Effect of Soil Matric Potential on the Formation and Indirect Germination of Sporangia of *Phytophthora parasitica*, *P. capsici*, and *P. cryptogea*

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ABSTRACT

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Mycelial disks of *Phytophthora parasitica* and *P. capsici* incubated in soil at a constant matric potential (ψ_m) of −300 millibars (mb) formed abundant sporangia within 24 hr, but *P. cryptogea* required 4 days. Both *P. capsici* and *P. parasitica* did not form sporangia in saturated soil, unless first incubated for 2 days at −200 to −300 mb ψ_m. The effect of ψ_m on zoospore discharge (indirect germination) by sporangia of *P. parasitica* was determined by changing ψ_m from −300 mb, at which 13% of the sporangia had germinated indirectly after 6 days, to 0, −10, −25, −50, and −100 mb. Within 24 hr, a significant increase to 40% indirect germination occurred, but only if ψ_m was adjusted to 0 mb. Zoospore discharge by sporangia formed in soils of different textures was more closely related to changes in ψ_m than to soil water content. Sporangia of *P. parasitica* consistently germinated indirectly less frequently in saturated soil than did those of either *P. cryptogea* or *P. capsici*. Indirect germination by sporangia of *P. parasitica* was increased by longer periods of incubation in soil at −300 mb ψ_m prior to saturation. Sporangia were formed and zoospores were released by *P. parasitica* at temperatures from 15 to 33 C, and in PEG 6000 solutions at −4.6 bars solute potential.

Additional key words: buckeye rot, tomato (*Lycopersicon esculentum*).

Phytophthora root and crown rot of tomatoes is a serious disease caused most commonly in California by *P. parasitica* but also by *P. capsici* (20). Although a fruit-rotting phase of the disease called buckeye rot is important in the south and west on fresh market tomatoes, root and crown rot causes the most serious losses on processing tomatoes in California. In fields the pattern of disease appears to be related to poor soil drainage or excessive irrigation. Although soil moisture is recognized as one of the most important parameters influencing sporulation and infection of plants by soilborne *Phytophthora* spp. (6), little is known about the effects of soil moisture on the species attacking tomato. The influence of the matric potential (ψ_m) component of soil water potential (Ψ) on sporangium formation by *P. parasitica* has been studied (7,10), and an isolate of this species from tomato was found to form sporangia abundantly at ψ_m values between −25 and −300 millibars (mb) (10), whereas an isolate from citrus formed sporangia abundantly at ψ_m values between −50 and −700 mb ψ_m (7). However, no sporangia were produced in saturated soil (7,10). The influence of ψ_m on zoospore release also has been studied for other *Phytophthora* spp., but not for *P. parasitica* or *P. capsici*. In the case of *P. cryptogea*, Duniway (4,5) determined by counting empty sporangia that, although 100% of the sporangia that formed in soil at −300 mb ψ_m (field capacity) germinated indirectly within 1 day after the soil was saturated, a significant amount of indirect germination occurred in sporangia maintained for 6 days at −300 mb ψ_m. MacDonald and Duniway (11) found by counting motile zoospores of *P. megasperma* and *P. cryptogea* that maximum indirect germination of sporangia formed in soil during 3–4 days at −150 mb ψ_m occurred when they were wetted to 0 mb, with much less germination at −10 mb ψ_m, and none at −25 mb ψ_m. Zoospore release began about 1 hr after the soil was saturated and was nearly completed within 4 hr (11). Pfender et al (17) counted empty sporangia of *P. megasperma* and reported that 100% germinated indirectly within 3 days when maintained at 0 mb ψ_m. Gisi (8) reported that only 15% of the sporangia of *P. cactorum* germinated in soil at 0 mb ψ_m, but that 60% germinated after the sporangia were transferred to glass-distilled water.

Because of reports (7,10) that *P. parasitica* formed sporangia best in soils drained to about field capacity (−300 mb ψ_m), we wanted to know if field observations that correlated disease with saturated soil conditions could be attributed primarily to a stimulation of zoospore release or if cyclic changes in soil ψ_m accompanying irrigation could induce sporangium formation in saturated soils where it would not otherwise be expected (7,10). Furthermore, we were interested in knowing to what extent sporangia could release zoospores in unsaturated soils and if the effect of soil ψ_m on sporulation differed among *P. parasitica*, *P. capsici*, and other *Phytophthora* spp.

