# Relationship of Matric Water Potential and Air-filled Porosity of Container Media to Development of Phytophthora Root Rot of Rhododendron

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## ABSTRACT

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Matric water potential and air-filled porosity were determined at four sampling dates during the growing season for trickle-irrigated pine bark and peat-based media that differed in composition and particle size distribution. At low and high inoculum densities (nine and 30 infested oat grains per container) of *Phytophthora cinnamomi*, severity of Phytophthora root rot of *Rhododendron* sp. was significantly less in pine bark media than in peat/sand/soil. Differences in root rot severity between the pine bark media and the peat/sand/soil medium were best explained by differences in air-filled porosity and matric water potential among media. Matric water potential generally fluctuated from −1.0 to −3.0 kPa between irrigations in the pine bark media and from 0 to −1.0 kPa between irrigations in the peat/sand/soil medium. Pine bark media had volumetric air-filled porosities that fluctuated from about 40% just after irrigation to about 45% 48 h later, whereas peat/sand/soil had an air-filled porosity near 10% after irrigation and about 20% 48 h later. Irrigation water ponded on the surface of containers with peat/sand/soil immediately after trickle irrigation. This was not observed in containers with pine bark media. Relatively large pores that provide high air-filled porosity in pine bark media account for the rapidity with which pine bark media drain after irrigation, which resulted in matric potentials unfavorable for zoospore discharge and dispersal.

*Additional keyword*: moisture retention curve.

Hammermilled pine bark has been used extensively in many nursery and greenhouse potting media in the commercial production of woody ornamentals in the southeastern United States (5,21,23). The benefits of pine bark as a container medium include the suppression of soilborne plant pathogens (22). Suppression of Phytophthora root rot, the most important disease in nursery production of woody ornamentals in the United States (1), has been reported in pine bark media (28,29).

Mechanisms of disease suppression in pine bark media are not fully understood. Physical factors within pine bark container media, such as air-filled porosity and matric water potential, may create a container environment that favors root development and expression of host resistance (22), but not pathogen reproduction and pathogenicity (16).

Soil water matric potential is a primary physical factor in the regulation of sporangium production and zoospore release, movement, and chemotaxis, as well as germination and survival of chlamydospores of *Phytophthora* spp. (6,9,10,14). Host susceptibility to Phytophthora root rot is affected by air-filled porosity of container media, which affects root generation and growth (4,32), root exudation (17), and plant metabolism related to host resistance (4).

Previously, we reported that severity of Phytophthora root rot for plants in peat- and pine bark-based container media was negatively correlated with total porosity and air space and positively correlated with bulk density and volumetric water content at 5.0- to 10.0-kPa tension of the container medium (20). In this study, we have examined different, yet related, physical properties of the various media with respect to their effects on disease severity. Our objectives were to quantify matric water potential and air-filled porosity in pine bark- and peat-based container media between irrigation events during the growing season, and to assess the relationship of these parameters to root rot of *Rhododendron* sp. caused by *Phytophthora cinnamomi* Rands. A preliminary report has been published (13).

## MATERIALS AND METHODS

**Container media and plant culture.** Three pine bark-based media, pine bark, pine bark/sand (3:1, v/v), and pine bark/peat (3:1, v/v), were compared with a peat/sand/soil medium, (1:1:1, v/v) for development of Phytophthora root rot. Pine bark media were prepared from a commercial grade, hammermilled pine bark (Summit Lumber Co., Louisburg, NC) with particles ≤5.0 cm. The sand was a washed commercial builder's sand, and the peat moss was shredded Canadian sphagnum. The soil was a sandy loam (68% sand, 17% silt, 15% clay [7]). Macro- and micronutrients were incorporated into all media as described previously (20). The size distribution of medium particles for the four media are presented in Ownley et al (20), as determined by procedures described by Bilderback et al (3). Pine bark and pine bark/peat had the largest proportion of particles greater than 6.3 mm. The two media with soil components, peat/sand/soil and pine bark/

sand, had larger proportions of particles passing through the 0.355-mm sieve (see Figs. 3, 4 in ref. 20). After 20 wk, the bulk densities of the four uninfested container media were 0.188, 0.492, 0.163, and 0.776 g $cm^{-3}$ for pine bark, pine bark/sand, pine bark/peat, and peat/sand/soil, respectively. The bulk densities of these media infested with nine colonized oat grains per container were 0.201, 0.519, 0.161, and 0.896 g $cm^{-3}$, respectively.

