The Influence of Matric Potential, Soil Texture, and Soil Amendment on Root Disease Caused by Phytophthora cinnamomi

R. E. Sterne, G. A. Zentmyer, and M. R. Kaufmann

Graduate Research Assistant and Professor, Department of Plant Pathology, and Associate Professor, Department of Plant Sciences, respectively, University of California, Riverside, CA 92502. Present address of senior author, Department of Plant Pathology, University of Arkansas, Fayetteville, AR 72701.

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ABSTRACT

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The amount of root disease caused by chlamydospores and mycelium of *Phytophthora cinnamomi* was examined in a sandy loam and a clay soil of matric potentials adjusted to 0, -0.05, -0.10, or -0.25 bar with ceramic tension plates. Data also were collected on the influence of glucose and asparagine amendments on root disease and chlamydospore germination in sandy loam soil at various matric potentials. Root disease was rated as the percentage of the root system of *Persea indica* seedlings with black lesions caused by *P. cinnamomi*. Infection was confirmed by plating roots on a selective medium. When 100 g of sandy loam soil was infested with chlamydospores (15 spores/g dry soil) or mycelium (four 0.5-mm-long fragments/g dry soil) disease ratings with either inoculum averaged 50-100% at -0.10 bar or less negative matric potentials but only averaged 4-8% at -0.25 bar. In soil infested with diseased roots of avocado seedlings (forty 5-mm-long segments/g dry soil), again disease ratings were much lower at -0.25 bar than at higher matric potentials. In clay soil infested with chlamydospores (15 spores/g dry soil), no sharp difference was observed between disease ratings at -0.25 bar and -0.10 bar or less negative matric potentials. Average disease rating at -0.25 bar was 50% in clay soil. At −0.25 bar in sandy loam soil amended with glucose and asparagine, 0.9 and 0.225 mg/g dry soil respectively, disease ratings averaged 86%. Chlamydospore germination and germ tube growth in sandy loam soil were reduced significantly at -0.25 bar matric potential compared to potentials approaching zero. When the soil was amended with glucose and asparagine, germination and germ tube growth at -0.25 bar were as high as in nontreated soil at -0.10 bar or less negative matric potentials. The results suggest that at -0.25 bar matric potential in sandy loam soil nutrient availability rather than matric potential per se limited disease development.

Soil water content and the permeability of soil in relation to drainage influence the development of avocado root rot caused by *Phytophthora cinnamomi* more than any other factor (17). Yet there are few studies defining the relationship of soil water status to infection by soilborne inocula of *Phytophthora* spp. or other Phycomycetous plant pathogens. In experiments with *Phytophthora cryptogea*, Duniway (3) found that zoospores could swim through a sand-peat soil mix and infect roots of safflower seedlings only when the water content of soil corresponded to matric potentials between 0 and −0.01 bar. In soil with finer texture, zoospore movement occurred primarily with flooding. Stanghellini and Burr (8) studied the effects of the potential of water in soil on oospores of *Pythium aphanidermatum*. Oospores did not germinate in nontreated soil at matric potentials from 0 to −15 bars. In soil amended with asparagine (100 μg/g soil) oospores germinated and germ tubes developed when soil matric potential was between -0.01 and -0.1 bar; however, at -1.0 bar, germination and germ tube development were 50% lower than at the less negative potentials. In a naturally infested soil, *P. aphanidermatum* colonized alfalfa seeds at matric potentials of -1.0 bar or higher.

Chlamydospores of *Phytophthora* are a primary survival structure and form of inoculum in soil (14). *Phytophthora cinnamomi* forms chlamydospores in soil and in roots of diseased avocado trees. Zentmyer and Mircetich (16) suggested that chlamydospores and oospores play an important role in the survival of *P. cinnamomi* in soil, when the water content is greater than 3% in a sandy loam soil. Mircetich et al. (4, 5) reported that chlamydospore germination depended on an adequate supply of exogenous nutrients. Chlamydospore germination in natural soil was enhanced by glucose (0.05 M) and asparagine (0.0125 M) and germination was much higher in soil containing root exudates of avocado than in fallow soil. Apparently, the effectiveness of chlamydospores as inoculum may be influenced by the availability of certain nutrients in soil.