MATERIALS AND METHODS

Three *Phytophthora* spp. were studied: *P. parasitica* Dastur (culture 30-2 DM [10]) isolated from an infected tomato root near Davis, CA; *P. capsici* Leonian (culture 1520) isolated from an infected tomato root near Brentwood, CA (19), and obtained from E. E. Butler; and *P. cryptogea* Tucker (culture 201) isolated from safflower and obtained from J. M. Duniway (3–5,11,12). Fungi were grown on lima bean agar (LBA) (1) or V-8 juice agar (V8A). Unless specified otherwise, experiments were conducted at 22–24 C.

Soils. Two soils were used: a Yolo fine sandy loam (YFSL) that had been autoclaved for 90 min and wet sieved to obtain the coarse sand fraction (⩾250 μm) (11), and a Marvin silty clay loam (MSCL) collected from a tomato field with a history of Phytophthora root rot located near Davis, CA. The latter soil was air-dried at about 20 C and sieved through a 1.4-mm screen. Soil water retention curves were obtained by drying soils to known matric potentials on tension plates and then drying portions of soil for 3 days at 105 C to determine water content.

Sporangium formation and germination in soil. Soil matric potential (ψ_m) was controlled with Büchner funnel tension plates (4,5). The center of the sintered-glass base in the funnels served as the reference in adjusting ψ_m. Soil depth in funnels was limited to a maximum of 2 mm to facilitate rapid equilibration of ψ_m (11). Soil on the plates initially was wetted to saturation by water infiltration through the sintered-glass plate and then was drained to −150 mb

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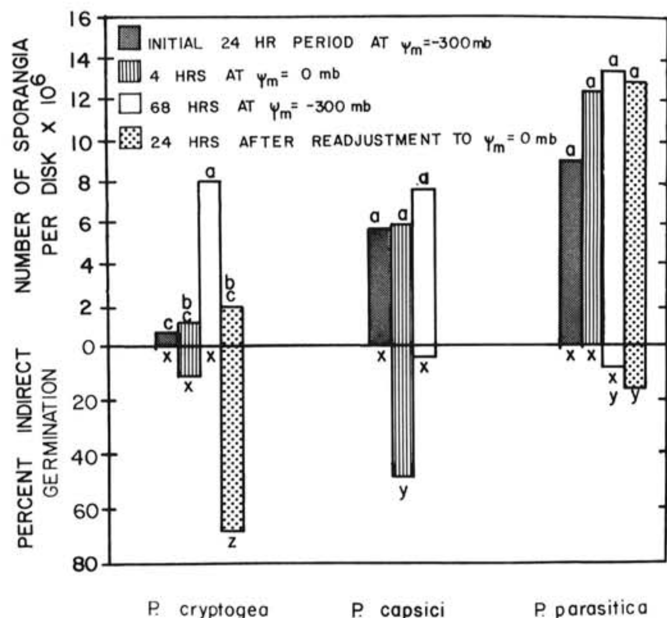

Fig. 1. Influence of changes in soil matric potential (ψ_m) on sporangium formation and indirect germination by *Phytophthora cryptogea*, *P. capsici*, and *P. parasitica*. Mycelial disks were incubated in the ≥250-μm fraction of Yolo fine sandy loam at $\psi_m = -300$ mb for 24 hr, followed by 4 hr at $\psi_m = 0$ and then 68 hr at $\psi_m = -300$ mb, and finally were returned to 0 mb for 24 hr. The numbers of sporangia and percentages of germination were determined at the end of each incubation period for each ψ_m value. Numbers of sporangia or percentages of germination within a species with letters in common do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.

