Effect of Soil Salinity on the Formation of Sporangia and Zoospores by Three Isolates of *Phytophthora*

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ABSTRACT

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Formation of sporangia and zoospores by three isolates of *Phytophthora* was studied in naturally and artificially salinized soils and soil extracts. Sporangium formation by isolates of *P. cryptogea* and *P. parasitica* 153, both orginally obtained from plants growing in nonsaline soils, gradually decreased in soils in which the electrical conductivity of the saturated soil extract (EC_e) was >5 decisiemens per meter (dS/m). In contrast, sporangium formation by an isolate of *P. parasitica* from a saline soil in the Coachella Valley, CA, was greatest in saline soils (EC_e = 5–44 dS/m) and was reduced in nonsaline soil or at very high salinity ($EC_e \geq 50$ dS/m). When sporangia of all three isolates were formed in soils at various levels of salinity and placed in salt solutions or saline soil extracts to stimulate indirect germination, zoospore release was greatest at $EC_e \leq 2.5$ dS/m and was restricted at $EC_e > 10$ dS/m. Sporangia of *P. cryptogea* formed in soil at $EC_e \geq 10$ dS/m failed to release zoospores in any solution, while sporangia of both isolates of *P. parasitica* formed in soil at $EC_e \leq 37$ dS/m released zoospores in solutions at $EC_e \leq 10$ dS/m. These results show that isolates of *Phytophthora* differ in their tolerance of high levels of salinity but that all three isolates studied are likely to produce sporangia and zoospores at salinity levels stressful to most crop plant species.

Additional key words: citrus.

Considerable research has been devoted to effects of soil moisture on the development of Phytophthora root rots (19,21,23) and on the life cycles of *Phytophthora* spp. (2,6,8,13,17,24). In some recent studies (4,5,7,15,16), it has been shown that plants of some agronomic and ornamental species stressed by extremes in soil moisture (eg, drought or flooding) or high salinity can become predisposed to Phytophthora root rots. While the impacts of environmental stresses on plant growth and crop yields are well documented, little is known of how these stresses affect soilborne pathogens or the mechanisms by which they promote disease. This is particularly true of salinity stress.

Although the relative sensitivity of agronomic plants to salinity varies, yields of most crops are reduced when salts accumulate to such a level that the electrical conductivity of the saturated soil extract (EC_e) reaches a value ≥4 decisiemens per meter (dS/m; 1 dS/m = 1 millimho/cm) (3,25). It is not known how these, or the higher levels of salinity that may predispose plants to root disease (16), influence the growth, reproduction, and survival of *Phytophthora* spp. While recent work has described the soil moisture requirements for sporangium formation (2,6,8), germination (8,17), and zoospore motility (6) of many *Phytophthora* spp., there have been no systematic studies describing effects of soil salinity on these processes. Some effects of various osmotica on growth (21,22,26), sporangium formation (6,12,21), and indirect germination (14,17,21) have been determined, but many of these studies were conducted in axenic systems or used single salts or osmotica not usually associated with soil. It often is difficult to relate the results of such studies to the saline soil environment, and they may not accurately reveal the salt tolerance of fungi (6,10).

The purposes of our study were to examine the effects of soil salinity on the formation of sporangia and zoospores by three isolates of *Phytophthora* in artificially and naturally saline soils, and to relate the results to levels of salinity known to adversely influence host plants and their susceptibility to disease.

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MATERIALS AND METHODS

Three isolates of *Phytophthora* were used: one of *P. cryptogea* Pethyb. and Laff. originally cultured from safflower (obtained from J. M. Duniway, University of California, Davis); one of *P. parasitica* Dastur. cultured from citrus growing in nonsaline soil (isolate 153 obtained from S. M. Mircetich, University of California, Davis), and one of *P. parasitica* (isolate BV-1) isolated by the senior author from diseased citrus growing in the saline soils of the Coachella Valley in California.