One-year-old plants of *Rhododendron* sp. cv. Nova Zembla were potted into 6-L polyvinyl containers and maintained under 50% shade at a research nursery (Horticultural Crops Research Station, Unit 4, North Carolina State University, Raleigh). Water was applied with two trickle irrigation rings around each plant once every 48 h between 1100 and 1130 hour. Pine bark media were irrigated to near saturation and the peat/sand/soil medium to saturation during this period, as evidenced by water ponding on the latter medium but not on the former media.

**Pathogen inoculum.** Oat inoculum of four isolates of *P. cinnamomi* from North Carolina (101 [ATCC 46292], 116, and 128 from rhododendron and 150 from azalea) and one isolate from Ohio (100; H. A. J. Hoitink, Ohio State University) were prepared as described previously (20). Oat inoculum of *P. cinnamomi* was added at the rate of nine or 30 colonized oat grains per container 4 wk after potting. Inoculum was placed into each of three sites around the periphery of the root ball at a depth of 2.5–5 cm. Inoculum was introduced on day of the year 160 and 180 in trial 1 and trial 2, respectively, as described below. Uninfested controls received no inoculum.

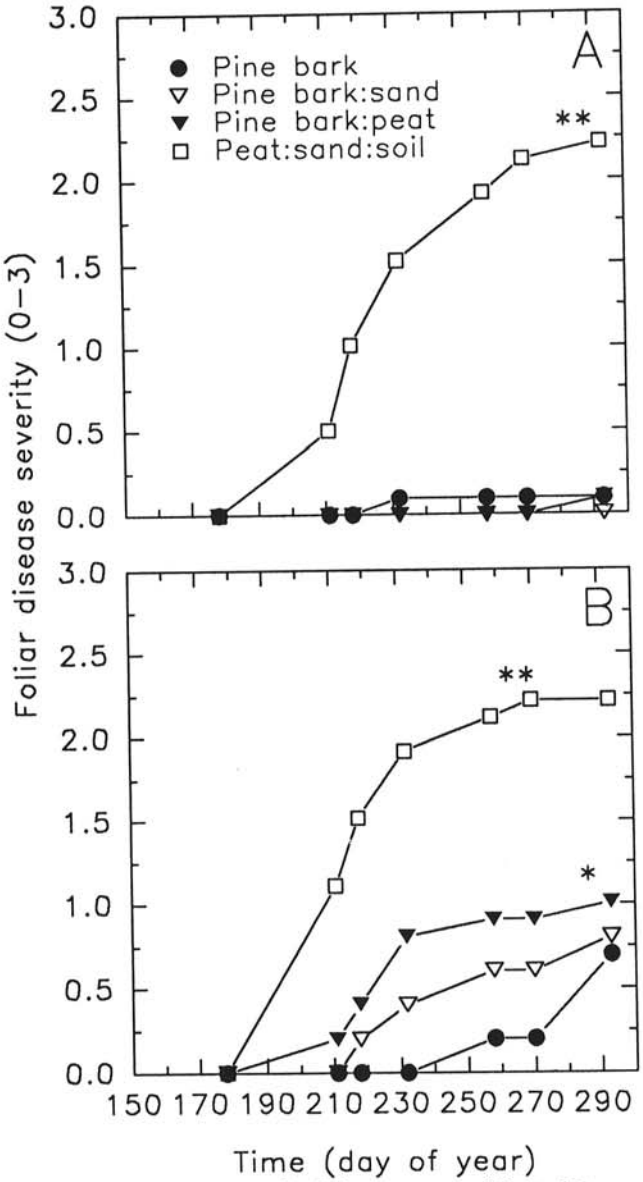


**Fig. 1.** Disease progress curve for foliar symptoms of Phytophthora root rot of rhododendron in pine bark, pine bark/sand, pine bark/peat, and peat/sand/soil media. **A,** media infested with nine oat grains per container colonized by *Phytophthora cinnamomi*. **B,** media infested with 30 colonized oat grains per container. Lines for pine bark/sand, pine bark/peat, and pine bark overlap in A. One or two asterisks denote that differences were significant compared with uninfested controls at $P = 0.01$ and $P = 0.001$, respectively.

