Effect of Soil-Water Matric Potential and Periodic Flooding on Mortality of Pepper Caused by *Phytophthora capsici*

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ABSTRACT

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Periodic flooding increased the mortality of pepper plants (*Capsicum annuum* L. 'Early Calwonder') grown in soil infested with 25 oospores of *Phytophthora capsici* per gram of soil as compared with those grown in infested soil at constant soil-water matric potentials of −2.5 and −12.5 kPa. Plant mortality increased as the number of 24-hr flooding periods at 10-day intervals increased. Plants grown in infested soil at a constant soil-water matric potential of −12.5 kPa were not infected 37 days after transplanting. However, when infested soil was periodically flooded, 20, 53, and 100% of the plants died after one, two, and three flooding periods, respectively. With a soil-water matric potential of −2.5 kPa, 0, 80, and 100% of the plants died after one, two, and three flooding periods, respectively. Only one of 15 plants was infected at a constant soil-water matric potential of −2.5 kPa. Our results support field observations associating heavy rainfall and subsequent flooding of the soil with increases in disease progress.

Soil-water matric potential (ψ_m) is important in the production of secondary inoculum, zoospore release, zoospore movement, and disease development for various species of *Phytophthora* (6,10–13,18,27–29). The optimal ψ_m for sporangium production was between −1.0 and −30.0 kPa when washed mycelium or mycelial disks of several species of *Phytophthora* were used as inoculum (12). *Phytophthora capsici* Leonian formed abundant sporangia within 24 hr when mycelial disks were buried in soil at a constant ψ_m of −30.0 kPa (3). No sporangia were formed in saturated soil unless the soil was first incubated at −20.0 to −30.0 kPa. Zoospore release occurred readily when sporangia formed at −30.0 kPa were exposed to saturated soil. Sporangium production by other *Phytophthora* spp., however, may occur readily in saturated soil if sporulation occurs on infested organic matter or infected roots. The optimum ψ_m for sporangium production was 0 kPa when root radicles infected with *P. megasperma* Drechs. (19,26) or leaf disks colonized by *P. cryptogea* Pethybr. & Lafferty, *P. cambivora* (Petri) Buisman, *P. drechsleri* Tucker, and *P. megasperma* (6,33) were used as inoculum.

Soil-water matric potential and changes in the soil-water status are also important factors in disease development. A decline in infection (27,29) and disease incidence (19,30) with a corresponding decline in ψ_m has been reported for several pathosystems involving *Phytophthora* spp. A single 24-hr saturation period reversed the effect of a low ψ_m on infection of tobacco by *P. parasitica* var. *nicotianae* (27,29); infection increased in the saturation treatment over that in the unsaturated treatment throughout a range of initial inoculum densities (27). Lengthening the flooding period from 4 to 48 hr every 2 wk increased disease severity of four *Phytophthora* spp. on Mahleb cherry seedlings (33) and *P. cactorum* on apple (6). Other researchers also have reported increases in disease development with flooding for *P. cinnamomi* on Fraser fir (17); *P. cryptogea, P. citrophthora*, and *P. citricola* on walnut (23); and *P. cryptogea* and *P. megasperma* on cherry (32). Cyclic changes in the soil-water status in the field were associated with cyclic changes in the mortality of tobacco caused by *P. p. nicotianae* as the result of repeated infection periods associated with conditions favorable for propagule germination and infection (13).

Generally, repeated flooding or lengthening the duration of flooding increased disease in various pathosystems involving species of *Phytophthora* (6,17,23,32–34). Changes in ψ_m apparently alter the inoculum-infection relationship substantially through probable influences on the increase of inoculum by the formation of sporangia and the subsequent release of zoospores. Zoospores of *P. p. nicotianae* were detected in the water above infested soil less than 0.5 hr after the soil was flooded (27), and an increase in the inoculum density of *P. cinnamomi* was reported after flooding in infested soil planted to Fraser fir (17).

