigation (13).

The present study was undertaken to compare the influence of various flooding durations on the severity of Phytophthora root and crown rots on two cherry rootstocks. In addition, we sought to determine whether prolonged periods of flooding predispose cherry to infection by *Phytophthora* spp. and to examine the influence of temporary postinoculation soil oxygen deficits on disease development. A portion of this work has been reported previously (20).

MATERIALS AND METHODS

Inoculum production. Inocula were prepared from the same cherry isolates of *P. cryptogea* and *P. megasperma* used in previous studies (21,22). In experiments employing artificially-infested potting medium, the fungi were initially grown on vermiculite soaked with dilute vegetable juice, and the colonized vermiculite was incorporated into steam-pasteurized UC mix (composed primarily of equal volumes of peat and sand) (2), as described before (14,21,22). In all other experiments, plants were inoculated with zoospores of *P. cryptogea*, which were obtained from sporangia that formed on colonized leaf disks of Mahaleb cherry (18,22). To produce this inoculum, disks were first cut with a 7-mm-diameter cork borer from freshly-excised, surface disinfested leaves and placed at the edge of a colony of *P. cryptogea* growing on V-8 juice agar. After 24–48 hr of incubation at 24 C, colonized disks were removed from the agar plates and buried 1 cm deep in UC mix maintained at $\psi_m = -25$ mb on a tension plate (6). Disks were subsequently recovered from the UC mix after 3 days; by that time *P. cryptogea* had formed numerous sporangia along the leaf disk margins. Next, the disks were immersed in quarter-strength Hoagland's solution 2 at room temperature, where most of the adhering sporangia released zoospores within 90–120 min. Finally, 2 hr after immersion of the leaf disks, the concentration of motile zoospores in the nutrient solution was determined by using a haemocytometer, and adjusted to 10^3 zoospores per milliliter. Designated plants were inoculated immediately with 50 ml of this final preparation (i.e., 5×10^4 motile zoospores per plant).

Influence of flooding duration on disease severity. Mahaleb and Mazzard (*Prunus avium* L. 'Silverbark Mazzard') cherry seedlings with lignified hypocotyls and rootballs filling their containers were produced 6 wk after stratified seed were planting into 30-cm^3 cups filled with steam-pasteurized UC mix. Individual seedlings were then transplanted into 9-cm-diameter Büchner funnels, within which were sealed fritted glass tension plates for the control of soil ψ_m (6). The potting medium in one half of these tension-controlling apparatuses consisted of 500 cm^3 of UC mix artificially infested with either *P. cryptogea* or *P. megasperma*, while the remainder contained an equal volume of uninfested UC mix. The transplanting procedures used were identical to those described previously (22) except that, in this experiment, seedlings were not subsequently covered with plastic bags. Immediately after transplanting, soil ψ_m was established at −1 7 mb midway up each of the 7-cm-high soil columns. This ψ_m value was maintained throughout the experiment, except during periodic flooding ($\psi_m = 0$) treatments of 0 (i.e., briefly wetted), 8, 12, 24, or 48 hr duration. The flooding regimes were initiated 2 wk after transplanting and continued at 2-wk intervals thereafter; the same procedures described previously (22) were used. There were five replicate seedlings for each cherry species × flooding duration combination in both the infested and uninfested UC mix. Each experiment was conducted for 3 mo in a greenhouse, where natural light was supplemented as necessary to provide a 15-hr photoperiod. Due to seasonal differences, soil temperatures ranged from 18–22 C when the UC mix was infested with *P. megasperma*, and from 18–24 and 19–29 C in two experiments with the UC mix infested with *P. cryptogea*. At the end of each experiment, differences among treatments were assessed according to a visual estimate (0–100 scale) of the percentage of the root mass rotted, the fresh weights of roots and shoots, and the incidence of crown rot and plant death. Because results for the two experiments with *P. cryptogea* were similar, a detailed analysis is presented for only one (soil temperature range 18–24 C).