Sporangium formation in saline soil. The isolates of *Phytophthora* were grown on pea-dextrose agar (17) at 25 C for 7 days. Disks of aerial mycelium were cut with a 7-mm-diameter cork borer, lifted from the agar surface, and buried 2-4 mm deep in soil in Büchner funnel tension plates (11). Except as stated otherwise, the sand used in these experiments was a coarse sand fraction (>250 μm) of Yolo fine sandy loam (YFSL) (17) which was maintained at a constant matric potential (ψ_m) in Büchner funnel tension plates.

Mycelial disks were immersed for 5 min in various salt solutions before placement in the Büchner funnels, and salt solutions identical to those in which disks had been immersed were used to fill the funnel reservoirs and to flood the sand after the disks were buried. The sand was allowed to drain to the desired ψ_m, and the tops of the funnels were covered with plastic bags to minimize evaporation. The funnels were adjusted to provide ψ_m values of −150 millibars (mb) for *P. cryptogea* and −50 mb for *P. parasitica*. Preliminary studies had shown sporangium formation to be optimum at those ψ_m values. The funnels were maintained at ambient laboratory temperature (24–26 C) throughout each experiment.

Several salts commonly associated with salt-affected soils in California were used, including combinations of NaCl and $CaCl_2$ (1:1, equivalent weight [eq]), $NaNO_3$ and $Ca(NO_3)_2$ (1:1, eq), KCl and $CaCl_2$ (1:1, eq), and synthetic sea salt (Instant Ocean , 33208 Lakeland Blvd., Eastlake, OH 44094). Magnesium sulfate was also used individually. In addition to artificially salinized media, sporangium formation was examined in several naturally saline soils collected from agricultural areas in the Coachella Valley in California. These included an Indio very fine sandy loam (EC_e ~ 150 dS/m) and a Carsitas gravelly sand (EC_e = 10 dS/m). A range of salinities was achieved for each soil type by leaching subsamples

to various extents with distilled water. The soils then were placed in Büchner funnels. Reservoirs were filled with distilled water, and the soils were saturated with distilled water and allowed to drain to a constant ψ_m. At the termination of the experiment, the soil samples were removed from the funnels and their final EC_e values were measured (25).

Sporangium formation was evaluated by removing mycelial disks from the soils after 4 days for *P. cryptogea* and 2 days for *P. parasitica*, and blending them individually in 10 ml of water for 30 sec at medium speed in a microcontainer on a Waring blender. The resulting suspension was centrifuged at 1,600 *g* for 1 min and the pellet was resuspended in water to a final volume of 2.0 ml. Four drops of acid fuchsin in lactophenol were added to the suspension to stain the sporangia and a drop of the suspension was placed under a coverslip supported over a glass slide at a uniform height of 0.1 mm. Slide mounts were examined at ×100 magnification and the number of sporangia in 50 fields of view were counted for each of four replications in each treatment. Data were analyzed by using a two-way analysis of variance.

Effect of salinity on zoospore release. Sporangia were formed on mycelial disks in sand amended with various concentrations of NaCl and $CaCl_2$ (1:1, eq) as described above. Mycelial disks bearing sporangia were removed from the funnels and rinsed with salt solutions having concentrations equal to those of the funnels to remove adhering sand. Excess wash solution was drained uniformly from the disks by placing them for 30 sec on a clean Büchner funnel tension plate adjusted to −100 mb ψ_m. Ten mycelial disks from each salinity treatment then were placed in 60 × 15-mm petri plates containing 5 ml of glass-distilled water or various salt solutions at ambient laboratory temperature (24–26 C) to stimulate zoospore release. The salt solutions were adjusted to provide a range of electrical conductivity (EC) values simulating EC_e values of soil extracts. After 2 hr, solutions were swirled to uniformly disperse the zoospores. Four 10 µl samples were removed from each zoospore suspension and placed individually on PVP medium (19). After 10–18 hr of incubation at 25 C, the spots were stained with acid fuchsin in lactophenol and examined at ×100 magnification to count the number of germinated zoospore cysts (17). In similar experiments, sporangia of *P. cryptogea* and *P. parasitica* BV-1 were formed in sand amended with 10 dS/m and 24 dS/m solutions of NaCl and $CaCl_2$ (1:1, eq), respectively, after which they were immersed in saturated soil extracts from naturally saline soils from the Coachella and Imperial valleys. The extracts were diluted with distilled water to produce a range of salt concentrations. Zoospore release was evaluated by using the methods described above and data were analyzed by using a two-way analysis of variance.