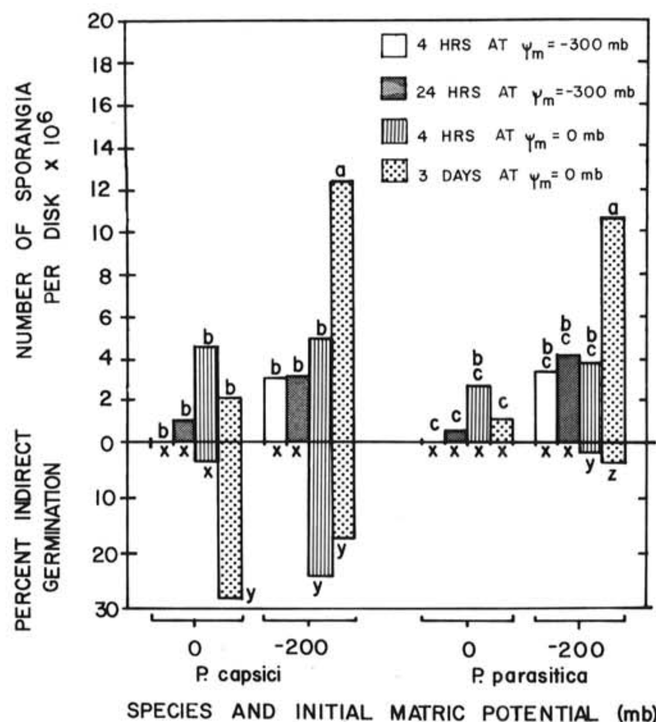

Fig. 2. Influence of changes in soil matric potential (ψ_m) on sporangium formation and indirect germination by *Phytophthora parasitica* and *P. capsici* in the ≥250-μm fraction of Yolo fine sandy loam. Mycelial disks initially incubated for 24 hr at either saturation ($\psi_m = 0$) or at -200 mb ψ_m, were incubated for 24 hr at $\psi_m = -300$ mb, followed by 3 days at $\psi_m = 0$. The number of sporangia and percentages of germination were determined 4 and 24 hr after adjustment to $\psi_m = -300$ mb, and 4 hr and 3 days after readjustment to 0 mb ψ_m. Numbers of sporangia with letters in common within a species do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.

ψ_m. Disks of mycelium were lifted from 9- to 11-day-old LBA cultures, placed on soil, and covered with 1–2 mm of dry soil, which quickly equilibrated with contiguous soil. Funnels then were set at the desired matric potentials. To observe sporangia, mycelial disks and surrounding soil were removed from the funnels and immediately fixed and stained with several drops of acid fuchsin in lactophenol. The stained disks were blended in 5 ml of water and centrifuged for 10 min at 1,600 *g* in a clinical centrifuge and the supernatant fluid above the pellet was removed until a volume of 1 ml remained. The pellet was resuspended in 1 ml with a Vortex mixer, and a drop of the suspension was placed on a slide and covered with a coverslip supported at each corner by small pieces of glass to give a uniform depth of 0.1 mm. The slide was examined at ×400 magnification, and sporangia in 50 random fields were counted for each replication. The totals for three replications were averaged for each treatment to estimate the total number of sporangia and the percent indirect germination per mycelial disk.

The influence of ψ_m on both sporangium formation and indirect germination was determined in every experiment. Disks were generally sampled at the end of the incubation period at a particular ψ_m. Disks were incubated at either -200 or -300 mb ψ_m for periods of time ranging from 1 to 6 days, and then in saturated soil at 0 mb ψ_m for 24 hr. In an experiment comparing *P. parasitica*, *P. capsici*, and *P. cryptogea*, disks incubated at -300 mb ψ_m for 24 hr were saturated for 4 hr and then returned to -300 mb ψ_m for 3 additional days. To determine the effect of cyclic changes in ψ_m on sporulation by *P. parasitica* and *P. cryptogea*, disks were incubated in soil at either 0 or -200 mb ψ_m for 24 hr prior to incubation at -300 mb ψ_m for 24 hr.

Sporangium formation in solutions. Soil extract was obtained by mixing 100 g of unsieved YFSL in 1 L of glass-distilled water for 1 hr, after which the suspension was centrifuged for 10 min at 5,000 *g* and the supernatant was filtered through Whatman #2 paper. A weft of mycelium was removed from a 5-day-old V8A culture of *P. parasitica* with a transfer needle and placed in a drop of soil extract on a coverslip that was inverted on a Van Tieghem cell. Sporangium formation and zoospore release were observed periodically with a light microscope at ×50 magnification. To determine the temperature limits for sporangium formation and zoospore release, 7-mm-diameter disks were cut from the margins of 4-day-old LBA or V8A colonies and placed in petri dishes containing 15 ml of either glass-distilled water or soil extract. Plates were incubated at constant temperatures ranging from 15 to 36 C in 3-C increments and observed at 24 and 48 hr for sporangium formation and indirect germination. The influence of solute potential (ψ_s) on sporangium formation and indirect germination was examined by placing disks from 13-day-old LBA cultures in 5-cm-diameter petri dishes containing 10 ml of either 0.05 M NaCl ($\psi_s = -2.3$ bars), PEG 6000 ($\psi_s = -1.8, -4.65, -10,$ or -18.2 bars) (15), glass-distilled water, tap water, or MSCL soil extract and incubating at 22–24 C. Disks were observed 24 hr later to determine the extent of sporangium formation and then chilled to 15 C for 20 min to observe indirect germination.