Infection of plants with oospore inoculum of *Phytophthora* spp. with different ψ_m has been reported only once as near as we can determine. Kuan and Erwin (19) reported a decrease in mortality of alfalfa seedlings with decreasing ψ_m (100, 50, 20, and 10% disease incidences at ψ_m of 0, −1.0, −5.0, and −10.0 kPa, respectively) and an inoculum density of 10 oospores of *P. megasperma* f. sp. *medicaginis* per gram of soil. The effect of flooding the soil on plant mortality was not studied.

Information on the effect of ψ_m on sporulation, germination, and disease development for propagules of *P. capsici* is lacking, and very little is known about the role oospores of heterothallic species of *Phytophthora* play in the ecology of the pathogen and the epidemiology of disease under different water regimes. Therefore, the objective of this research was to investigate the effect of constant ψ_m and periodic flooding on mortality of pepper seedlings exposed to oospores of *P. capsici* with a defined initial inoculum density.

MATERIALS AND METHODS

Oospores of *P. capsici* were produced by placing four 1-cm^2 pieces of clarified V-8 juice agar (100 ml of clarified V-8 juice [cleared by centrifuging Campbell's V-8 juice amended with 15 g of $CaCO_3$ L^{-1}], 20 g of Difco agar [Difco Laboratories, Detroit, MI], and 900 ml of deionized water) with actively growing hyphae of two opposite compatibility types in an Omni-mixer (Ivan Servall, Inc., Norwalk, CT) with 50 ml of clarified V-8 juice broth (prepared as described above but without agar) and homogenizing for 30 sec. One milliliter of the resultant suspension was added to 40 ml of clarified V-8 juice broth amended with cholesterol

at 30 mg L^{-1} (Eastman Kodak Co., Rochester, NY) in a 250-ml Erlenmeyer flask. The cultures were incubated in the dark at 25 C for 2 mo.

Oospores were harvested from mycelial mats grown in liquid culture. Six mycelial mats were combined in 55 ml of 10^{-3} M 2-(N-morpholino)-ethanesulfonic acid (MES, Sigma Chemical Co., St. Louis, MO) in the Omni-mixer and homogenized for 30 sec. Buffer pH was adjusted to 6.1–6.2 with 0.1 N KOH. The resultant suspension of hyphae and oospores was diluted 1:1 (v/v) with a 1% solution of cellulase (EC 3.2.1.4; from *Penicillium funiculosum*; Sigma Chemical Co., St. Louis, MO) in 10^{-3} M MES, which gave a final concentration 0.5% cellulase, and the suspension was sonicated for 30 sec at 150 W (Braunsonic 1510, B. Braun Instruments, San Francisco, CA). After incubation for 18–24 hr in the dark at 25 C, the suspension was remixed in the Omni-mixer, sonicated again, and successively filtered through 150-μm and 75-μm nylon mesh with suction. Oospores were concentrated and the cellulase and hyphal fragments removed by successive centrifugations in 10^{-3} M MES for 2.5 min at approximately 1500 rpm in a clinical centrifuge (International Equipment Co., Needham Heights, MA). Supernatant was drawn off with a Pasteur pipette. Centrifugation speed was reduced as the suspension became free of debris and until a reasonably pure suspension of oospores was obtained. Oospores were resuspended in 10^{-3} M MES, stored at 5 C overnight, and used the next day in experiments. Suspensions were plated on clarified V-8 juice agar (CV-8) and a selective medium (PARPH) containing 10 mg pimaricin, 250 mg ampicillin, 10 mg rifampicin, 100 mg pentachloronitrobenzene, 50 mg hymexazol, and 17 g Difco cornmeal agar in 1 L of deionized water (16,25) to test for the presence of viable hyphal fragments and sporangia. Viable hyphal fragments or sporangia were not present in the inoculum for any trial, and very few oospores germinated (<1%) on either CV-8 or PARPH. Isolate Cp-8 (A1 compatibility type) was paired with isolate Cp-7 (A2 compatibility type). Isolates were maintained on CV-8 and periodically transferred.