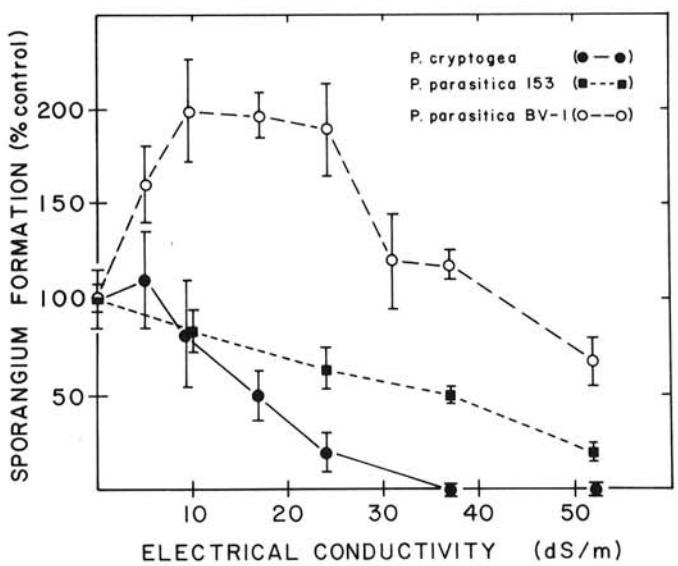

Fig. 1. Sporangium formation by three isolates of *Phytophthora* in a coarse sand fraction of Yolo fine sandy loam amended with solutions of NaCl and $CaCl_2$ (1:1, eq) to obtain a range of salinities with electrical conductivities of 0–52 decisiemens per meter (dS/m). Sporangium formation is expressed as a percentage of the number of sporangia formed per mycelial disk in nonsalinized sand, which was 9.7×10^5 for *P. cryptogea*, 1.8×10^6 for *P. parasitica* 153, and 2.1×10^6 for *P. parasitica* BV-1. Vertical lines represent standard deviations from the mean.

RESULTS

Sporangium formation in saline soil. Sporangium formation by *P. cryptogea* steadily decreased as the EC_e of the sand increased from 5 to 37 dS/m (Fig. 1). At an EC_e of 24 dS/m, there was an 80% reduction in the number sporangia present when compared with the number formed in nonsaline sand (9.7×10^5 sporangia per disk). *P. parasitica* 153 also showed a decrease in sporangium formation with increasing salinity, although this isolate generally appeared to be more tolerant of high salinity (Fig. 1). Compared with the number of sporangia formed in nonsaline sand (1.8×10^6 sporangia per disk), there were 30 and 80% fewer in sand having EC_es of 24 dS/m and 52 dS/m, respectively. In contrast to both these isolates, sporangium formation by *P. parasitica* BV-1 appeared to be greatly stimulated by salinity (Fig. 1). In sand amended with NaCl and $CaCl_2$ to an EC_e of 10–24 dS/m, sporangium formation was increased nearly two-fold relative to that in nonsalinized sand (2.6×10^6 sporangia per disk). Furthermore, large numbers of sporangia formed in salt-amended sand with EC_e values as high as 52 dS/m.

When the coarse sand fraction of YFSL was amended with other salts or combinations of salts to acheive soil EC_e values of 0–50 dS/m, the effect of increasing salinity on sporangium formation by each isolate was similar to that of soil amended only with NaCl and $CaCl_2$ (1:1, eq) (*unpublished*).

In naturally saline soils from the Coachella Valley, sporangium formation by *P. cryptogea* (Fig. 2) and *P. parasitica* 153 (*unpublished*) followed a pattern similar to that observed in artifically saline soils (Fig. 1). Likewise, sporangium formation by *P. parasitica* BV-1 followed a similar pattern, and appeared to be stimulated by salinity levels in the range of 5–60 dS/m (Fig. 2).