Influence of preinoculation and postinoculation flooding periods on disease severity. Mahaleb and Mazzard seedlings were grown for 8 wk in individual pots containing uninfested UC mix, then flooded for various durations immediately before and/or after inoculation with zoospores of *P. cryptogea*. Flooding periods were initiated in designated pots 24–44 hr prior to inoculation by placing them in individual watertight containers and establishing a water table 5–10 mm above the soil surface. Just before inoculation, the UC mix in these pots was minimally drained by lowering the water tables to within 2–3 cm of the pot bottoms. At this time, the remaining pots that had not yet been flooded were thoroughly irrigated, briefly allowed to drain, and then placed in similar containers with water tables 2–3 cm above the bottom of each pot. Fifty milliliters of zoospore suspension (or 50 ml of quarter-strength Hoagland's solution 2 in the case of uninoculated controls) was then poured evenly over the soil surface of each pot and allowed to infiltrate into the UC mix, which at this point became nearly saturated. Plants were flooded 10 min after inoculation by first adding water to the UC mix, then reestablishing the water table 5–10 mm above the soil surface. Plants remained flooded for 4–48 hr after inoculation, then the pots were removed from the watertight containers and allowed to drain freely. Plants were subsequently watered as needed for 3 wk, at which time the root systems were gently washed and examined for decay. Disease severity was evaluated for each plant based on the proportion of the root mass visibly rotted, by using a scale in which 0 = no disease; 1 = 1–25% root rot; 2 = 26–50% root rot; 3 = 51–75% root rot; 4 = 76–99% root rot, no crown rot, plant alive; and 5 = 100% root rot, crown rot present, and the plant dead or collapsing. *P. cryptogea* was confirmed as the cause of root and crown rots by reisolating the pathogen on a modified PVP medium (14). The experiment was repeated four times in a greenhouse, where the soil temperature ranged from 19–24 C.

Influence of postinoculation oxygen concentration on disease severity. Mahaleb seedlings were grown for 8 wk in individual pots containing uninfested UC mix, then temporarily subjected to different soil oxygen concentrations immediately following inoculation with zoospores of *P. cryptogea*. To accomplish this, pots were first irrigated, briefly allowed to drain, then placed in watertight containers in which a water table was established 2–3 cm above the bottom of each pot. Seedlings were then quickly inoculated with 50 ml of zoospore suspension (or dilute nutrient solution for uninoculated controls) and flooded within 10 additional minutes, as described above. Pots remained flooded for 6 hr to facilitate inoculum dispersal. After this period, pots were removed from the watertight containers and allowed to drain for 10–15 min, except for one group which was kept flooded for an additional 42 hours. Drained pots were subsequently placed in individual plastic bags, and the top of each bag was tied around the base of the seedling's stem, approximately 1–2 cm above the surface of the UC mix. Two glass tubes were inserted approximately 4 and 6 cm, respectively, into the UC mix through slits in the plastic bag, and the slits were resealed with cellophane tape. The deeper tube was then connected to a manifold which distributed air, a mixture of 90% nitrogen:10% air (v:v), or nitrogen alone, at a rate of 10 L per pot per hour. The second tube, situated on the opposite side of the pot and providing access to the central plane of the root zone, was capped with a rubber bulb through which gas samples were drawn with a syringe for chromatographic analysis. Displaced soil gas was allowed to escape through small gaps between the plastic bag and the stem of the seedling. Gas samples drawn from the access tubes 24 and 40 hr after initiation of the gas treatments

indicated oxygen concentrations of 21%, 2.5%, and 0.5% by volume in soil atmospheres treated with air, the nitrogen/air mix, and nitrogen alone, respectively.

The various gas treatments were maintained continuously for 42 hr following the initial 6-hr flooding period, after which time the pots were disconnected from the manifolds and removed from the plastic bags. At the same time, pots that had remained continuously flooded for 48 hr were removed from the containers and allowed to drain. All plants were subsequently watered as needed for 3 wk without further treatment, then the roots were washed and evaluated for disease severity by using the 0–5 scale described above.