RESULTS

When incubated at -300 mb ψ_m interrupted by a brief 4-hr period of saturation at 24 hr, mycelial disks of *P. parasitica*, *P. capsici*, and *P. cryptogea* formed similar numbers of sporangia by 4 days (Fig. 1). Essentially all of the sporangia formed by *P. parasitica* and *P. capsici* were formed within the first 24 hr of incubation, while the numbers of sporangia formed by *P. cryptogea* increased significantly from 1 to 4 days of incubation (Fig. 1). Results identical to those in Fig. 1 were obtained with mycelial disks washed for 3 hr in distilled water prior to incubation in soil. When mycelial disks of *P. parasitica* and *P. capsici* were incubated in saturated soil for 24 hr, no sporangia were formed (Fig. 2). However, sporangia did form in saturated soil if the mycelial disks were first incubated for 24 hr at -200 mb ψ_m followed by 24 hr at -300 mb ψ_m (Fig. 2). When the incubation period at -200 mb ψ_m was extended past 48 hr, no new sporangia of *P. parasitica* formed when the disks were saturated (Fig. 3). Results similar to those in

Fig. 3 were obtained by initially incubating disks at −300 mb ψ_m. Likewise, disks initially held at either −150 or −300 mb ψ_m for 5 days did not show an increase in sporangia during 3 subsequent days of saturation (*unpublished*).

Sporangia of *P. parasitica* formed readily in both glass-distilled water and YFSL soil extract at all temperatures tested except 36 C. At 22–24 C, sporangial initials were observed 90 min after the hyphae of *P. parasitica* were placed in YFSL soil extract. Within 2.5 hr, the development of many sporangia had advanced to papilla formation; by 4.75 hr, many swimming zoospores and empty sporangia were observed. Abundant sporangia also formed on disks incubated at 22–24 C in tap water, MSCL soil extract, PEG 6000 solutions at −1.7 bars, and NaCl solutions at −2.3 bars. Fewer sporangia were formed in PEG 6000 solutions at −4.65 bars and none were formed in PEG 6000 solutions at −10 or −18.2 bars.

The influence of ψ_m on zoospore release varied among the three species tested. Sporangia of *P. capsici* and *P. cryptogea* formed at −300 mb ψ_m germinated readily when exposed to saturated soil, although sporangia of *P. parasitica* did not always do so (Fig. 1). When sporangia of *P. parasitica* that had formed during 4 days in soil at −300 mb ψ_m were adjusted to 0 mb ψ_m, only 15% germinated indirectly within 24 hr, while 70% of *P. cryptogea* sporangia did so (Fig. 1). None of the sporangia formed by *P. parasitica* during 24 hr in soil at −300 mb ψ_m germinated indirectly when saturated for 4 hr, while 50% of *P. capsici* sporangia did so (Fig. 1). Sporangia of *P. capsici* formed during 2 days in soil under cyclic changes in ψ_m germinated to a much greater extent following saturation than did those of *P. parasitica* (Fig. 2). Sporangia of *P. parasitica* did not show indirect germination comparable to that of *P. capsici* unless they had been maintained at −200 mb ψ_m for 6 days before ψ_m was adjusted to 0 mb (Fig. 3). In two soils with different water content-matric potential curves (Fig. 4), between 5 and 18% of *P. parasitica* sporangia germinated indirectly when maintained in soil at −300 mb ψ_m for 6 days (Fig. 5). When ψ_m was adjusted from −300 mb to higher values, the amount of indirect germination increased, but only when sporangia were adjusted to 0 mb ψ_m where indirect germination was 35% in YFSL, and 40% in MSCL, was this increase significant.

The amount of indirect germination by sporangia of *P. parasitica* in solutions was much greater than that occurring in soil. Zoospore release occurred at all temperatures and in all osmotic solutions in which sporangia formed. The highest amount of indirect germination, about 65%, occurred with sporangia incubated at 21, 24, or 27 C in YFSL soil extract. Chilling the sporangia or aerating the cultures did not significantly increase the percentage of indirect germination.