Soil-water matric potential was controlled by the use of 600-ml Büchner funnels with porous glass plates as tensiometers as described by Duniway (10). Soil used in all experiments was a Myakka sand (sandy, siliceous, hyperthermic Aeric Haplaquod) (2) with an organic matter content of 0.95% and a pH of 6.6 in water. Raw field soil was air-dried, passed through a 2-mm-mesh screen, and stored until used. Five kilograms of soil (at approximately 2% moisture) were microwaved for 7 min on high power (700 W) and stored for at least 1 wk before use (14). The infested-soil-layer technique was used to allow uninjured roots to grow down into an infested layer of soil (16,24). Soil was placed in the funnels in two, 2-cm-deep layers. The bottom layer of either infested soil or microwaved uninfested soil, depending on the experimental treatment, was covered with a top layer of microwaved uninfested soil. Each layer was gently tamped down and leveled. Soil in the funnels was flooded briefly by raising the level of the reservoir. The reservoir was then lowered to establish the desired ψ_m. The reference points were 1 cm above the porous glass plate (the middle of the infested soil layer) and the top of the reservoir (250-ml Erlenmeyer flasks). Approximately 1 cm in height separating the reference points was equal to 0.1 kPa of tension (0.1 kPa = 1.0 mbar = 1.022 cm H_2O) (15). Autoclaved deionized water was used throughout.

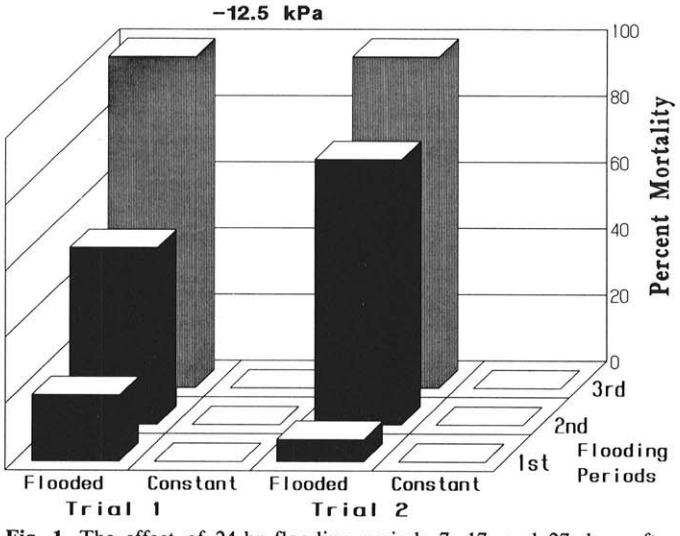

Fig. 1. The effect of 24-hr flooding periods 7, 17, and 27 days after transplanting and a constant soil-water matric potential of −12.5 kPa on the mortality of pepper seedlings infected by *Phytophthora capsici*; the height of each bar represents the percentage of 15 plants that died.

Pepper seeds (*Capsicum annuum* L. 'Early Calwonder') were germinated in vermiculite and transplanted into the top uninfested layer (one plant per funnel) when the first true leaves began to expand. A plastic disk with an opening for the plant stem was placed over the top of the soil in each funnel to retard evaporation. Experiments were conducted in a plant growth room at 25–27 C with a 14-hr photoperiod (approximately 94 μmol m^{-2} s^{-1} photosynthetically active radiation [PAR] at the top of the plants [LI-COR, Inc., Lincoln, NE]). Soil was infested and placed in the funnels, and pepper seedlings were transplanted on the same day.