In a previous study we found that root disease of indicator plants in soil infested with chlamydospores of *P. cinnamomi* occurred at matric potentials ranging from 0 to -0.1 bar (10). At -0.25 bar, disease ratings were reduced to near zero. At various matric potentials, we adjusted the osmotic potential of soil to levels that might occur in avocado orchards and found no significant difference in disease ratings with different osmotic potentials at any matric potential. Thus, matric potential dominated the effect of the total water potential of soil on

the disease ratings. Because changes in matric potential might determine the development of Phytophthora root rot in the field, this investigation was undertaken to examine more closely how matric potential influences root disease caused by several nonmotile forms of inoculum of *P. cinnamomi*. Information was sought on the relationship of soil texture and soil amendments to root disease at matric potentials from 0 to -0.25 bar. Data are also presented on chlamydospore germination at various matric potentials with and without a soil amendment.

MATERIALS AND METHODS

Inoculum.—The isolate of *Phytophthora cinnamomi* Rands used in all experiments was Pc 40, ATCC 32992 (Phytophthora Culture Collection, Department of Plant Pathology, University of California, Riverside). Chlamydospores were obtained from mycelial mats grown for 30 to 40 days in the dark at 24 C in 250- ml bottles containing 25 ml of V-8 juice broth (100 ml V-8 juice, 2 g $CaCO_3$, and 900 ml demineralized water). Suspensions of chlamydospores were prepared and stored by methods previously described (10). The suspensions were used in experiments within 16 hr after preparation. The germinability and viability of chlamydospores were measured by the methods described by Tsao (11). On the average, 85% of the spores in suspensions were viable. Only viable spores were considered when the concentration of spores in soil was calculated for root disease assays in infested soil.

Mycelial inoculum was prepared from mats of *P. cinnamomi* grown in petri dishes containing 25 ml of a minimal medium described previously (9). The mats were grown in the dark at 24 C for 5 days, washed twice with demineralized water and suspensions of mycelial fragments were prepared by comminuting the mats in demineralized water in a Waring Blendor at low speed for 30 sec. The procedure provided mycelial fragments that averaged 0.5 mm long. The concentration of fragments in a suspension was determined with a 1-ml-capacity eelworm, counting chamber (German Hawksley Ltd., Lancing, England). Mycelial suspensions were diluted and immediately used to infest soil.

Fragments of avocado roots infected with *P. cinnamomi* were used for inoculum in some disease assays. Roots were uniformly infected by *P. cinnamomi* in a complete nutrient solution as described by Zentmyer and Mircetich (15). The roots were cut into 5-mm-long pieces and plated on $P_{10}VP$ agar, a medium selective for *Phytophthora* and *Pythium* spp. (12). After 24 hr, fragments of roots with hyphae of *P. cinnamomi* growing from them were removed from the agar with forceps and used to infest soil saturated with water.

Control of soil matric potential.—Hollow ceramic tension plates were used to regulate soil matric potentials (Ψ_m) in 1.5-cm layers of soil (10). Plexiglass cylinders were sealed to the edges of the tension plates and provided a container 8.5 cm diameter × 8.5 cm tall. The cylinder allowed room for soil and air space for shoots of seedlings growing in the soil. The open tops of the cylinders were covered with polyethylene film to reduce evaporation. The height of the water column between the surface of the hollow plate and a reservoir of water controlled the hydrostatic head supported by matric forces in the ceramic plate and a layer of soil on the surface of the plate. The apparatus functioned as the Büchner funnel tension plates described by Duniway (3). The water content of soil on the tension plates was measured by sampling soil from a tension plate and then drying the soil to constant weight at 110 C. The water content data indicated that the adjustment of soil matric potential was essentially complete within 30 min. A comparison of the water content of soil on the tension plates with soil equilibrated in a pressure plate apparatus confirmed that Ψ_m was accurately controlled (10).

Two soils of different texture were used. A coarse sandy loam soil (52% sand; 27.6% silt; 20.4% clay) from an avocado grove on the University of California, Riverside, campus was used in most experiments, and in some studies an Omni-clay soil (13.5% sand; 32.2% silt; 54.3% clay) was used. Prior to use, the soils were sieved (1.5 mm screen) and in certain experiments they were autoclaved (120 C for 50 min) on two successive days. Osmotic potentials were determined by electrical conductivity measurements of saturation extracts of the soil (13). The osmotic potential of the coarse sandy loam was -0.37 bar and accounts for the differences between matric potentials reported here and the total water potential reported elsewhere (10). The Omni-clay soil had an osmotic potential of -0.80 bar. The pH of saturation extracts was 6.0 and 7.7 for the sandy loam and clay soil, respectively. During experiments, soil temperatures on the tension plates ranged from 24 to 26 C but varied only 1 C among plates at one time. Photosynthetically active radiation (400-700 nm) averaged 4.1 nanoeinsteins $\cdot$ cm^{-2} $\cdot$ sec^{-1} for 10 hr per day at the soil surface on the tension plates.