DISCUSSION

The speed with which sporangia form in soil, even at optimum ψ_m, seems to vary among species. Gisi et at (9) reported that the numbers of sporangia formed by *P. palmivora* at −10 mb ψ_m increased steadily from 1 to 4 days of incubation in soil, whereas the maximum numbers of sporangia of *P. cinnamomi* were formed at −160 mb ψ_m within 1 day and declined thereafter. Thus, based on time required for sporangium formation, *P. palmivora* (9), *P. cactorum* (8,21), and *P. cryptogea* (4) can be placed in a group requiring several days, whereas *P. cinnamoni* (9) and *P. megasperma* (17) can form large numbers of sporangia in as little time as 24 hr. We found that although −300 mb ψ_m is favorable for production of sporangia by all three species tested, *P. parasitica* and *P. capsici* formed maximum numbers of sporangia within the first 24 hr, whereas *P. cryptogea* formed very few sporangia within that time (Fig. 1). Gisi et al (9) found that varying ψ_m did not stimulate formation of sporangia by *P. cinnamomi*. We found, however, that large numbers of sporangia of *P. parasitica* were formed in saturated soil if the mycelial disks were first incubated in soil at −200 to −300 mb ψ_m for 48 hr, even though none were produced when disks were introduced directly into saturated soil (Fig. 2) (7,10). If the disks were incubated for longer than 48 hr (Fig. 3), they lost the ability to form more sporangia when subsequently saturated, perhaps due to a change in the physiology of the hyphae