Effect of salinity on zoospore release. Sporangia of *P. cryptogea*, formed in sand amended with NaCl and $CaCl_2$ (1:1, eq) at a constant ψ_m of −150 mb, germinated by release of zoospores when placed in solutions of greater (hypertonic), equal (isotonic), or lower (hypotonic) salt concentration (Fig. 3A). After 2 hr in

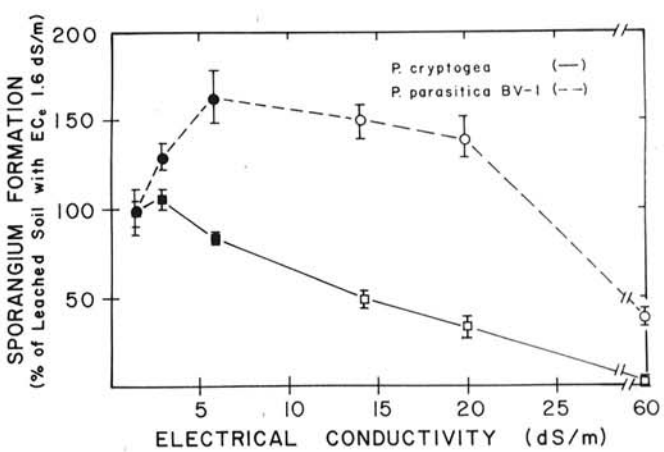

Fig. 2. Sporangium formation in an Indio very fine sandy loam (open points) and Carsitas gravelly sand (closed points). The electrical conductivity of the saturated extracts (EC_e) of these soils were 150 and 10 decisiemens per meter (dS/m), respectively, and they were leached to obtain a range of EC_e values from 1.6 to 60.0 decisiemens per meter (dS/m). Sporangium formation was expressed as a percentage of the number of sporangia formed per mycelial disk in soil at EC_e of 1.6 dS/m which was 6.2×10^5 for *P. cryptogea* and 1.5×10^6 for *P. parasitica* BV-1. Vertical lines represent the standard deviation from the mean.

solution ($\psi_m = 0$), sporangia formed in sand having an EC_e of 5.0 or 10.0 dS/m released maximum numbers of zoospores in hypotonic solutions, while fewer zoospores were released in isotonic and hypertonic solutions (Fig. 3A). No zoospores were released in any solution from sporangia formed in saline sand at 24 dS/m (Fig. 3A). In contrast to sporangia of *P. cryptogea*, those of *P. parasitica* BV-1 formed in soil with an EC_e as high as 37 dS/m were capable of releasing zoospores (Fig. 3B). Like *P. cryptogea*, zoospore release by sporangia formed by *P. parasitica* BV-1 in salinized sand was maximum in very hypotonic solutions of 2.5 dS/m but was greatly restricted in solutions with EC ≥10 dS/m. *P. parasitica* 153 (*unpublished*) showed a pattern of indirect germination similar to that of *P. parasitica* BV-1 (Fig. 3B). In all three isolates, zoospore release was slightly lower in glass-distilled water than in a dilute saline solution (EC = 2.5 dS/m). Furthermore, zoospore release was depressed when sporangia were formed in the absence of any added salt (0 dS/m) (Fig. 3A and B). Differences between the isolates in the number of zoospores released per 100 sporangia indicate that not all the sporangia released zoospores after 2 hr in solution. While the mean numbers of zoospores released per 100 sporangia in the first 2 hr after immersion in solution appeared to be low, the numbers are consistent with those indicated in other reports (2,14,17). Zoospore release continued for several hours in each of the salt solutions, but the relative proportion of zoospores in the various solutions remained constant. Sporangia that failed to release zoospores in saline solutions were observed to germinate directly; however, no quantitative measurements were made.