Two sets of experiments were performed: one with a constant ψ_m of −2.5 kPa and the other at −12.5 kPa. These ψ_m were chosen based on the examination of the soil-water release curve and the diameter of water-filled pores at each ψ_m. Each experiment was repeated once and consisted of the following four treatments: uninfested soil and a constant ψ_m; uninfested soil and periodic flooding (soil flooded for 24-hr periods 7, 17, and 27 days after transplanting); infested soil (25 oospores per gram of dry soil) and a constant ψ_m; and infested soil and periodic flooding. In preliminary experiments, symptoms were usually present 3–4 days after a flooding period, and no further symptom development was observed 7–9 days after a flooding period. Thus, flooding periods at 10-day intervals precluded misclassification of the flooding period and associated symptom development. Each trial consisted of 15 funnels per treatment, with one plant per funnel, arranged in a completely randomized design.

Reservoirs were filled and plants observed daily for symptoms. Symptom development consisted of incipient wilt followed by constriction of the stem by a brown lesion extending up from the soil line. Plants were harvested as they became moribund. Roots and a small portion of the stem were washed free of soil in running water, dipped in 70% EtOH for 5–10 sec, rinsed twice in deionized water, and blotted dry on paper towels. Root systems were then plated on PARPH and incubated at room temperature in the dark. The plates were observed for the characteristic growth of *P. capsici* from the stem and roots and checked microscopically. Small portions of agar with hyphae from the edge of the advancing colony were transferred to PARP (PARPH without hymexazol) with embedded Van Tiegham cells and incubated in the dark at room temperature to confirm that the hyphae growing from the roots was *P. capsici* and not a *Pythium* sp. *P. capsici* grew slowly on the PARP medium with dense colony morphology and no aerial mycelium, whereas a *Pythium* sp. grew much faster with loose colony morphology and aerial mycelium. The *Pythium* sp. was rarely isolated and was not associated with symptom development. All symptomless plants were harvested at the conclusion of the trials (37–40 days after transplanting), and the roots were plated on the selective medium to assess for the presence of symptomless infected plants. Extensive root growth was observed throughout the volume of soil in each funnel at the conclusion of the trials.

RESULTS

Periodic flooding dramatically increased disease incidence in all trials when oospores of *P. capsici* were used as inoculum (Figs. 1 and 2). No disease was observed and no infection detected in plants when the roots were plated on the selective medium after 37 days in infested soil that had been maintained at a constant

ψ_m of −12.5 kPa (Fig. 1). However, when infested soil was periodically flooded, 20, 53, and 100% of the plants died after one, two, and three 24-hr flooding periods, respectively. No disease was observed and no infection detected in plants growing in the uninfested soil. The experiment was repeated with similar results; 7, 80, and 100% of the plants grown in infested soil died after one, two, and three flooding periods, respectively.

Periodic flooding also increased the percentage of plant mortality in infested soil over those in infested soil held at a constant ψ_m of −2.5 kPa. When infested soil was periodically flooded, 0, 80, and 100% of the plants died after one, two, and three 24-hr flooding periods, respectively (Fig. 2). A much lower level of disease was observed with a constant ψ_m of −2.5 kPa; only one of 15 plants was diseased after 17 days, and no further disease was observed and no infection detected at the conclusion of the trial. No disease was observed and no infection detected in plants growing in the uninfested soil. The trial at −2.5 kPa was also repeated with similar results; 20, 73, and 80% of the plants grown in infested soil died after one, two, and three flooding periods, respectively. One of 15 plants was diseased at the conclusion of the trial when infested soil was held at a constant ψ_m. No disease was observed and no infection detected in plants growing in the uninfested soil.

DISCUSSION

Mortality of pepper plants grown in soil infested with 25 oospores of *P. capsici* per gram of soil was influenced by periodic flooding. Other investigators also have shown an increase in disease with either a single flooding period or periodic flooding (6,17,23,27,29,32–34). The results also reinforce field observations where heavy rainfall with subsequent flooding of the soil was associated with increases in disease progress of *P. capsici* on pepper (5).