**Experimental design.** The experiment was a 4 × 3 factorial in a randomized complete block design, with four media and three inoculum rates. Two trials were conducted, with five replicates and two observations (plants) per replicate per trial. Both observations were used for disease assessment, whereas only one observation of each replicate was used for determinations of physical properties. Analysis of root rot severity data from the two trials yielded similar results and comparable mean square errors; therefore, trials were combined in further analyses, resulting in a total of 10 replicates and two plants per replicate per treatment. Data for trial 2 are presented for area under the disease progress curve (AUDPC), matric water potential, and air-filled porosity.

**Moisture retention curves.** Moisture retention curves for each medium have been characterized (20). Briefly, undisturbed, 7.5-cm-high cores of media, 347.5 $cm^3$ in volume, were removed from the center of each container at the end of the growing period and were used to generate the soil moisture retention curves (20). Cores were saturated on a porous pressure plate apparatus, and the volume of water drained after 24–48 h at each constant pressure selected between 0 and 29.35 kPa was measured (3,12). A five-parameter nonlinear model (19,33) was used to fit the moisture retention curve for each medium. Pine bark and pine bark/peat retained more water than the other media over the 0- to 29.35-kPa (10 mb = 1 kPa) tension range (see Figs. 1, 2 in ref. 20). Replacement of pine bark with sand or soil greatly reduced the moisture-holding capacity of container media.

**Calculation of water content, air-filled porosity, and matric water potential of container media during the growing season.** Determinations of changes in water content of container media planted with rhododendron were based on changes in total mass that occurred during the time between irrigation events. Total mass was determined by weighing each containerized plant several times between scheduled irrigation events. Trial 1 was performed between days of the year 160 and 290, with measurements started on days 168, 190, 218, and 269, corresponding to 8, 30, 58, and 109 days after introduction of *P. cinnamomi*, respectively. Trial 2 was conducted between days of the year 180 and 290, and measurements were started on days 210, 218, 259, and 271, which corresponded to 30, 38, 79, and 91 days after introduction of *P. cinnamomi*, respectively. Containerized plants were weighed five to eight times over a period of 48 h between rain-free irrigation events.

The mass of water at each weight determination was based on the equation:

$$M_w = M_t - [(\rho_b)(V_t) + M_p] \quad (1)$$

in which $M_w$ = mass of water in the medium; $M_t$ = mass of water, medium solids, medium air, and plant; $\rho_b$ = bulk density; $V_t$ = total volume of medium solids, water, and air within the container; and $M_p$ = mass of plant shoot. Plant shoot mass determinations during the course of the experiment were based on regressions of shoot mass against canopy width for each treatment. The total volume of medium in each container was monitored carefully by recording any changes in the distance of the container medium surface from the container rim due to settling of medium or splashing of medium during thunderstorms. The percentage of volume of water in the medium, $P_v$, was calculated from the ratio of $V_w$ to $V_t$, in which $V_w$ is equal to $M_w$ when the density of water is 1.0 g $cm^{-3}$ (15).

Matric water potential was determined for each medium × inoculum combination at each sampling time by inputing the

calculated $P_v$ in a computer program written with Symphony (Lotus Development Corp., Cambridge, MA). Because the moisture retention curve is a plot of matric water potential versus $P_v$, the computer program interpolated a matric water potential value from the characteristic moisture retention curve of the container medium based on the calculated $P_v$.

Because cores of media were removed from the center of the containers to generate the moisture retention curves, matric water potentials calculated were based on moisture retention characteristics for the midpoint in the container. After drainage of gravitational water following irrigation, each centimeter interval below or above the midpoint would be at −0.1 kPa values higher or lower than the average or midpoint values reported. However, results are presented in terms of average or midpoint values of matric water potential of the medium in the container.

The percentage of air-filled porosity ($E_a$) was determined as:

$$E_a = T_p - P_v \quad (2)$$

in which $T_p$ (total porosity) = mass of water at saturation, and $P_v$ = percentage of volume of water (15).

**Disease assessment.** Plants were observed for foliar symptoms of Phytophthora root rot during the course of the experiments. A visual assessment scale, with 0 = healthy, 1 = chlorotic, 2 = stem necrotic, and 3 = plant dead, was used to assign a foliar symptom rating for each plant. Disease severities were averaged over replicates for each treatment, and disease progress curves were plotted. For each plot, AUDPC was calculated as described by Shaner and Finney (26).