RESULTS

Influence of flooding duration on disease severity. When seedlings were grown in UC mix infested with *P. cryptogea*, root rot severity increased progressively and dramatically as biweekly flooding periods increased from 0 to 48 hr (Table 1, Fig. 1). For instance, root rot on Mahaleb seedlings increased from only 6% in nonflooded UC mix to 15, 18, 65, and 99% after periodic flooding episodes of 8, 12, 24, and 48 hr duration, respectively. In general, fresh root weights were inversely proportional to estimated root rot percentages (Fig. 1), and mean values for both parameters showed a strong linear trend with respect to flooding duration (Table 1). Crown rot and seedling mortality occurred only after 48-hr flooding periods. When subjected to this treatment, seven of ten Mahaleb seedlings and four of ten Mazzard seedlings developed crown rot and died in the two experiments.

Although the different flooding durations affected Mahaleb and Mazzard root weights similarly, there was a significant rootstock × inoculum × flooding duration interaction with respect to percent root rot (Table 1). Whereas Mahaleb and Mazzard responded similarly to the 0-, 8-, 12-, and 48-hr flooding treatments, Mazzard appeared significantly less susceptible to root rot (22 versus 65% for Mahaleb) under the intermediate disease pressure provided by the 24-hr flooding periods (Fig. 1).

Disease severity caused by *P. megasperma* was negligible when seedlings were flooded for 0-, 8-, or 12-hr periods; however, disease severity increased to moderate and high levels as flooding durations increased to 24 and 48 hr, respectively (Fig. 2). There were no significant rootstock × inoculum × flooding duration interactions (Table 2), and *P. megasperma* did not cause crown rot or death of any seedling in this experiment.

Although plants flooded in the absence of a *Phytophthora* sp. had little observable root rot, they usually had significantly lower root fresh weights than the nonflooded controls in the same experiment (Figs. 1 and 2). These decreases ranged from 0–54% (relative to the weights of the nonflooded controls) on Mazzard, and from 30–58% on Mahaleb. Weight differences were generally more pronounced at higher soil temperatures and with longer flooding durations.

Influence of preinoculation versus postinoculation flooding periods on disease severity. When seedlings were flooded for various lengths of time immediately before and/or after inoculation with zoospores of *P. cryptogea*, disease severity increased dramatically as the postinoculation flooding period increased from 4 to 48 hr. In contrast, preinoculation flooding periods, regardless of their length, had little influence on disease severity (Table 3). For example, Mahaleb seedlings flooded for 4 hr after inoculation had an average disease index (DI) of only 1.1 when they received no preinoculation flooding treatment, and had a similarly low DI of 1.4 when flooded for 44 additional hours prior to inoculation (Table 3). However, when Mahaleb seedlings were flooded for 48 hr entirely after inoculation, the average DI increased to 4.2 (Table 3). On Mazzard, disease development was influenced by the various preinoculation and postinoculation flooding periods in the same manner, although DIs were lower than on Mahaleb in every treatment (*unpublished*).

Influence of postinoculation oxygen concentration on disease severity. In one experiment, disease severity was comparably high whether seedlings were flooded continuously for 48 hr after

TABLE 1. Analysis of variance for fresh root weight and percent root rot of Mahaleb and Mazzard cherry seedlings (rootstock) flooded for five different periods (hours) in the presence and absence of *Phytophthora cryptogea* (inoculum)

