Movement of Zoospores of Phytophthora cryptogea in Soils of Various Textures and Matric Potentials

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ABSTRACT

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Active movement of *Phytophthora cryptogea* zoospores in soils was examined by placing susceptible safflower seedlings at various distances from a source of motile zoospores for 24 hours. The presence of *P. cryptogea* in seedlings was determined by symptom development and by isolation on a selective medium. Tension plates were used to control soil moisture at various matric potentials (ψ_m). The bottom of soil samples 1.5-cm thick was the reference point for ψ_m values which are expressed in millibars (mb). Sporangia that formed in soil at $\psi_m = -300$ mb and were used to inoculate soils at higher ψ_m values only released zoospores at $\psi_m \geqslant -10$ mb. When either sporangia or motile zoospores were used to inoculate soil, zoospores readily swam 25 to 35 mm in the surface water over flooded soils or through a coarse textured U.C.-type soil mix at $\psi_m \geqslant -1$ mb. Active zoospore movement in the soil mix was reduced at $\psi_m = -10$ mb and was only detected over a distance of 5 mm at $\psi_m = -50$ mb. No detectable zoospore movement occurred at $\psi_m \leqslant -100$ mb. Active zoospore movement in sieved and reconstituted silt loam and fine sandy loam soils was limited to a distance of 5 mm at $\psi_m = -1$ mb and was not detected at $\psi_m = -10$ mb. Zoospores moved a distance of 5 mm in a clay loam soil at $\psi_m = -10$ mb. Water flow down through 40 mm soil columns carried zoospores to depths of 8-12 mm in the loam soils and 40 mm in the coarse soil mix.

Additional key words: Phytophthora root rot, *Phytophthora drechsleri, Carthamus tinctorius,* water potential.

Taxis of zoospores to plant roots in water has been demonstrated for a number of phycomycetous plant pathogens including several members of the genus *Phytophthora* (8, 9). Active zoospore movement to host roots may be an important event leading to root infection and a few experiments on *Phytophthora* spp. have shown that zoospore taxis to roots can occur at least in some wet soils. Zoospores of *P. cinnamomi* can swim 12 mm through capillary tubes of the same diameter (190 μm) as relatively large soil pores (1). Infections of belowground plant parts by *P. infestans* and *P. cinnamomi* occur in soil at distances of 13-25 mm from the nearest sporangia when zoospores were probably the inoculum (15, 16). When zoospores are added to soil, motile zoospores of *P. palmivora* cause more death of papaya seedlings than do the same numbers of nonmotile zoospores (14). More specifically, zoospores of *P. palmivora, P. drechsleri,* and *P. megasperma* accumulate on plant roots after motile zoospores are added to soil (10, 14, 19). In one such experiment, zoospores of *P. megasperma* were observed to accumulate on roots in sand, but not in a finer textured garden soil (10). Unfortunately, the literature does not contain more precise data on the influence of soil texture or water status on the movement of fungus zoospores.

Soil structure and water status determine the size distribution of water-filled pores in soil and, therefore, can be expected to greatly influence active zoospore movement and taxis in soil (3, 6). Interactions between soil texture, water status, and the movement of bacteria and nematodes in soils have been investigated (6, 7, 13). However, because of great differences in size and/or means of locomotion (13), the behavior of zoospores in soils probably cannot be predicted from the behavior of bacteria or nematodes. The present study examines the influence of soil water status and texture on the active movement of *Phytophthora* zoospores to plant roots. As measured here, active zoospore movement probably includes taxis and refers to the movement brought about by flagella. Data on the passive movement of zoospores in soil with water flow and on the indirect germination of sporangia in soil are also presented.

MATERIALS AND METHODS

The isolate of *Phytophthora cryptogea* Pethyb. and Laff. used in all experiments was the A^2 mating type originally isolated from safflower. [This is the same isolate (P201) that was used previously (4, 5) under the name, *P. drechsleri* Tucker. Its morphology, however, fits the description of *P. cryptogea* more closely than the description of *P. drechsleri* (S. M. Mircetich, *personal communication*). Furthermore, Bumbieris (2) has suggested that *P. drechsleri* and *P. cryptogea* should be considered as one species under the name *P. cryptogea.*] For experiments in which mycelial disks were put into soil, *P. cryptogea* was grown on agar medium made with

frozen lima beans (4). Mycelial disks were lifted from 10- to 14-day-old cultures and were treated with fluorescent brightener by the methods used previously (4, 5). For those experiments in which motile zoospores were added to soil, *P. cryptogea* was grown in petri plates of Difco lima bean agar at 25 C. Numerous sporangia formed in 10-16 days and motile zoospores were obtained by flooding cultures containing sporangia with autoclaved soil extract (200 g moist soil per liter) for 12 hours at 18 C.