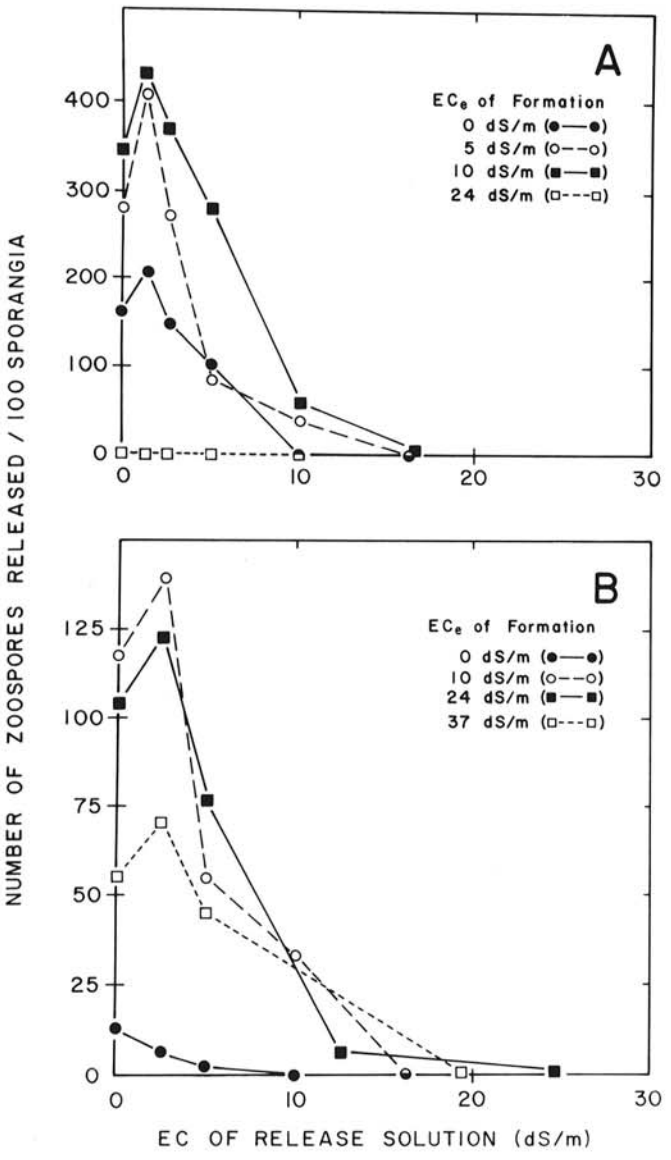

Fig. 3A and B. Influence of salinity on zoospore release by **A,** *P. cryptogea* and **B,** *P. parasitica* BV-1. Sporangia were formed at −50 mb ψ_m and −150 mb ψ_m, respectively, in the coarse sand fraction of Yolo fine sandy loam amended with solutions of NaCl and $CaCl_2$ (1:1, eq) to give the conductivities (EC_e in decisiemens per meter [dS/m]) indicated in the legends. After formation under constant conditions, sporangia were placed in solutions of NaCl and $CaCl_2$ (1:1 eq) having EC values indicated on the horizontal axes. The number of zoospores released was determined 2 hr after disks were placed in solution. At $P = 0.05$, both the EC_e at which sporangia were formed and the EC of the release solution had a significant effect and interaction on zoospore release for both *P. cryptogea* and *P. parasitica* BV-1.

In other experiments, sporangia of *P. cryptogea* and *P. parasitica* BV-1 were formed in sand amended with NaCl and $CaCl_2$ (1:1, eq) to an EC_e of 10 and 24 dS/m, respectively, and then were placed in solutions of NaCl and $CaCl_2$, $NaNO_3$ and $Ca(NO_3)_2$, and $MgSO_4$ having EC values of 0–10 dS/m to induce zoospore release. At the same EC values, all salt solutions appeared to be equally stimulatory or inhibitory to zoospore release (*unpublished*). Sporangia of *P. cryptogea* and *P. parasitica* BV-1 also were formed in salt-amended sand as described above (EC_e = 10 and 24 dS/m, respectively) after which they were placed in dilutions of water extracts made from naturally saline soils. Zoospore release was maximum in very dilute extracts (EC_e 2–6 dS/m) and was reduced at EC_e values ≥10 dS/m (Fig. 4A and B). The overall pattern of zoospore release in soil extracts was similar to that in NaCl and $CaCl_2$ solutions at similar EC values.