Source of variation	df	Fresh root weight[a] MS	Fresh root weight[a] F	Root rot (%)[a,b] MS	Root rot (%)[a,b] F
Rootstock	1	71.57	12.93**	1,631.13	27.58**
Inoculum	1	553.19	99.97**	15,521.63	262.47**
Hours	4	154.47	27.91**	3,994.91	67.55**
Linear	1	464.99	84.03**	15,912.59	269.08**
Quadratic	1	54.07	9.77**	61.36	1.04
Deviations	2	49.41	8.93**	2.84	0.08
Rootstock × hours	4	12.41	2.24	100.63	1.70
Linear	1	11.34	2.05	80.16	1.36
Quadratic	1	34.29	6.20*	118.63	2.01
Deviations	2	2.00	0.36	101.87	1.72
Inoculum × hours	4	20.24	3.66**	3,466.48	58.62**
Linear	1	59.78	10.80**	13,665.64	231.01**
Quadratic	1	0.00	0.00	176.69	2.99
Deviations	2	6.72	1.21	11.79	0.12
Rootstock × inoculum	1	1.25	0.28	187.05	3.12
Rootstock × inoculum × hours	4	0.65	0.12	206.65	3.49*
Linear	1	0.00	0.00	175.35	2.97*
Quadratic	1	0.05	0.01	232.18	3.93**
Deviations	2	1.27	0.23	209.53	3.54*
Residual	80	5.53		59.14	

[a] *F* values are significant at $P = 0.05$ (*) and $P = 0.01$ (**) as noted.
[b] Percent root rot was analyzed following arcsin transformation of the data.

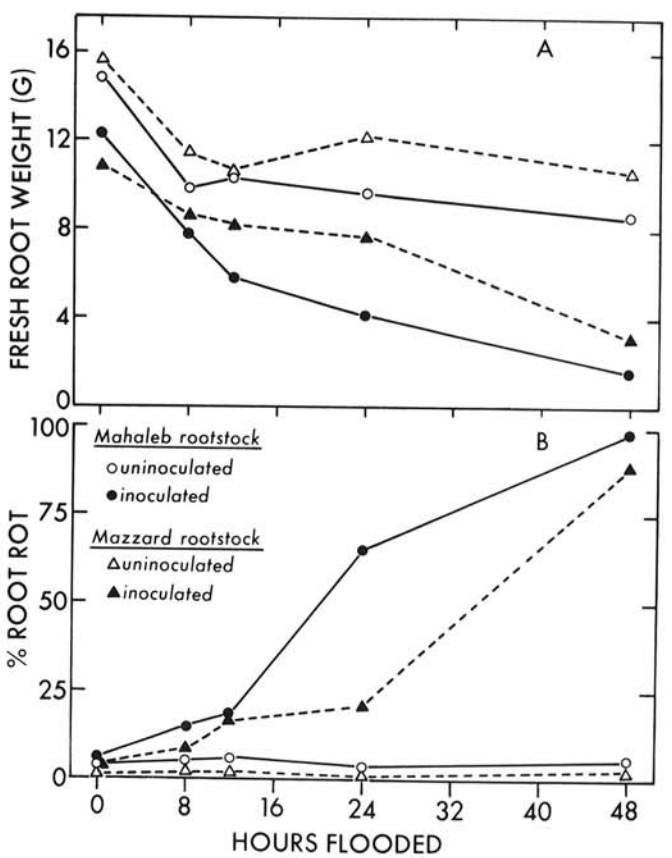

Fig. 1. Influence of periodic flooding duration on **A,** fresh root weight and **B,** percent root rot of Mahaleb and Mazzard cherry seedlings grown for 3 mo in UC mix in the presence and absence of inoculum of *Phytophthora cryptogea*. Soil water matric potential (ψ_m) was maintained at −17 mb except during biweekly flooding ($\psi_m = 0$) episodes of the durations indicated. Data points represent averages of five replicate seedlings per treatment.

inoculation, or if they were flooded for only 6 hr and their roots were exposed to an atmosphere containing 0.5% O_2 for an additional 42 hr (Table 4, Fig. 3). In a second experiment, seedlings exposed to the 0.5% O_2 atmosphere following inoculation had significantly less root rot than those flooded for 48 hr, but significantly more root rot than seedlings exposed to a temporary postinoculation atmosphere of 2.5% or 21% O_2 (Table 4). The latter two treatments caused only moderate root rot in both experiments (Table 4, Fig. 3). Uninoculated seedlings had no root or crown rot, regardless of flooding duration or oxygen concentration.