Root disease assay.—*Persea indica* (L.) seedlings, a sensitive indicator plant for *P. cinnamomi* in soil (Zentmyer, *unpublished*), were used to assay root disease caused by different forms of nonmotile inoculum of *P. cinnamomi* in soil at various levels of matric potential. Two seedlings were planted in infested soil on a tension plate, and eight plates were used for each combination of matric potential and type of inoculum. After 12 days, plants were removed from soil, roots were washed, and the portion of the root system with black lesions caused by *P. cinnamomi* was estimated. Infection by *P. cinnamomi* was confirmed by plating roots from infested soil on $P_{10}VP$ medium. All experiments were repeated at least once.

In one set of experiments we rated the amount of disease in autoclaved sandy loam soil infested with chlamydospores and adjusted to matric potentials of 0, -0.05, -0.10, and -0.25 bar. A stock suspension of chlamydospores was diluted to provide 15 spores/g of dry soil when 25 ml of the dilution was used to saturate 100 g of soil. Infested soil was placed on a tension plate, *P. indica* seedlings were planted in the soil, and matric potential was adjusted as described earlier. In other experiments in sandy loam soil, suspensions of mycelial fragments were diluted to provide approximate inoculum levels of 4 or 16 fragments/g of dry soil when autoclaved soil was infested by the procedure described for chlamydospores. When infected root fragments were used as inoculum (infection confirmed on P_{10} VP medium), 100 g of autoclaved sandy loam soil was saturated with water

and forty 5-mm-long fragments were thoroughly mixed into the soil. To study disease caused by chlamydospores in clay soil, we diluted a spore suspension with demineralized water to provide 15 spores/g of dry soil when 60 ml of the dilution was used to saturate 100 g of dry soil. Indicator plants and matric potentials were set as in experiments with sandy loam soil.

The influence of a soil amendment and Ψ_m on root disease caused by chlamydospores was examined by infesting samples of amended sandy loam soil with chlamydospores. For experiments involving amended soil, we suspended spores in a glucose and asparagine solution (0.02 M glucose and 0.0065 M asparagine) which provided 0.9 mg glucose and 0.225 mg of asparagine per gram of dry autoclaved soil on the tension plates. Matric potential adjustment and rates of infestation were the same as in experiments with chlamydospores described previously.

Chlamydospore germination in soil.—For some experiments, chlamydospores were treated with the fluorescent brightener "Calcofluor White M2R New" (11) and fluorescence microscopy was used to follow chlamydospore germination in soil at different matric potentials. Spores were placed in a solution (300 μg/ml) of the brightener for 8 hr, concentrated by centrifugation, and washed twice with demineralized water. The germinability and viability of spores were measured as described by Tsao (11). Treating with the fluorescent brightener did not change germinability or viability of chlamydospores. In demineralized water only 3% of the spores germinated, whereas in a glucose-asparagine solution (0.01 M each) germination averaged 88% with or without Calcofluor.

Chlamydospores treated with Calcofluor were added to 2 g of sandy loam soil and placed between two layers of 10 μm Nitex monofilament nylon screen (6). The screens were buried in saturated sandy loam soil on tension plates with or without *P. indica* seedlings and the matric potential of the soil was adjusted as described earlier.

Analysis of variance and Duncan's multiple range test were employed to analyze differences among treatments and to compare means.

RESULTS

Figure 1 shows the influence of matric potential on root disease in sandy loam soil infested with different types of inoculum of *P. cinnamomi*. With chlamydospore inoculum disease ratings averaged 86% and 77% at Ψ_m levels of 0 and -0.05 bars, respectively. The average rating was 46% at -0.10 bar, and at -0.25 bar the average number of roots with lesions was only 4%. When the soil was infested with either four or 16 fragments of mycelium per gram of dry soil, there was no significant difference between disease ratings with the two levels of inoculum at any one matric potential. With four fragments per gram of dry soil (Fig. 1), the disease ratings at Ψ_m values from 0 to -0.10 bar were similar to ratings when the soil was infested with chlamydospores and there was a similar tendency for disease to decrease sharply between -0.1 bar and -0.25 bar. With autoclaved soil infested with diseased root fragments disease ratings also were lower at -0.25 bars than at less negative matric potentials. The only significant difference between disease ratings for the different types of inoculum occurred at -0.10 bar, where the average rating with root fragment inoculum was significantly higher than with soil infested with chlamydospores or mycelial fragments.