Wilcox and Mircetich (33) suggested that the influence of different soil moisture regimes on disease parallels the influence of ψ_m on sporangium production and zoospore discharge and motility. They reasoned that the low levels of infection by several *Phytophthora* spp. and negligible disease development on Mahaleb cherry, which occurred in their studies at constant ψm as opposed to the higher levels of disease observed with periodic flooding, may have been due to the low frequency of sporangium production or the failure of sporangia to discharge zoospores at the tested ψ_m. Sporangium production has been reported to take place over a wide range of ψ_m, depending on the soil and form of inoculum used in the study, but zoospore release is generally thought to occur only in near-saturated, saturated, or flooded conditions (3,6,11,12,20–22,26,33). Thus, the limiting factor to infection under the conditions of these experiments appears to be ψ_m that affect zoospore release.

Stolzy et al (31) suggested that zoospores of *Phytophthora* spp. require water-filled pores of at least 40–60 μm in diameter to move through soil, but this probably represents the smallest pore diameters that will facilitate zoospore movement for even short distances (8). Allen and Newhook (1) demonstrated that the helical motion of zoospores required water-filled pores to be about 190 μm in diameter. The maximum pore diameter that remains filled with water as the ψ_m is lowered from saturation can be determined by the capillary rise equation (9,15). Thus, zoospore movement would be restricted to ψ_m above approximately −1.5 kPa.

These conditions may be modified, however, by the texture and pore size distribution of various soils. Zoospores of *P. cryptogea* swam horizontally through surface water or through a coarse-textured soil mix at ψ_m of $\geq$ −0.1 kPa for distances of 25–35 mm to reach seedlings (10). However, movement of zoospores through soil was reduced at −1.0 kPa and was not observed at −5.0 kPa. Zoospore movement was limited to 5 mm at −0.1 kPa in reconstituted loam soils and further restricted at −1.0 kPa. Thus, a lower limit of pore size diameters of 40–60 μm realistically may not allow movement. Duniway (10,12) suggested that not only must there be continuous, water-filled channels that are large enough to accommodate zoospores, but that the larger and less tortuous the water-filled pore, the more suitable that will be for active zoospore movement. We observed high plant mortality in the treatments with periodic flooding as a result of the conducive soil environment for zoospore formation, release, and movement.

The largest water-filled pore size in a soil with a ψ_m of −2.5 kPa would be approximately 120 μm in diameter, which is greater than the limiting pore size of 40–60 μm necessary for zoospore movement but still less than the 190 μm pore size reported by Allen and Newhook (1). This may account, however, for the few plants that were infected at a constant ψ_m of −2.5 kPa. A small number of zoospores resulting from oospore germination may have been able to move short distances through water-filled pores to root surfaces and initiate infection. In contrast, only pore sizes of 12 μm and less would be water-filled at a ψ_m of −12.5 kPa, and zoospore movement in the soil would be prevented. No infection was observed in plants growing in infested soil at a constant ψ_m of −12.5 kPa.

The method of oospore germination and infection in our study is not known. Oospores of *P. m. medicaginis* in soil maintained at a constant ψ_m of −10.0 kPa did not germinate (19). Thus, the lack of infection of pepper seedlings when grown in soil infested with oospores of *P. capsici* maintained at a constant ψ_m of −12.5 kPa may have been due to the lack of oospore germination. Shew (27) reported that one 24-hr flooding period was enough to overcome the inhibitory effect of ψ_m of −3.0 to −5.0 kPa on infection of tobacco plants grown in soil naturally infested with *P. p. nicotianae*. The failure of *P. p. nicotianae* to cause infection at ψ_m lower than those that favor zoospore release and motility indicated that, under the conditions of the study, direct germination of propagules other than zoospores (presumably chlamydospores) was not important in the infection of tobacco roots. Similarly, in our study, a single 24-hr flooding period was sufficient to allow oospore germination and infection, which led to plant death, but infection and subsequent plant mortality were not observed at ψ_m not conducive to zoospore release (20). This circumstantial evidence indicates that oospores of *P. capsici* probably germinate at high ψ_m and produce germ sporangia, which then release zoospores. Kuan and Erwin (19) also noted this mode of germination at high ψ_m with oospores of *P. m. medicaginis*. Infection and plant mortality observed with *P. capsici* at a constant ψ_m of −2.5 kPa, however, indicates that oospore germination and zoospore release may occur under less than optimal conditions, but that the germinating oospore would have to be very close to the root in accordance with the arguments presented above for the diameter of water-filled pores in soil at certain ψ_m.