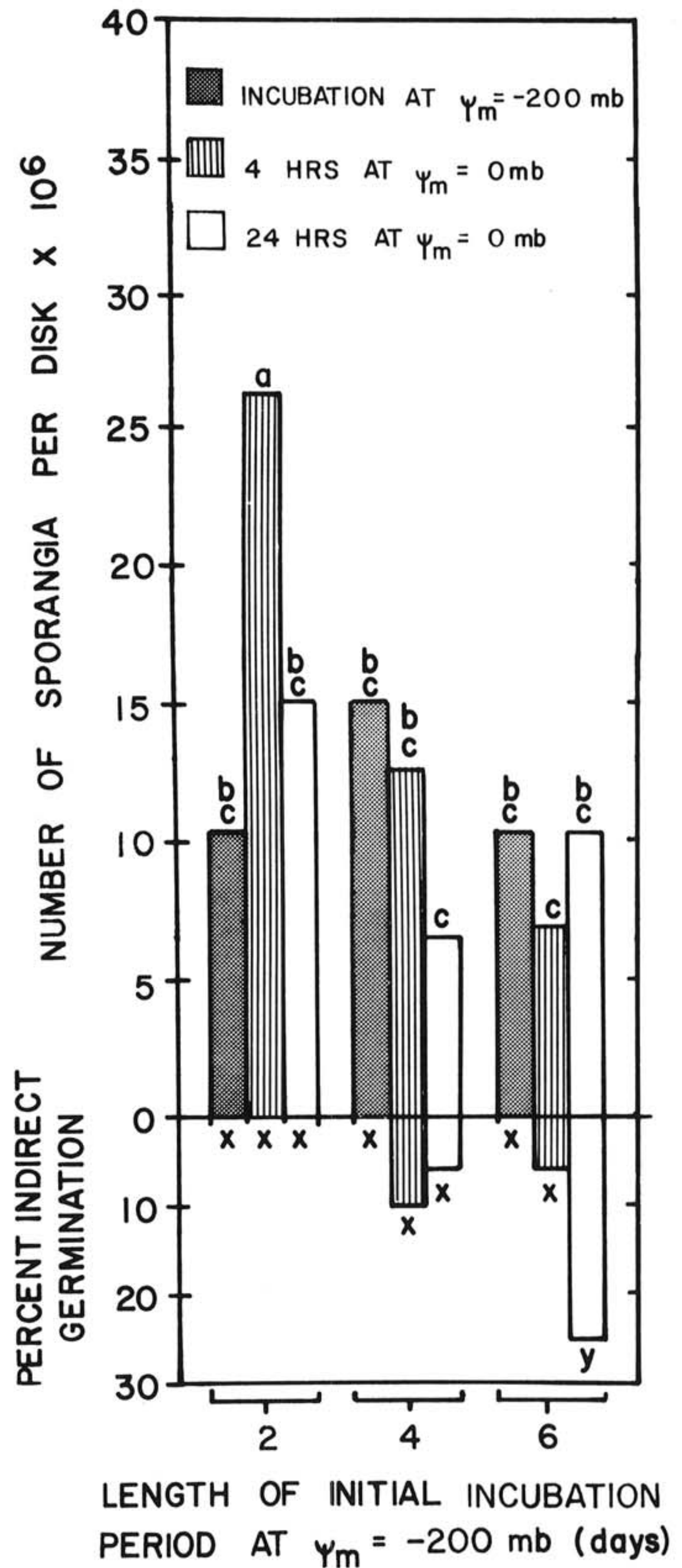

Fig. 3. Influence of length of incubation at $\psi_m = -200$ mb and a subsequent 24-hr period at $\psi_m = 0$ on sporangium formation and germination by *Phytophthora parasitica* in the ⩾250-μm fraction of Yolo fine sandy loam. Mycelial disks were exposed initially to $\psi_m = -200$ mb for 2, 4, or 6 days, followed by 24 hr at saturation. The numbers of sporangia and percentages of germination were determined with mycelial disks from the same Büchner funnel just before, 4 hr, and 24 hr after ψ_m was changed from −200 mb ψ_m to saturation ($\psi_m = 0$). Numbers of sporangia and percentages of germination with letters in common do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.

or hyphal lysis by soil microorganisms. Gisi et al (9) in a survey of the literature on sporangium formation by *Phytophthora* spp. suggests that mycelia introduced into soil in infected plant tissues form sporangia at higher ψ_m values than mycelia introduced as washed disks. They also suggested that sensitivity to aeration can determine the upper ψ_m limit for sporangium production in soil (9). Sporangium production in culture by *P. parasitica* requires an O_2 concentration of greater than 1% and is inhibited at a CO_2 concentration of 5% (16). Thus, while nutrition, CO_2, and O_2 levels may interact to determine the optimum ψ_m for initiation of sporangium formation, our results clearly show that once sporangia are initiated, other ψ_m values may be conducive to their formation. This was also shown with *P. cambivora*, which initiated sporangium formation only in saturated soils, although formation continued at −50 mb ψ_m (22).

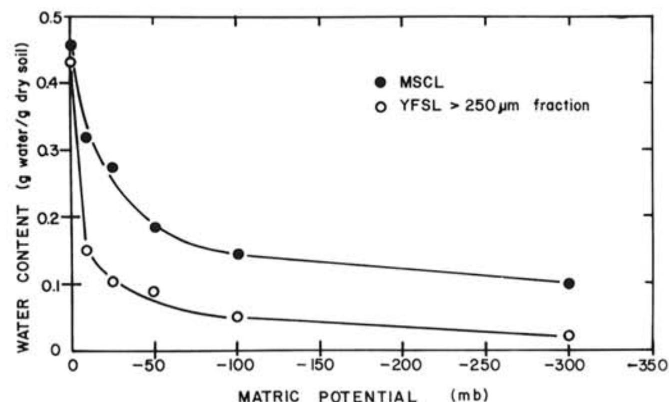

Fig. 4. The relationship between water content and decreasing matric potential for a Marvin silty clay loam (MSCL) and the ⩾250-µm fraction of Yolo fine sandy loam (YFSL).