In tests with clay soil infested with chlamydospores, we did not observe a sharp difference between disease ratings at Ψ_m values of -0.10 bar and -0.25 bar (Fig. 2). At $\Psi_m = 0$, the disease rating (76%) was lower than the rating for any inoculum at that potential in the sandy loam soil (Fig. 1). With a reduction in Ψ_m of -0.05 bar in the clay soil, the average rating was 50% and was approximately that value for more negative matric potentials, even at $\Psi_m = -0.25$ bar.

Table 1 reports the influence of a soil amendment on root disease of indicator plants in autoclaved soil that was infested with chlamydospores and adjusted to different Ψ_m levels. The disease ratings in nontreated soil at Ψ_m values from 0 to -0.25 bar corresponded to the percentages for chlamydospore inoculum in the previous study (Fig. 1). In contrast to an average disease rating of 4% at $\Psi_m = -0.25$ bar, in nontreated sandy loam soil, the average rating was 86% at that potential in the same soil amended with glucose and asparagine.

The germination of chlamydospores of *P. cinnamomi* in sandy loam soil was significantly reduced at $\Psi_m = -0.25$ bar (Table 2). Three days after the spores were buried in soil, germination varied from 69% to 80% in soil with or without roots of *P. indica* at Ψ_m values ranging from 0 to -0.10 bar. Germination percentages were slightly higher at those Ψ_m levels after 7 days (76% to 85%) but neither the

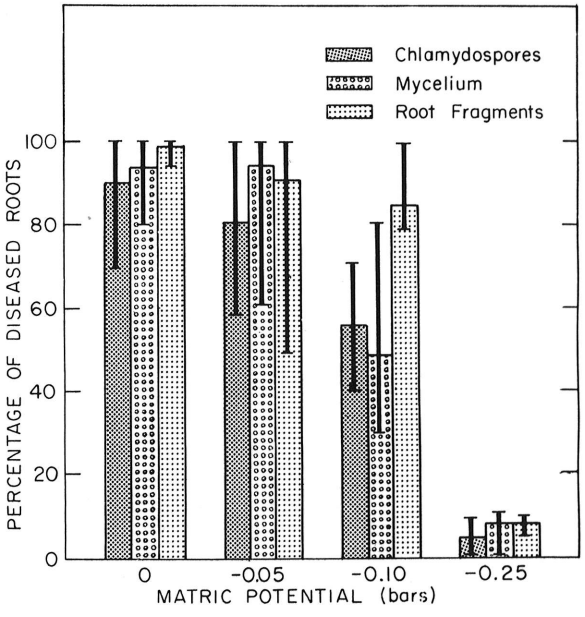

Fig. 1. The influence of matric potential in a sandy loam soil on the percentage of diseased roots of *Persea indica* seedlings in soil infested with different types of inoculum of *Phytophthora cinnamomi*. One hundred grams of autoclaved soil was infested with either 15 chlamydospores/g of dry soil, four mycelial fragments/g dry soil, or forty 5-mm-long avocado root fragments infected with *P. cinnamomi*, and the matric potential adjusted with ceramic tension plates. Lines at the height of bars indicate ranges of percentage disease caused by one type of inoculum at one matric potential.

presence of roots of *P. indica* plants nor Ψ_m influenced spore germination significantly ($P = 0.05$). However, at $\psi_m = -0.25$ bar, germination was significantly reduced to 33% to 45% but the presence of roots did not affect germination. Amending soil at $\Psi_m = -0.25$ bar with glucose and asparagine, 0.9 mg and 0.225 mg/g of dry soil, respectively, increased germination in soil with or without roots to levels comparable to those in nontreated soil at Ψ_m values from 0 to -0.10 bar.