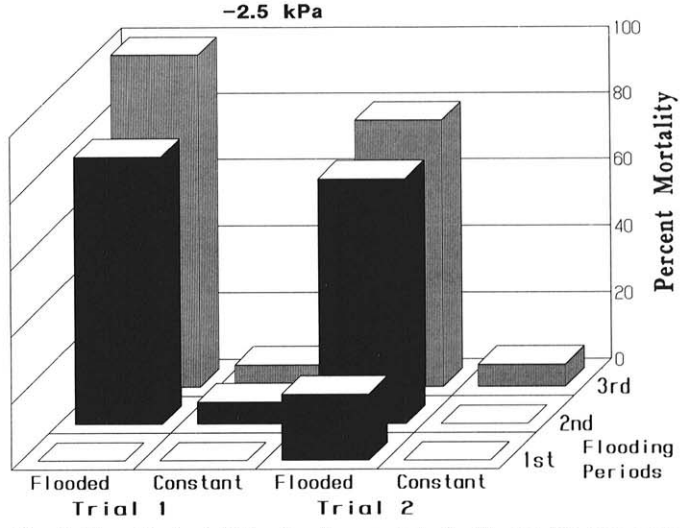

Fig. 2. The effect of 24-hr flooding periods 7, 17, and 27 days after transplanting and a constant soil-water matric potential of −2.5 kPa on the mortality of pepper seedlings infected by *Phytophthora capsici*; the height of each bar represents the percentage of 15 plants that died.

Although the conditions for oospore germination, sporangium production, and zoospore release existed, one 24-hr flooding period did not result in 100% infection. Roots of the transplanted seedlings may not have grown down into the infested layer of soil and contacted the oospore inoculum at the time of the first 24-hr flooding period. Thus, oospores were not stimulated to germinate. With time, more roots contacted oospore inoculum, which probably germinated indirectly with subsequent flooding and resulted in infection and plant mortality.

Another aspect of disease development that has not been investigated sufficiently is the effect of secondary inoculum produced on roots on subsequent disease development. Oospore germination during flooding periods may result in infection, but it is not known whether the initial inoculum is sufficient to result in plant death. A low percentage of the plants died as a result of just one flooding period, indicating that sufficient inoculum was present to result in plant mortality. In a related study, low numbers of zoospores of *P. capsici* were able to cause high percentages of plant mortality in pepper when zoospores were added to free water over a flooded soil (4). Shew (27) observed zoospores in the surface water over flooded soil in as little time as 0.5 hr, which demonstrated the direct effect of high ψ_m on the pathogen through increasing zoospore production and dispersal. Others have also shown this effect (10,17,20,26). The migration of zoospores to the surface water via negative geotaxis (7) may have produced the same effect in our study.

The increase in inoculum during a flooding period may be enough to infect the plant, but may not be enough to cause plant mortality. In this instance, sporangium production may occur on infected root segments during periods of lower ψ_m, and zoospores could be released once a sufficiently high ψ_m is again reached. Thus, more than one flooding period may be required for substantial increases in secondary inoculum and disease incidence. This may have been the case in our study where repeated flooding of the soil was required before high levels of plant mortality were obtained. Only when experiments are conducted with low numbers of oospores and zoospores placed directly on host roots under defined ψ_m will this question be answered.

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