Four soils of different textures were used. Columbia silt loam, Yolo fine sandy loam, and a Yolo clay loam were collected from the Sacramento Valley of California. The fourth soil was a U.C.-type soil mix (18) formulated from, among other ingredients, equal volumes of fine sand and peat. Before use, all soils were sieved (1.4 mm openings) and were autoclaved at 121 C for 1 hour on 2 successive days.

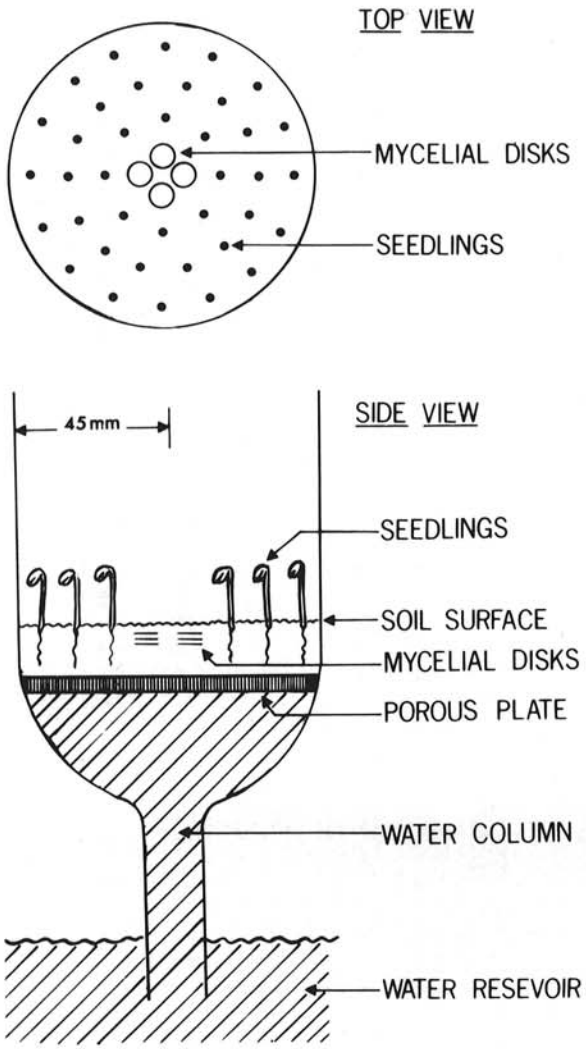

Fig. 1. Spatial arrangement of mycelial disks of *Phytophthora cryptogea*, safflower seedlings, and soil on tension plates. At $\psi_m = 0$ the surface of the water reservoir was at the level of the porous plate. The water surface was 5 mm above the soil surface in flooded treatments.

Soil moisture was controlled by using 9-cm diameter Büchner funnels with fritted glass plates of fine porosity (Kimble 28400-90F) as tension plates (4). The height of the water column between the porous plate and the surface of a water reservoir (Fig. 1) was adjusted to give the desired matric potential (ψ_m). [With the exception that ψ_m values are negative, ψ_m is equivalent to soil-water suction or tension and ψ_m values are given in millibars (mb). One mb is equivalent to the pressure exerted by a 1.022-cm-high column of water and 1,000 mb = 1 bar = 0.99 atmosphere. Solute potential of the soil solution accounts for the difference between ψ_m values reported here and total water potential (4, 5)]. The tension plates were set at $\psi_m = -50$ mb and filled to a depth of 1.5 cm with soil. The soil was wetted and allowed to equilibrate for several hours. To consolidate the soil, 200 ml of water was added to the soil surface and the tension plates were reset to $\psi_m = -250$ mb for 12 hours before they were set to the desired ψ_m values. Tension plates were covered with loosely fitting plastic bags to reduce evaporation. Soil temperature ranged between 23 and 27 C, but variation between soil samples was less than 1 C at any one time. The rate of change in soil temperature was less than 0.4 C per hour. Soil water content and bulk density were determined by sampling a known volume of soil from the tension plates and drying the soil to a constant weight at 105 C.