DISCUSSION

The results obtained in the present study confirm previous experimental results (15,22) and field observations (14) that have linked severe Phytophthora root and crown rots on cherry trees with prolonged periods of soil flooding. Additionally, this study suggests that disease incidence and severity are influenced by the duration of the flooding period, the *Phytophthora* species present, and the cherry rootstock involved.

Disease severity was clearly proportional to the duration of regular flooding periods for both *P. cryptogea* (Table 1, Fig. 1) and *P. megasperma* (Table 2, Fig. 2). Although both pathogens caused near-total destruction of the seedlings' root systems with 48-hr floodings, *P. cryptogea* appeared to cause significantly more severe symptoms than *P. megasperma* after shorter flooding durations (Figs. 1 and 2). This may be partially related to a more rapid availability of zoospores of *P. cryptogea* upon the initiation of flooding (22). However, it is also possible that seedlings became highly susceptible to infection or colonization by *P. megasperma* only after relatively long periods of flooding, although this was not investigated.

Unlike alfalfa (9) and rhododendron (3), Mazzard and Mahaleb seedlings were not predisposed to infection by flooding periods that occurred prior to inoculation. Rather, the severe root and crown rots caused by *P. cryptogea* following prolonged flooding episodes (21,22; Fig. 1) appear to result from phenomena which occur in flooded soils after zoospore release (Table 3), as well as from the stimulatory effect of flooding on the zoospore-release process (10,22). Although it seems probable that one such phenomenon is the optimized movement of zoospores under flooded conditions (6), the zoospores of many *Phytophthora* spp. appear to remain motile in soil or irrigation water for only a relatively few hours (11,12,19). Therefore, it seems unlikely that the dramatic increase in disease development that occurred as flooding durations were extended to 48 hr (Fig. 1; Table 3) is due solely to enhanced inoculum dispersal throughout this period. Furthermore, although it is possible that a secondary cycle of zoospore production and

TABLE 2. Analysis of variance for fresh root weight and percent root rot of Mahaleb and Mazzard cherry seedlings (rootstock) flooded for five different periods (hours) in the presence and absence of *Phytophthora megasperma* (inoculum)

Source of variation	df	Root weight[a] MS	Root weight[a] F	Root rot (%)[a,b] MS	Root rot (%)[a,b] F
Rootstock	1	685.39	31.30**	164.94	12.10**
Inoculum	1	292.41	13.36**	7,662.92	562.34**
Hours	4	498.23	22.76**	3,258.36	239.11**
Linear	1	1,976.30	90.27**	12,273.80	900.70**
Quadratic	1	0.00	0.00	684.99	50.27**
Deviations	2	8.32	0.38	37.32	2.74
Rootstock × hours	4	97.38	4.45**	27.74	2.04
Linear	1	0.36	0.02	0.00	0.00
Quadratic	1	310.96	14.20**	62.30	4.57*
Deviations	2	39.09	1.79	24.32	1.79
Inoculum × hours	4	126.21	5.77**	3,054.19	224.13**
Linear	1	464.86	21.23**	10,866.13	797.40**
Quadratic	1	28.95	1.32	1,340.19	98.35**
Deviations	2	5.52	0.25	5.22	0.38
Rootstock × inoculum	1	8.41	0.38	7.15	0.53
Rootstock × inoculum × hours	4	2.04	0.93	33.62	2.47
Residual	80	21.89		14.25	

[a] *F* values are significant at $P = 0.05$ (*) and $P = 0.01$ (**) as noted.
[b] Percent root rot was analyzed following arcsin transformation of the data.