Observations of zoospore motility of *P. cryptogea* and *P. parasitica* BV-1 indicated that, although zoospore release was high

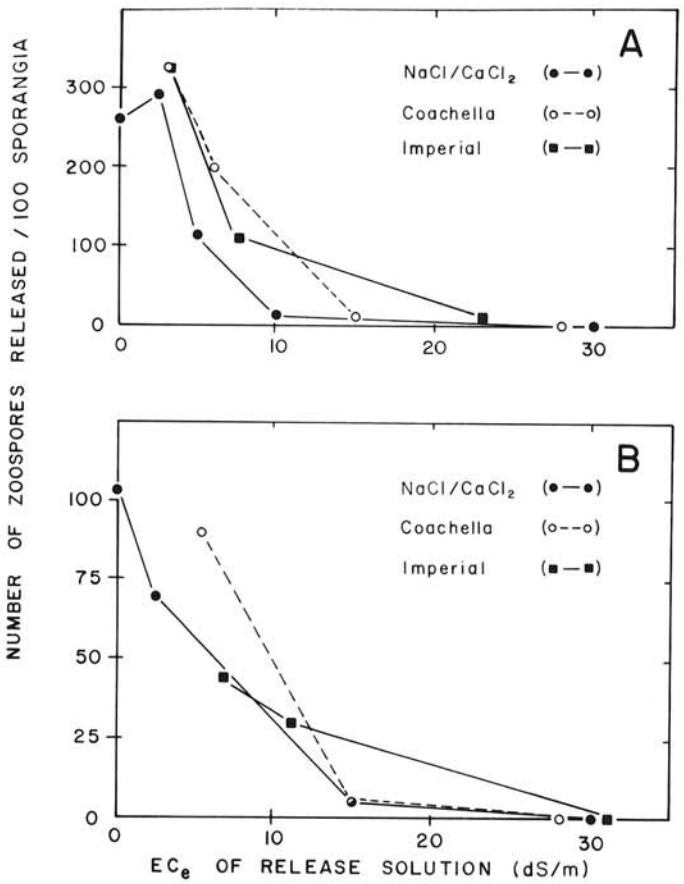

Fig. 4A and B. Influence of extracts from artificially and naturally saline soil on zoospore release by **A,** *P. cryptogea* and **B,** *P. parasitica* BV-1. Sporangia were formed in the coarse sand fraction of Yolo fine sandy loam at −50 mb ψ_m and 10 dS/m for *P. cryptogea* and −150 mb ψ_m and 30 dS/m for *P. parasitica*. Sporangia were placed in either NaCl and $CaCl_2$ solutions or extracts made from saline soils from the Coachella and Imperial valleys diluted to obtain a range of electrical conductivity (EC_e) values from 0 to 30 dS/m.

in saline solutions or soil extracts, the duration of zoospore motility was reduced at conductivity values >2.5 dS/m. Four hours after release, many zoospores had encysted and germinated in solutions >2.5 dS/m, and within 5 hr a visible mycelial mat had formed on the solution surface. In solutions with conductivities ≤2.5 dS/m, most zoospores were motile 4 hr after release, with a few remaining motile for as long as 20 hr.

DISCUSSION

Our results indicate that some isolates of *Phytophthora* from inland agricultural areas have a greater tolerance of soil salinity than the crop plants they attack. All three isolates of *Phytophthora* used in this study were capable of forming large numbers of sporangia and releasing zoospores in soil at $EC_e \geq 4.0$ dS/m, a level that is damaging to many agricultural crops (3,25). Even at an EC_e of 8–10 dS/m, which causes reduced yield in many salt-tolerant agronomic plants (3,25), the isolate of *P. parasitica* from saline soils (BV-1) produced maximum numbers of sporangia (Fig. 1) and measurable numbers of zoospores (Fig. 3B).