Active zoospore movement was examined by arranging susceptible safflower seedlings (*Carthamus tinctorius* L. 'Nebraska 10') at various distances from a source of zoospores in soils on tension plates. Sporangia that formed on mycelial disks in U.C.-type soil mix were sources of zoospores for most of the experiments. Mycelial disks from culture were buried 3-8 mm below the surface of the soil mix and were maintained at $\psi_m = -300$ mb for 6 days. During this time each disk formed an average of 8×10^4 sporangia and more than 90% of the sporangia were full of cytoplasm and were ungerminated. The number and condition of sporangia were determined for four-to-six replicate disks by the fluorescence microscopy methods given elsewhere (4, 5). After mycelial disks had been in the soil mix for 6 days, the tension plates were either reset to a higher ψ_m value (less negative than −300 mb; e.g., −50 mb), in which case safflower seeds were planted in the soil 2 days before ψ_m was changed, or the mycelial disks were moved to other tension plates containing 2-day-old seedlings in soil. Tension plates into which mycelial disks were moved were maintained at $\psi_m = -50$ mb during seed germination and were reset to their final ψ_m values 12 hours before the disks were moved. The soil was sprinkled lightly with water immediately after mycelial disks were buried. Unless stated otherwise, 12 mycelial disks were positioned 3-8 mm below the surface at the center of each soil sample. The seedlings were in three concentric rings at distances of 5, 15, and 25 mm from the nearest mycelial disks. The relative position of the mycelial disks and seedlings is illustrated in Fig. 1.

The number and condition of the sporangia again were determined 24 hours after the mycelial disks and seedlings were placed together at the final ψ_m values. Empty sporangia were assumed to have germinated indirectly by the release of zoospores (4). At the time sporangia were examined, seedlings were removed from the soil and were

washed under running water. Four seedlings from each concentric ring were individually transplanted into autoclaved soil mix in 150-ml paper cups with drain holes. Four additional seedlings from each ring were cut into 1-cm segments and transferred to a petri dish containing a selective medium that consisted of cornmeal agar supplemented with pimaricin and other antibiotics (4, 5). Plates of selective medium were incubated at 25 C and were examined for growth of *P. cryptogea* daily for 10 days. Transplanted seedlings were maintained in a 27 C greenhouse for 14-20 days where they were periodically examined for symptoms of infection by *P. cryptogea*. No seedlings from noninoculated soils developed symptoms after transplanting or yielded mycelial growth on selective medium that could be confused with *P. cryptogea*. Occasionally roots had penetrated soil to the porous plant (Fig. 1) and had grown horizontally. When this occurred, the location of the root was noted, and if any portion of the root was less than 15 or 25 mm from the mycelial disks, the seedling was grouped with those in a correspondingly closer position.

Motile zoospores rather than mycelial disks were used to inoculate the soil in some experiments. Tension plates and 2-day-old seedlings were used in the arrangement described above (Fig. 1), with the exception that the seedlings were 15, 25, and 35 mm from the point of inoculation. One milliliter of suspension containing 2.5×10^5 motile zoospores was added at the center of each tension plate. The zoospore suspension was in a syringe with a 1-mm orifice and was added by touching one drop at a time to the soil over the course of 30 minutes. The zoospore suspension did not splash or run across the soil surface. Tension plates at ψ_m values less negative than -10 mb were adjusted to $\psi_m = -10$ mb before inoculation and were reset to their final ψ_m value after the inoculum had penetrated the soil. Seedlings were transplanted to cups of soil and transferred to selective medium 24 hours after the soil was inoculated.

The movement of zoospores downward in soil with water flow was examined in tension plates filled to a depth of 6 cm with soil. Soil was consolidated by watering after the tension plates were set at $\psi_m = -300$ mb where they were maintained for the rest of the experiment. A depression 2 cm deep by 6 cm in diameter was dug at the center of the soil surface and the tension plates were allowed to equilibrate for several days. A 50-ml suspension containing 3.5×10^6 motile zoospores was poured into each depression. After the suspension had completely penetrated the soil, an additional 50 ml of water was allowed to penetrate the soil. The following day soil was aseptically dug from the central 6-cm diameter area of the tension plates in 4-mm-deep increments. Soil samples were transferred to planting holes into which 4-day-old safflower seedlings were transplanted. The seedlings were observed for symptom development as in the other experiments.