TABLE 3. Relative influence of preinoculation and postinoculation flooding periods on the severity of disease caused by *Phytophthora cryptogea* on Mahaleb cherry

Flooding period (hr) Preinoculation[x]	Flooding period (hr) Postinoculation[y]	Disease index[z]
0	4	1.1 d
44	4	1.4 cd
0	8	1.4 cd
40	8	1.5 cd
0	24	2.1 b
24	24	1.7 bc
0	48	4.2 a

[x] Eight-wk-old seedlings grown in pots of uninfested UC mix were flooded for the periods indicated immediately before inoculation with *P. cryptogea* zoospores.
[y] Seedlings were flooded for the durations indicated immediately following inoculation.
[z] Disease index: 0 = no disease, 1 = 1–25% root rot, 2 = 26–50% root rot, 3 = 51–75% root rot, 4 = 76–99% root rot, and 5 = 100% root rot and/or crown rot present, plant dead or collapsing. Values given are the means of 20 observations (five replicates per experiment × four experiments). Means not followed by the same letter are significantly different ($P = 0.05$) according to Duncan's multiple range test. Uninoculated controls in all treatments showed no disease symptoms.

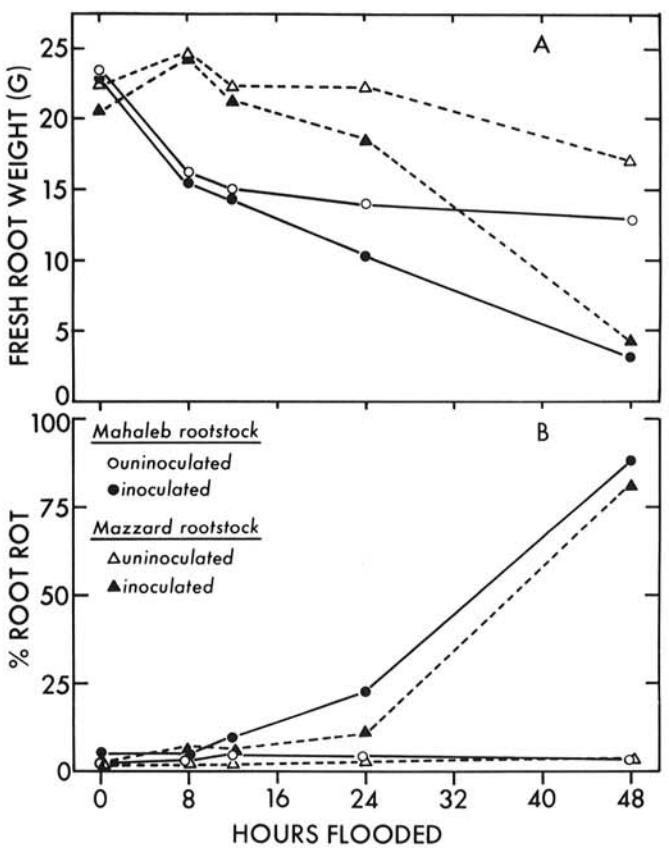

Fig. 2. Influence of periodic flooding duration on **A,** fresh root weight and **B,** percent root rot of Mahaleb and Mazzard cherry seedlings grown for 3 mo in UC mix in the presence and absence of inoculum of *Phytophthora megasperma*. Soil water matric potential (ψ_m) was maintained at −17 mb except during biweekly flooding ($\psi_m = 0$) episodes of the durations indicated. Data points represent averages of five replicate seedlings per treatment.

TABLE 4. The influence of flooding and postinoculation soil O_2 concentration on the severity of disease caused by *Phytophthora cryptogea* on Mahaleb cherry

Treatment[x]	Disease index[y]	
	Experiment 1[z]	Experiment 2[z]
Flooded 48 hr	4.2 a	4.2 a
Flooded 6 hr + 42 hr at 0.5% O_2	4.4 a	2.8 b
Flooded 6 hr + 42 hr at 2.5% O_2	1.8 b	1.6 c
Flooded 6 hr + 42 hr at 21% O_2	1.6 b	1.4 c

[x] Eight-wk-old seedlings were inoculated with 5×10^4 motile zoospores of *P. cryptogea* immediately prior to the indicated treatment. Soil O_2 concentrations were maintained for 42 hr immediately following an initial 6-hr flooding period.