As described previously (20), root samples were collected from each plant after 20 wk, and root rot severity was assessed on a visual scale of 1–5, with 1 = healthy, 2 = discolored and necrotic feeder roots, 3 = larger roots necrotic, 4 = stem necrotic, and 5 = plant dead. Washed roots then were transferred to a semiselective medium for *Phytophthora* spp. (11).

**Data analysis.** Disease data were analyzed for significance with the general linear models procedure and the least significant difference ($P = 0.05$) test of the Statistical Analysis System (24,25). AUDPCs were tested for significance by single degree-of-freedom contrasts.

## RESULTS

**Foliar symptoms.** In the peat/sand/soil medium, disease was severe, with a severity rating of >2.2 (on a 0–3 scale) after 90 days, regardless of initial amount of inoculum (Fig. 1). For plants in the infested peat/sand/soil media, the AUDPC for plants with nine or 30 oat grains per plant was greater ($P = 0.001$) than in the uninfested controls. In the infested medium at nine oat grains per plant, the AUDPC was 1,487 severity days compared with 1,795 severity days for plants with 30 oat grains of *P. cinnamomi* per plant.

In the pine bark-based media, foliar symptoms of root rot, as measured by AUDPC, were more severe at 30 oat grains of *P. cinnamomi* per plant than at nine oat grains per plant (Fig. 1). However, at 30 oat grains per plant, only the AUDPC for pine bark/peat (686 severity days) was greater ($P = 0.01$) than the respective uninfested control (Fig. 1B).

**Root symptoms.** Root rot symptoms were most severe on rhododendrons growing in the peat/sand/soil medium (Figs. 2, 3). No difference in severity was observed between nine and 30 oat grains per plant for plants in the peat/sand/soil medium, and disease was greater ($P = 0.05$) than for plants in uninfested controls (Fig. 2D). Rhododendrons in the pine bark-based media had less severe root rot ($P = 0.05$) than plants in peat/sand/soil (Fig. 3B,C). At nine oat grains per plant, severity of root rot for plants in pine bark and pine bark/sand was similar to the uninfested controls (Fig. 2A,B), whereas in pine bark/peat, root rot severity was intermediate compared with the high inoculum treatment and the uninfested control (Fig. 2C). At the high inoculum level, however, plants in all media had more severe root rot than the corresponding plants in uninfested controls (Fig. 2A–D).

**Matric water potential and air-filled porosity of container media.** Changes in matric water potential for the uninfested pine bark/sand medium between irrigation events fluctuated more sharply than in the other media at the 30-day sampling period (Fig. 4A). Matric water potential reached below −30 kPa at 26 h after irrigation. The same pattern of change in matric water potential occurred at 30 days for pine bark/sand infested with nine oat grains per container (Fig. 4B). In the other pine bark

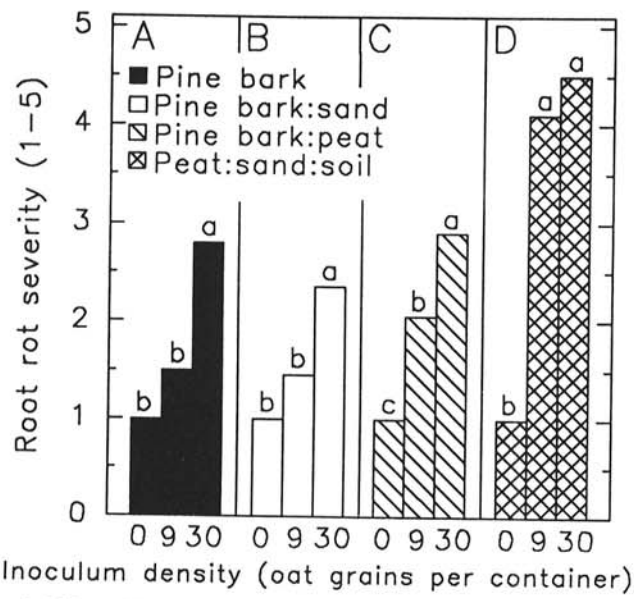


**Fig. 2.** Effect of four container media on Phytophthora root rot severity of rhododendron. Media were infested with zero, nine, or 30 oat grains per container colonized by *Phytophthora cinnamomi*. Data for each medium (**A–D**) were analyzed separately. Bars with the same letter within each medium are not significantly different at $P = 0.05$ according to *F*-protected LSD tests.