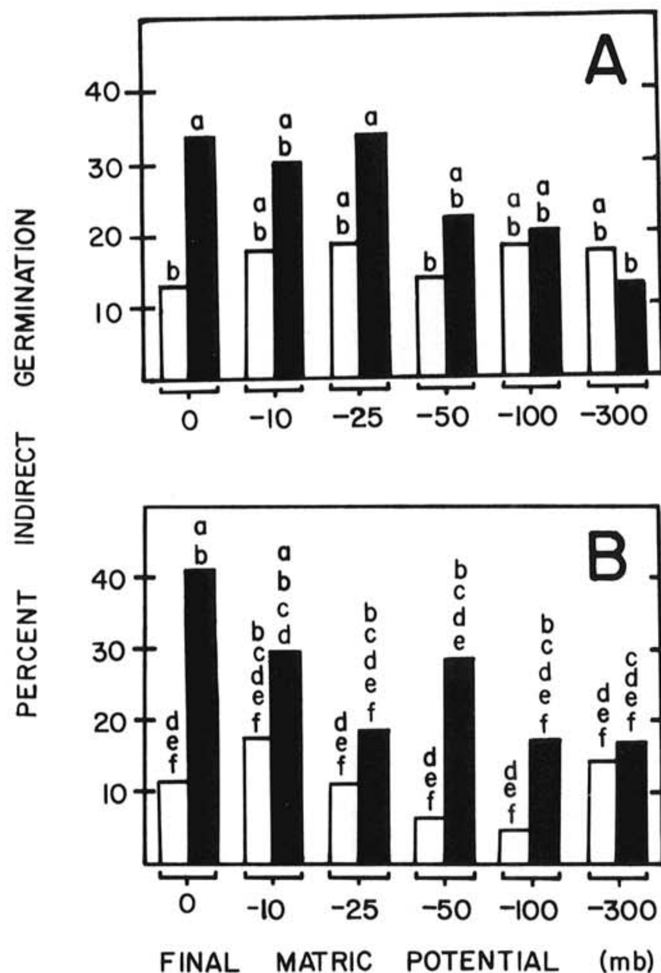

Fig. 5. Influence of a change in matric potentials on indirect germination by *Phytophthora parasitica* sporangia in **A**, Marvin silty clay loam, and **B**, the ⩾250-µm fraction of Yolo fine sandy loam. The initial and final percentages of germination were determined with mycelial disks from the same Büchner funnel held for 6 days at $\psi_m = -300$ mb (□) and 24 hr after ψ_m was changed from −300 mb to the final value given (■). Percentages with letters in common (above each bar) do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.

The dynamics of zoospore release also varied among the three species that we tested. In as little as 24 hr after mycelial disks of *P. capsici* were placed in soil at a ψ_m favorable for sporangium formation, zoospore release occurred when the soil was saturated (Fig. 1). Owing to its slower sporangium formation, *P. cryptogea* did not release zoospores when mycelial disks were subjected to the same treatment. Once sporangia had formed, they germinated readily when saturated (Fig. 1). However, although *P. parasitica* formed large numbers of sporangia within 24 hr at −300 mb ψ_m, no indirect germination occurred when the sporangia were saturated. It was not until sporangia were maintained in soil at −300 mb ψ_m for 6 days that appreciable amounts of indirect germination occurred upon saturation (Fig. 3). On the other hand, sporangia formed on mycelial disks in solutions, including unsterile soil extract, germinated readily after 1–2 days of incubation. The results shown in Figs. 1 and 2 indicate that if a soil factor is inhibiting indirect germination by *P. parasitica*, it is one to which *P. cryptogea* and *P. capsici* are much less sensitive and one that does not function in soil extract. Alternatively, *P. parasitica* may have some constitutive inhibitor of zoospore release that is leached away much more quickly in solutions than in soil.

As was found by Duniway (4,5) for *P. cryptogea* and by Reeves (18) for *P. cinnamomi*, some indirect germination by *P. parasitica* sporangia occurred at ψ_m values as low as −300 mb, although the maximum amounts of indirect germination were in saturated soil (Fig. 5). Although indirect germination can occur at ψ_m values too low for significant zoospore motility (5,13), the increased inoculum density in soil could be epidemiologically significant (2,14). As with other *Phytophthora* spp. (11), the sensitivity of zoospore discharge to the ψ_m component of Ψ is not paralleled by a similar sensitivity to ψ_s, as zoospore discharge by *P. parasitica* occurred in PEG 6000 solutions at $\psi_s = -4.65$ bars.

Phytophthora parasitica and *P. capsici* in infected tissues can probably form sporangia under two sets of circumstances: when the soil dries from saturation to values near field capacity, and when the soil is subsequently rewetted by irrigation. Although even relatively short (5–6 hr) periods of soil saturation resulting from irrigation may be ample for zoospore release by sporangia of *P. capsici* (Figs. 1 and 2), zoospore release by *P. parasitica* appears to require longer periods of saturation (Fig. 3). When caused by *P. capsici*, the association of Phytophthora root and crown rot with poor soil drainage may be due mostly to the effects of prolonged periods of saturation on zoospore motility and infectivity. In the case of *P. parasitica*, however, prolonged periods of soil saturation are also required for substantial amounts of indirect germination. Although sporangia of *P. capsici* can germinate indirectly as soon as formed (Fig. 1), sporangia of *P. parasitica* require a lag period before they can germinate (Fig. 3). Thus, increase in zoospore inoculum during the early phases of an epidemic may be slower with *P. parasitica* than with *P. capsici*.