While all three isolates produced sporangia when exposed to saline soil conditions, there were differences among the isolates in their ability to tolerate soil salinity. Sporangium formation by isolates of *P. cryptogea* and *P. parasitica* from nonsaline areas was reduced by 50% at salinity levels of 17 and 35 dS/m, respectively (Fig. 1). In contrast, an $EC_e \geq 55$ dS/m was required for the same reduction in sporangium formation by *P. parasitica* BV-1, which originated from a saline soil (Figs. 1 and 2). At lower salinities (5–37 dS/m), sporangium formation by this isolate appeared to be stimulated (Figs. 1 and 2). The variability in salt tolerance among these isolates of *Phytophthora* may indicate a potential for ecological adaptation within *Phytophthora* spp. In studies comparing marine and terrestrial isolates of other zoosporic fungi, similar ecological adaptations to salinity have been shown (6). Studies of sporangium formation by *Phytophthora* spp. at various ψ_s values have suggested that isolates from inland soils are relatively sensitive to salinity levels above 28 dS/m ($\psi_s \leq -12$ bars) (6,21), whereas marine isolates are capable of abundant sporulation at −24 bars ψ_s (equivalent to an EC_e of ~54 dS/m) (6). While we did not sample extensively to obtain many isolates, our results show that at least one isolate of *P. parasitica* from a salt-affected soil in an inland valley of California tolerated levels of salinity similar to those tolerated by marine species (Figs. 1 and 2).

The isolates of *Phytophthora* used in this study also differed in ability to form and release zoospores in saline environments. In the case of *P. cryptogea*, only sporangia formed in salt-amended sand with an $EC_e \leq 10$ dS/m were capable of zoospore release (Fig. 3A). On the other hand, sporangia of both isolates of *P. parasitica* released abundant zoospores even if formed in sand having EC_e levels of 10–37 dS/m (Fig. 3B). In all three isolates, zoospore release was greatest when sporangia were placed in hypotonic solutions relative to those in which sporangia were formed, and was reduced in isotonic or hypertonic solutions (Fig. 3). Furthermore, zoospore formation was significantly reduced in extracts or solutions with conductivity values >12 dS/m (ψ_s ~−5 bars). This reduction was similar to the ψ_s limits of −3 to −6 bars reported to inhibit zoospore release in other *Phytophthora* spp. (9,14,17).

The primary effect of salinity on formation and indirect germination of sporangia appeared to be osmotic. Although work by others has suggested that Mg^{++} may inhibit zoospore release (9,17) or radial growth of colonies on agar (21), we detected only slight differences in sporangium formation and zoospore release among the various ionic solutes, including $MgSO_4$.

The results of our studies on zoospore formation in saline solutions (Fig. 3) tend to support the findings of Gisi (9), who suggested that hypotonic shifts in osmotic potential may stimulate zoospore release, while hypertonic conditions may reduce or inhibit release. Other research (17) has shown that zoospore release is more sensitive to changes in matric potential (ψ_m) than to solute potential (ψ_s), and in our work reported here, sporangia were exposed to changes in both. The ψ_m was changed from −5 0 or −150 mb to 0 mb at the same time sporangia were exposed to changes in ψ_s, and both ψ_m and ψ_s may have contributed to zoospore release. In saline soils, however, similar shifts in ψ_m and ψ_s can occur during irrigation cycles. For example, as water is removed from soil by evaporation and transpiration between irrigations, plants and microorganisms may be exposed to high levels of salinity as salts are concentrated in the remaining soil solution (20). When the soil then is irrigated and rewetted to $\psi_m = 0$, salts are diluted, resulting in concomitant increases in ψ_m and ψ_s, which would act together to stimulate zoospore release as in our experiments.

Despite the threat of increasing salinity in many irrigated agricultural areas of the world, studies of possible interactions between salinity stress and root diseases are limited. A few studies (4,16; and T. J. Swiecki and J. D. MacDonald, *unpublished*) have demonstrated that following brief exposures to high levels of salinity (11–22 dS/m), plants can be predisposed to Phytophthora root rot. Other reports (1,18) have attributed both increases and decreases in disease severity in saline soils to effects of salinity on the activity of the pathogens. For example, a recent study indicated that Pythium root rots may be suppressed in some saline soils of the San Joaquin Valley of California because of reduced colonization and reproduction by *Pythium ultimum* (18). In contrast to this, our study shows that some isolates of *Phytophthora* are potentially quite active at levels of salinity that can severely stress crop plants. This continued activity by the pathogen under conditions that could increase host susceptibility to infection, could result in severe Phytophthora root rot in some saline soils.

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