Germ tube growth also was reduced at $\Psi_m = -0.25$ bar compared to less negative matric potentials (Sterne and Zentmyer, *unpublished*). At the higher Ψ_m values (0 to -0.10 bar) and in the soil at -0.25 bar with glucose and asparagine, germ tubes grew up to 700 μm from chlamydospores and fluoresced brightly in ultraviolet light. Most of the germ tubes formed mycelia and grew through nylon screens into the soil. In contrast, in nontreated soil at $\psi_m = -0.25$ bar, germ tubes grew only 150 to 300 μm and fluoresced very faintly. In our experiments, the number of germ tubes per spore varied from one to eight, and in soil with roots, some spores produced a short germ tube bearing a sporangium.

DISCUSSION

The results reported here confirm our earlier conclusion that in a sandy loam soil root disease caused by *P. cinnamomi* can be considerably less severe at a matric potential of -0.25 bar than at -0.10 bar or less negative values (10). The high levels of disease at matric potentials from 0.00 to -0.10 bar agree with observations in the field that Phytophthora diseases are favored by high water content in soil (2, 14). The sharp reduction in disease at $\Psi_m = -0.25$ bar could be important in the epidemiology of Phytophthora diseases. For example, if the water status of soil in an avacado orchard remained generally below -0.1 bar matric potential, root rot caused by *P. cinnamomi* might not develop as rapidly. This is supported by the fact that *P. cinnamomi* probably survives in dead avocado roots as mycelium, chlamydospores, or oospores (16) and in our experiments in soil infested with either diseased roots, mycelium, or chlamydospores, there was considerably less disease at $\Psi_m = -0.25$ bar than at -0.10 bar. Zoospores of *Phytophthora* also seem to function best in soil at very high matric potentials. Duniway (3) observed that in sandy loam soil the movement of zoospores of *Phytophthora cryptogea* from sporangia to roots of safflower seedlings could only be detected at Ψ_m values less negative than -0.10 bar. Therefore, if over-irrigation or inadequate drainage cause Ψ_m levels above -0.10 bar then soil conditions probably favor disease initiated by several forms of inoculum of *Phytophthora*.

Chlamydospore germination was reduced and germ tube development was poor in sandy loam soil at -0.25 bar matric potential, and apparently both factors contributed to the low disease ratings at that potential. Since chlamydospore germination was not completely prevented at $\Psi_m = -0.25$ bar (only reduced to 33-45%), it is likely that the low disease ratings at that matric potential were more related to poor development of germ tubes and mycelium from spores than to reduced germination. Disease ratings in soil infested with mycelial fragments or with roots containing mycelium were also very low at $\Psi_m = -0.25$ bar. Evidently growth and perhaps subsequent infection of roots by mycelium from any source (spore or diseased root) was restricted at that potential. Interestingly, more disease occurred at -0.10 bar with diseased root inoculum than with the other inocula we tested (Fig. 1). The quantity of inoculum in soil with diseased roots probably

TABLE 1. The influence of matric potential (Ψ_m) and a soil amendment on the percentage of infection of roots of *Persea indica* by chlamydospores of *Phytophthora cinnamomi*[a]

Matric potential (bars)	Soil treatment[b]	Percentage diseased roots[c]
0.00	infested[b]	95
-0.05	infested	90
-0.10	infested	46
-0.25	infested	4
-0.25	noninfested	0
-0.25	infested + glu + asp	86

[a]Matric potential was adjusted with ceramic tension plates. The soil in some tension plates was amended with 0.02 M glucose + 0.006 M asparagine to provide 0.900 mg glucose (glu) and 0.225 mg asparagine (asp)/g dry soil and adjusted to $\Psi_m = -0.25$ bar.

[b]Soil was autoclaved at 120 C for 50 min on two successive days then 100 g samples of autoclaved soil were infested with 15 chlamydospores/g dry soil.

[c]Percentage diseased roots is the mean of 16 *Persea indica* seedlings, eight from two separate experiments. Disease rated as the portion of the root system with black lesions caused by *Phytophthora cinnamomi*. Infection confirmed by plating roots on $P_{10}VP$, a medium selective for *Phytophthora* spp.