TABLE 1. Influence of various matric potentials of U.C.-type soil mix on the indirect germination of *Phytophthora cryptogea* sporangia[a]

Final matric potential (mb)	Indirect germination (%)	
	Initial	Final
>0[b]	4.5 A[c]	91.8 E
−1	5.2 A	69.3 D
−10	4.0 A	48.4 C
−50	8.9 AB	21.9 B
-300	4.8 A	5.0 A

[a]The initial and final percentages of germination were determined with mycelial disks from the same Büchner funnel just before and 24 hours after ψ_m was changed from −300 mb to the final value given.

[b]Flooded.

[c]Percentages followed by different letters are statistically different by a Duncan's test on an arc sin $\sqrt{\text{percentage}}$ transformation at $P = 0.05$.

RESULTS

The influence of various ψ_m values of U.C.-type soil mix on the indirect germination of sporangia is shown in Table 1. Most of the sporangia germinated indirectly in flooded soil, whereas significantly fewer sporangia germinated indirectly at ψ_m values of −1 and −10 mb. There was no significant change in the condition of sporangia at $\psi_m = -50$ mb. The net effect of ψ_m value of U.C.-type soil mix on the release and active movement of zoospores is shown in Fig. 2. In this experiment, a barrier (Fig. 2) was sometimes used to block zoospore movement on or near the soil surface. In the absence of a barrier, zoospores moved to most of the seedlings if the soil mix was flooded or was at $\psi_m = -1$ mb. At ψ_m values of −10 and −50 mb, however, zoospores moved only 15 and 5 mm, respectively. With the exception of flooded soil, the

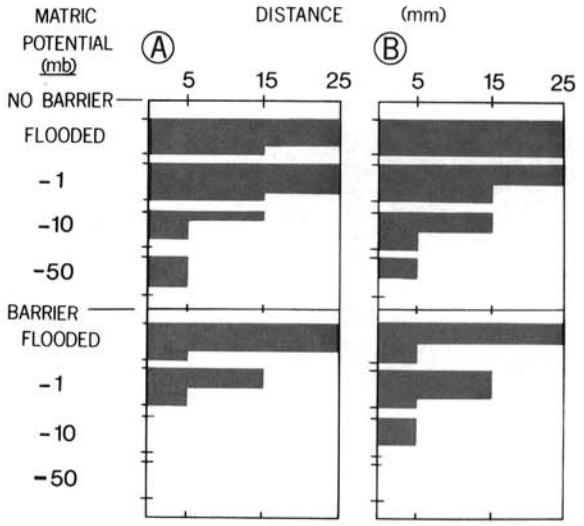

Fig. 2-(A,B). Effect of matric potential on the movement of *Phytophthora cryptogea* zoospores to safflower seedlings at various distances from mycelial disks with sporangia in U.C.-type soil mix. A barrier consisting of a 2-cm long by 2.5-cm diameter tube was pushed 5 mm down into the soil between the mycelial disks and nearest seedlings on some tension plates. *Phytophthora cryptogea* was detected in seedlings by **A)** symptom development and **B)** isolation on selective medium. Bar width is proportional to the incidence of *P. cryptogea* in seedlings with the distance between marks on the vertical axis representing 100% incidence.

presence of a barrier invariably reduced the distance at which *P. cryptogea* was detected.

Figure 3 gives the results of an experiment in which a suspension of motile zoospores was added to U.C.-type soil mix at various ψ_m values. Zoospores moved to a majority of the seedlings at $\psi_m = 0$. Considerable zoospore movement also occurred at $\psi_m = -1$ mb, but zoospore movement was reduced at $\psi_m = -10$ mb and was not detected at $\psi_m \leqslant -50$ mb. With the exception of slightly less zoospore movement at $\psi_m = -10$ mb, a repeat of the experiment in Fig. 3 gave the same results.

The average results of two experiments on active zoospore movement in four different soils are presented in Fig. 4. In addition to placing mycelial disks with sporangia in the soil, mycelial disks were placed in the water over flooded soils and were retained in their usual central position (Fig. 1) with a mesh ring. Zoospores invariably moved to all of the seedlings when sporangia were on the surface of flooded soils. Zoospore movement was noticeably reduced when sporangia were 3-8 mm below the surface of all flooded soils except U.C.-type soil mix. Zoospores moved at least 15 mm, and more commonly 25 mm, through U.C.-type soil mix at all ψ_m values tested. Zoospore movement was greatly reduced at $\psi_m = -1$ mb and was not observed at $\psi_m = -10$ mb in Columbia silt loam and Yolo fine sandy loam. Limited zoospore movement was observed at both $\psi_m = -1$ mb and $\psi_m = -10$ mb in Yolo clay loam.