LITERATURE CITED

1. Aragaki, M., Mobley, R. D., and Hine, R. B. 1967. Sporangial germination of *Phytophthora* from papaya. Mycologia 59:93-102.
2. Bernhardt, E. A. 1979. Epidemiology of tomato root rot caused by *Phytophthora parasitica* Dastur: I. Effect of soil moisture on zoospore production and disease incidence. II. Relationship between zoospore density and disease incidence. M. S. thesis, University of California, Davis. 51 pp.
3. Duniway, J. M. 1975. Limiting influence of low water potential on the formation of sporangia by *Phytophthora dreschsleri* in soil. Phytopathology 65:1089-1093.

4. Duniway, J. M. 1975. Formation of sporangia by *Phytophthora drechsleri* in soil at high matric potentials. Can. J. Bot. 53:1270-1275.
5. Duniway, J. M. 1976. Movement of zoospores of *Phytophthora cryptogea* in soils of various textures and matric potentials. Phytopathology 66:877-882.
6. Duniway, J. M. 1979. Water relations of water molds. Annu. Rev. Phytopathol. 17:431-460.
7. Feld, S. F., Menge, J. A., and Tsao, P. H. 1978. Influence of drip and furrow irrigation on populations of *Phytophthora parasitica* in citrus soil. (Abstr.) Phytopathol. News 12:147.
8. Gisi, U. 1975. Investigations on the soil phase of *Phytophthora cactorum* (Leb. u Cohn) Schroet. with fluorescent optical direct observation. Z. Pflanzenkrankh. Pflanzenschutz 82:355-377.
9. Gisi, U., Zentmyer, G. A., and Klure, L. J. 1980. Production of sporangia by *Phytophthora cinnamomi* and *P. palmivora* in soils at different matric potentials. Phytopathology 70:301-306.
10. Ioannou, N., and Grogan, R. G. 1977. The influence of soil matric potential on the production of sporangia by *Phytophthora parasitica* in relation to its isolation from soil by baiting techniques. (Abstr.) Proc. Am. Phytopathol. Soc. 4:173.
11. MacDonald, J. D., and Duniway, J. M. 1978. Influence of the matric and osmotic components of water potential on zoospore discharge in *Phytophthora*. Phytopathology 68:751-757.
12. MacDonald, J. D., and Duniway, J. M. 1978. Temperature and water stress effects on sporangium viability and zoospore discharge in *Phytophthora cryptogea* and *P. megasperma*. Phytopathology 68:1449-1455.
13. MacDonald, J. D., and Duniway, J. M. 1978. Influence of soil texture and temperature on the motility of *Phytophthora cryptogea* and *P. megasperma* zoospores. Phytopathology 68:1627-1630.
14. MacDonald, J. D., and Duniway, J. M. 1979. Use of fluorescent antibodies to study the survival of *Phytophthora megasperma* and *P. cinnamomi* zoospores in soil. Phytopathology 69:436-441.
15. Michel, B. E., and Kaufmann, M. R. 1973. The osmotic potential of polyethylene glycol 6000. Plant Physiol. 51:914-916.
16. Mitchell, D. J., and Zentmyer, G. A. 1971. Effects of oxygen and carbon dioxide tensions on sporangium and oospore formation by *Phytophthora* spp. Phytopathology 61:807-811.
17. Pfender, W. F., Hine, R. B., and Stanghellini, M. E. 1977. Production of sporangia and release of zoospores by *Phytophthora megasperma* in soil. Phytopathology 67:657-663.
18. Reeves, R. J. 1975. Behavior of *Phytophthora cinnamomi* Rands in different soils and water regimes. Soil Biol. Biochem. 7:19-24.
19. Satour, M. M. 1966. Phytophthora root and crown rot of tomato. Ph.D. thesis, University of California, Davis. 132 pp.
20. Satour, M. M., and Butler, E. E. 1967. A root and crown rot of tomato caused by *Phytophthora capsici* and *P. parasitica*. Phytopathology 57:510-515.
21. Sneh, B., and McIntosh, D. L. 1974. Studies on the behavior and survival of *Phytophthora cactorum* in soil. Can. J. Bot. 52:795-802.
22. Sugar, D. 1977. The development of sporangia of *Phytophthora cambivora*, *P. megasperma*, and *P. drechsleri* and severity of root and crown rot in *Prunus mahaleb* as influenced by soil matric potential. M.S. thesis, University of California, Davis. 56 pp.