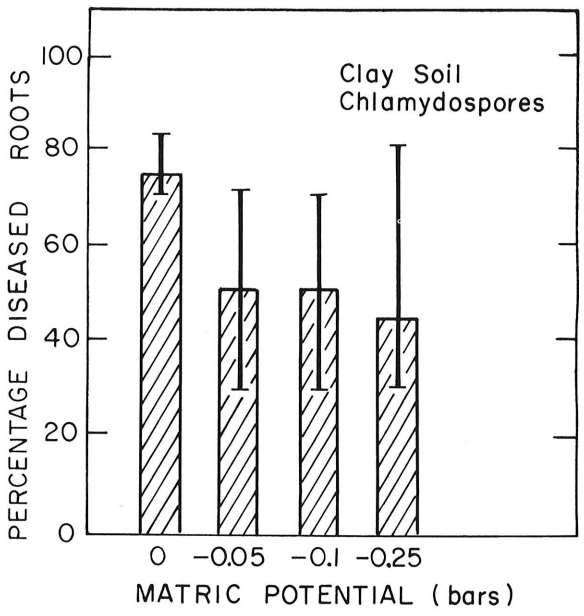

Fig. 2. The influence of matric potential in an Omni-clay soil (13.5% sand, 32.2% silt, and 54.3% clay) on the percentage of diseased roots of *Persea indica* seedlings in soil infested with chlamydospores of *Phytophthora cinnamomi*. One hundred grams of soil infested at a rate of 15 chlamydospores/g of dry soil.

exceeded the amount in soil infested with chlamydospores or mycelium, and root tissue may have supplied energy to spores for germination and to mycelium for growth and infection.

Experiments in clay soil and in soil amended with nutrients indicated that matric potential only indirectly influenced the amount of root disease in sandy loam soil infested with chlamydospores. In contrast to the effect of -0.25 bar matric potential in sandy loam soil, disease ratings at that potential in clay soil were as high as at -0.10 bar or at less negative potentials (Fig. 2). Likewise, disease ratings were as high at -0.25 bar in sandy loam soil amended with glucose and asparagine as at potentials approaching zero (Table 1); i.e., amending the sandy loam soil cancelled the effect of matric potential. Apparently, aeration could be eliminated as the factor limiting disease in sandy loam at -0.25 bar, because adding amendments at that potential should not influence aeration. Furthermore, the direct effect of water potential at -0.25 bar on fungal growth very likely was negligible, since most evidence indicates that growth reductions occur at much lower potentials than those used in our experiments (1, 2, 8, 10). Thus, the results suggest that at −0.25 bar in sandy loam soil the availability of nutrients rather than matric potential per se was the limiting factor for disease development.

In a study of the water potential relations of three *Phytophthora* spp., Sommers et al. (7) suggested that "the effect of soil water on fungal growth in soil should not be interpreted solely from a simple potential energy basis, but that the nutrient status and dynamics of ion and water uptake must also be considered". The data presented in this study suggest that the influence of soil water potential on disease caused by chlamydospores and mycelium of *P. cinnamomi* is primarily related to the effects of matric potential on nutrient availability. Our findings add to the present understanding of why diseases like avocado root rot caused by *P. cinnamomi* are usually severe and develop rapidly in finer-textured soils with poor drainage or in soils subjected to excessive irrigation.

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TABLE 2. The influence of matric potential and soil amendment on the germination of chlamydospores of *Phytophthora cinnamomi* in soil

Matric potential (bars) and soil treatment	Chlamydospore germination in soil without plants[a]		Chlamydospore germination in soil with plants[b]	
	3 days (%)[c]	7 days (%)[c]	3 days (%)[c]	7 days (%)[c]
0.00 nonamended	72	82	69	81
−0.05 nonamended	76	83	80	76
−0.10 nonamended	76	85	73	79
−0.25 nonamended	40*[e]	33*	45*	38*
−0.25 glu + asp[d]	67	79	68	78

[a]Chlamydospores labeled with Calcofluor White M2R Brightener and buried in autoclaved soil between layers of 10 μm nylon screen. Four samples buried for each treatment. Matric potential adjusted with ceramic tension plates.

[b]Chlamydospores labeled and buried as above. Roots of two *Persea indica* seedlings placed in direct contact with the nylon screens containing chlamydospores.

[c]Number of spores germinated per 100 spores counted. Figures are means of four samples for each treatment.

[d]Soil amended with 0.02 M glucose (glu) and 0.006 M asparagine (asp) solutions to provide 0.900 mg glucose and 0.225 mg asparagine/g dry soil.

[e]Mean values followed by asterisk are significantly different from unmarked means ($P = 0.05$) by Duncan's multiple range test, but not significantly different from each other.

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