The experiments in Fig. 4 confirmed the results in Table 1 in that the germination of sporangia in U.C.-type soil mix varied significantly with ψ_m value. At ψ_m values of 0, −1, and −10 mb, respectively, 95, 71, and 57% of the sporangia in the soil mix had germinated indirectly. However, the final percentages of sporangia that had germinated indirectly did not differ significantly with ψ_m value in the other soils (Fig. 4) and averaged 96, 81, and 78% at the respective ψ_m values of 0, −1, and −10 mb.

Water flow downward through 40-mm soil columns initially at $\psi_m = -300$ mb carried zoospores to the following depths: 8 mm in Columbia silt loam and Yolo fine sandy loam; 12 mm in Yolo clay loam; and 40 mm in U.C.-type soil mix.

Equilibrium relationships between the cumulative water loss and decreasing ψ_m for the soils that were used are shown in Fig. 5. Soil bulk densities averaged 1.09 g cm^{-3} for Yolo fine sandy loam, 1.12 g cm^{-3} for Yolo clay loam, 1.18 g cm^{-3} for Columbia silt loam, and 1.20 g cm^{-3} for U.C.-type soil mix.

DISCUSSION

Even though the seedling technique employed here only measured the presence or absence of *P. cryptogea*, there is little doubt that zoospores were the propagules that moved to the seedlings. For example, there was no

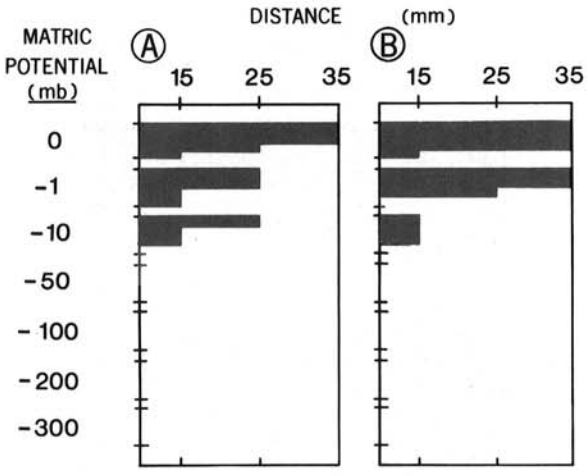

Fig. 3-(A,B). Effect of matric potential on the movement of *Phytophthora cryptogea* zoospores to safflower seedling roots at various distances from the point where a zoospore suspension was added to U.C.-type soil mix. *Phytophthora cryptogea* was detected in seedlings by **A)** symptom development and **B)** isolation on selective medium. Bar width is proportional to the incidence of *P. cryptogea* in seedlings with the maximum distance between marks on the vertical axis representing 100% incidence.