[y] Disease index: 0 = no disease, 1 = 1–25% root rot, 2 = 26–50% root rot, 3 = 51–75% root rot, 4 = 76–99% root rot, and 5 = 100% root rot, crown rot present, plant dead or collapsing.

[z] Average of five replicates per treatment. Values in a column not followed by the same letter are significantly different ($P = 0.05$) according to Duncan's multiple range test. Uninoculated controls showed no disease symptoms in any treatment.

discharge occurred only during the 48-hr flooding periods, preliminary efforts to demonstrate this were unsuccessful (*unpublished*). Nevertheless, the role of secondary inoculum or repeated zoospore emergence from microsporangia (19) during prolonged flooding episodes is worthy of further investigation.

Flooding periods that persist after zoospore release may influence disease severity by affecting the host as well as the fungus. In particular, it appears that Mahaleb root and crown tissues may be significantly more susceptible to colonization by *P. cryptogea* while the soil O_2 supply is very low than they are while the soil is well-aerated (Table 4). Thus, infections initiated within the first several hours following zoospore discharge may develop most extensively if oxygen becomes depleted in the root zone, as it often does while the soil remains flooded (5,7).

The mechanism(s) underlying this apparent relationship between soil O_2 supply and the susceptibility of Mahaleb to disease development was not investigated. However, there are reports that the active, postinfection defense responses of other plants may be inhibited by low-oxygen environments. For instance, phytoalexin biosynthesis by pea and bean is severely inhibited by O_2 concentrations of 1% (4), and phytoalexin biosynthesis by potato does not proceed in an atmosphere devoid of oxygen (1). Similarly, molecular oxygen is required by plant phenoloxidases involved in the inactivation of certain pathogens and in the formation of physical barriers to penetration (5). It has also been suggested (5) that modest oxygen deficiencies in the root zone might suppress lignin biosynthesis, which appears to be a defense response induced in some plants by attempted fungal invasion (16,17).

It appears, therefore, that flooding periods might increase the incidence and severity of Phytophthora root and crown rots on cherry by promoting a number of sequential events, including the production and discharge of zoospores (10,18,22); zoospore movement (6) and chemotactic response (9); zoospore cyst germination (8); and, finally perhaps by reducing host resistance to subsequent colonization by the pathogen. However, additional research is needed to determine the relative importance of these various factors insofar as they influence the development of Phytophthora root and crown rots on cherry and other plant species.

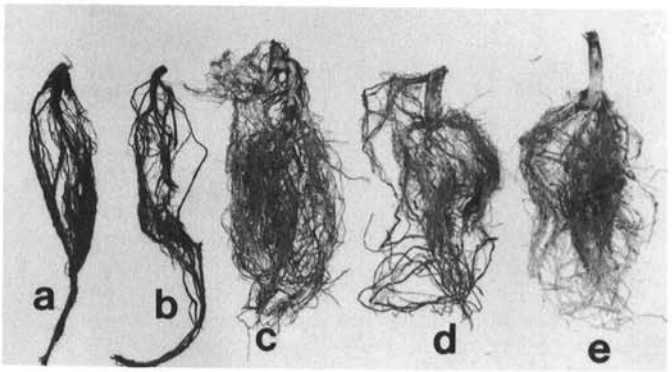

Fig. 3. The effect of postinoculation soil atmosphere on the development of Phytophthora root and crown rots of Mahaleb cherry. Seedlings grown in pasteurized UC mix were inoculated with motile zoospores of *P. cryptogea* and **a,** flooded for 48 hr thereafter; or, seedlings were flooded for 6 hr after inoculation, then drained and exposed for an additional 42 hr to a soil atmosphere containing **b,** 0.5% O_2, **c,** 2.5% O_2, or **d,** 21% O_2. The uninoculated control (**e**) was flooded for 6 hr before an additional 42 hr of exposure to a soil atmosphere containing 0.5% O_2.

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