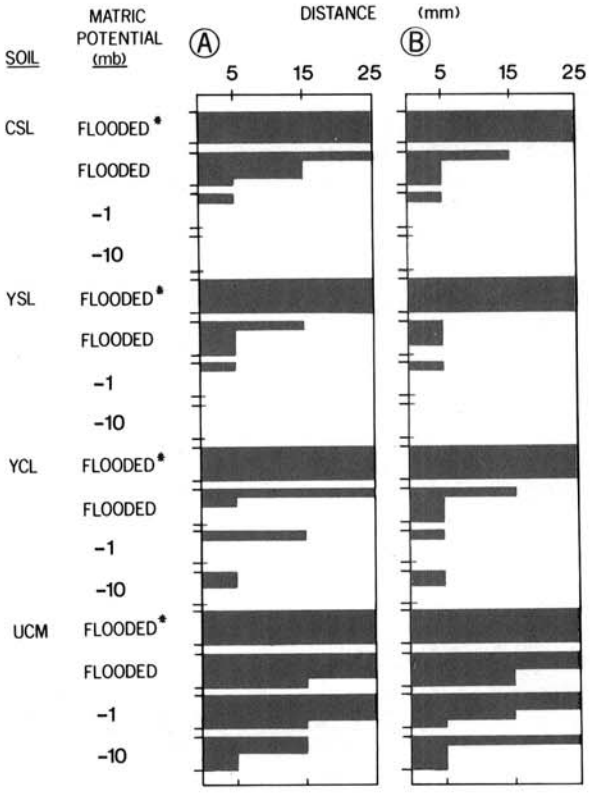

Fig. 4.-(A,B). Effect of matric potential and soil type on the movement of *Phytophthora cryptogea* zoospores to safflower seedlings at various distances from mycelial disks with sporangia. An asterisk indicates mycelial disks were on the soil surface and mycelial disks were 3-8 mm below the soil surface in the other treatments. *Phytophthora cryptogea* was detected in seedlings by **A)** symptom development and **B)** isolation on selective medium. Bar width is proportional to the incidence of *P. cryptogea* in seedlings with the maximum distance between marks on the vertical axis representing 100% incidence. Legend to soils: CSL = Columbia silt loam; YSL = Yolo fine sandy loam; YCL = Yolo clay loam; and UCM = U.C.-type soil mix.

release of zoospores and *P. cryptogea* was not detected in any seedlings when seedlings and mycelial disks with sporangia were left in the soil mix for 3 days at $\psi_m = -300$ mb. When mycelial disks were examined by fluorescence microscopy, there was no observable growth of mycelium from the disks into the surrounding soil. The few (<2%) sporangia that germinated directly invariably had germ tubes less than 0.2 mm long. Preliminary experiments showed that zoospores of *P. cryptogea* would swim several centimeters and would accumulate on the roots of safflower seedlings in water extracts (200 g soil per liter) of all the soils used. However, the number of zoospores that must reach a safflower seedling for *P. cryptogea* to be detected by the methods used is unknown. Therefore, the experiments reported here only provide a relative measure of zoospore movement. Water equilibration in the tension plates was rapid (4) and it is unlikely that water flow contributed to the horizontal movement of zoospores which was used as a measure of active zoospore movement. Attraction of zoospores to the nearest seedlings may have diverted zoospores from movement to seedlings at greater distances. However, the high incidence of *P. cryptogea* at all distances tested in the soil mix at $\psi_m \geq -1$ mb indicates diversion to the nearest seedlings was not a major factor.

Observations of indirect germination only at $\psi_m \geq -10$ mb (Table 1) agree with frequent statements in the literature that the indirect germination of *Phytophthora* sporangia requires free water (22, 23). Presumably, free water in soil would be at $\psi_m = 0$. There is also limited evidence that *Aphanomyces euteiches* releases zoospores only at $\psi_m \geq -10$ mb (12). The results of previous studies on *Phytophthora* spp., however, showed some indirect germination of sporangia at ψ_m values down to −300 or −400 mb (4, 21). Therefore, even though increasing the ψ_m value of soil to nearly zero enhanced indirect germination, ψ_m values approaching zero probably are not required for sporangia to germinate indirectly. In the present study, there was significantly more indirect germination at $\psi_m = -10$ mb in the loam soils than in U.C.-type soil mix, which indicates that soil texture and water content, as well as the ψ_m value of soil, may affect indirect germination of sporangia.

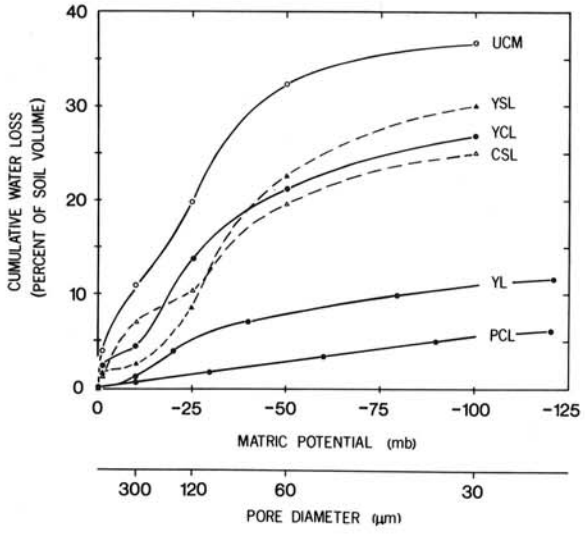

Fig. 5. The cumulative water loss from Columbia silt loam (CSL), Yolo clay loam (YCL), Yolo fine sandy loam (YSL), and U.C.-type soil mix (UCM) plotted as functions of decreasing matric potential. Data from the literature (17, 20) for undisturbed cores of Yolo loam (YL) and Panoche clay loam (PCL) from a soil depth of 30 cm are also shown and are referred to in the Discussion. Cumulative water loss is expressed as the percentage of the total soil volume which drained water as ψ_m was decreased from zero. The bottom axis gives the diameter of an idealized capillary pore which is expected to drain water at a given matric potential (3, 6, 13).

Flooded soils invariably were most suitable for active zoospore movement (Fig. 2, 4). When segments of seedlings from flooded soils were individually placed on a selective medium, *P. cryptogea* was recovered only from those segments that were near the water surface. The zoospores evidently rose from the soil and accumulated near the water surface (11). Because they can swim more freely in surface water than in soils (Fig. 4), and because they may be exposed to flowing or splashing water, it is conceivable that any tendency motile zoospores might have to rise in water may enhance their dispersal.

Zoospores readily swam 25-35 mm through U.C.-type soil mix at $\psi_m \geq -1$ mb. At $\psi_m = -10$ mb zoospores moved lesser distances and $\psi_m = -50$ mb is probably the lower limit for measurable zoospore mobility in the soil mix (Fig. 2, 3). Zoospores of *P. cryptogea* apparently require higher ψ_m values for active movement in soil than do either the nematodes (13) or bacteria (6, 7) for which data on movement in soil have been published. Furthermore, the water requirements for active zoospore movement are very much greater than those for growth of mycelium or formation of sporangia by *Phytophthora* spp. in soil (5, 21).

Limited diffusion of a zoospore attractant from the seedlings may contribute to the observed influence of ψ_m on zoospore movement. However, it is more likely that the confinement of active zoospore movement to high ψ_m values is due to the large size of soil pores that must be filled with water to accommodate swimming zoospores. At the ψ_m values that either slightly or almost completely limit zoospore movement [i.e. −10 and −50 mb, respectively (Fig. 2, 3)], soil pores on the order of 300 and 60 μm in diameter are expected to drain water (Fig. 5). A *Phytophthora* zoospore, even with its flagella extended, is considerably less than 60 μm in diameter (1) and water requirements for its movement in soil probably are related more to swimming habit than to size. Several workers have reported that swimming zoospores have a helical path (1, 8, 11) and that frequent contact of swimming zoospores with solid surfaces reduces zoospore motility (9, 11). Therefore, not only must there be continuous water-filled channels that can accommodate zoospores, but probably the larger and less tortuous the water-filled pores the more suitable they will be for active zoospores movement. Indeed, all increases in ψ_m above a minimum of −50 mb increased zoospore mobility (Fig. 2, 3, 4).

In comparison to that in the U.C.-type soil mix, movement of *P. cryptogea* zoospores was very much reduced in the loam soils tested (Fig. 4). The curves in Fig. 5 show that the loam soils also contained fewer large pores than did the soil mix (e.g. they drained less water at

$\psi_m = -50$ mb). The complete lack of active zoospore movement at $\psi_m = -10$ mb in Columbia silt loam and Yolo fine sandy loam suggests only the very largest of the pores in those soils were suitable for zoospore mobility. In contrast to earlier suggestions for finer textured soils (6, 9), passive movement of zoospores downward by water flow was not much more extensive in the loam soils than was movement by flagella.

The literature and the results presented here both indicate that pore spaces between the primary particles of most finer textured soils are too small to permit significant zoospore movement (3, 6, 9, 22). In fact, occurrence of the relatively large soil pores that can accommodate motile zoospores will depend on a number of other factors that are not the usual criteria for soil texture. Among the other factors are aggregate structure, the degree of compaction, and the prevalence of channels left by dead roots and burrowing animals. Unfortunately, the many factors that affect soil pore structure make it difficult to predict zoospore behavior in natural soils from the results obtained in sieved and reconstituted soils. Published data on the release of water from undisturbed loam and clay loam soils (17, 20), however, suggest some natural arid-zone soils have considerably less pore space than did the experimental soils used here (Fig. 5) and would, therefore, be less suitable for zoospore movement. A full understanding of the role of active zoospore movement in root disease not only requires experiments on zoospore mobility in undisturbed soils, but also requires more research on the distribution of *Phytophthora* propagules in soils relative to roots and their ability to infect roots after direct germination.

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