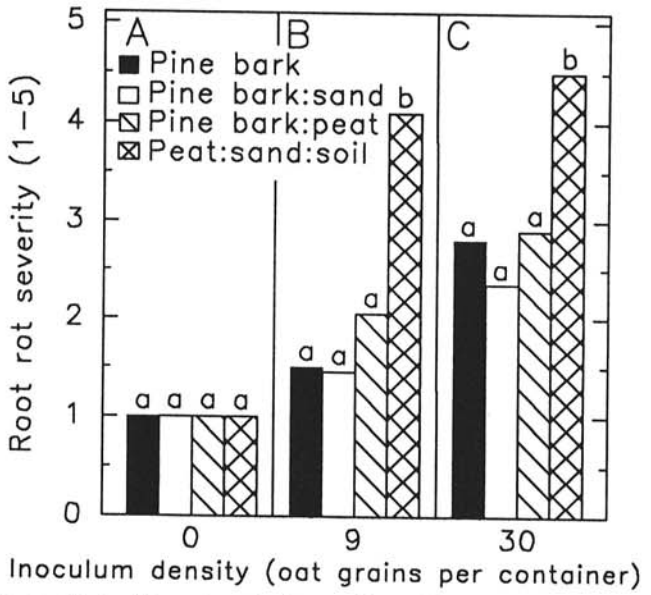


**Fig. 3.** Effect of inoculum density on Phytophthora root rot severity of rhododendron in four container media. Media were infested with zero (**A**), nine (**B**), or 30 (**C**) oat grains per container colonized by *Phytophthora cinnamomi*. Data for each inoculum density (A–C) were analyzed separately. Bars with the same letter within each inoculum density are not significantly different at $P = 0.05$ according to *F*-protected LSD tests.

media at 30 days, fluctuation in matric water potential between irrigation events occurred beginning about 28 h after irrigation but was of less magnitude than that found in pine bark/sand medium (Fig. 4A,B).

In general, no fluctuation in matric water potential occurred in the peat/sand/soil medium between irrigation events, where values at 30-, 79-, and 91-day sampling periods remained higher than −0.5 kPa regardless of the presence or absence of *P. cinnamomi* (Fig. 4A–F). At the 79- and 91-day sampling periods, the pattern of matric water potential fluctuation between irrigation events was similar for the three pine bark media in both uninfested and infested media (Fig. 4C–F). Generally, matric water potential remained between −1 and −3 kPa between irrigation events for the pine bark media at the three sampling dates. As the season progressed and temperatures declined, higher matric water potentials were maintained in all media.

The air-filled porosities of the pine bark media were similar (Fig. 5). Porosities ranged from 30–44% within 1.5–2 h after an irrigation to 35–50% at the end (48 h later) of the irrigation event, depending on medium, presence of the pathogen, and sampling date (Fig. 5). The absolute change in air-filled porosity between irrigations was about 12% for an individual pine bark medium regardless of sampling date or presence of *P. cinnamomi*.

In contrast, the air-filled porosity in the peat/sand/soil medium ranged from 3–12% just after an irrigation to 12–22% at 48 h after irrigation, depending on sampling date and presence or absence of *P. cinnamomi* (Fig. 5). In one exception, however, at 30 days in the uninfested medium, air-filled porosity reached 30% at 48 h after irrigation (Fig. 5A). The absolute change in air-filled porosity in the peat/sand/soil medium between irrigations was the same as that observed in pine bark media (Fig. 5). During irrigation, infiltration rate into the peat/sand/soil medium was so slow that water ponded on the surface and remained standing for several minutes after irrigation. This did not occur in the pine bark media.

## DISCUSSION

Root rot of rhododendron caused by *P. cinnamomi* was most severe in the peat/sand/soil medium, regardless of initial inoculum density. Matric water potential within this medium generally ranged from 0 to −0.5 kPa during the 48-h periods between irrigations. In pine bark media, root rot occurred but severity was affected by inoculum concentration. At nine oat grains per plant, disease severity for plants in peat/sand/soil was >4.0 on a 1–5 scale, whereas plants in pine bark media had disease severities <2.1. In pine bark/sand, and pine bark, root rot was not different from that in the uninfested control, whereas in pine bark/peat, root rot was intermediate compared with the uninfested control and the high inoculum treatment. On two of three sampling dates in trial 2, matric water potentials fluctuated from near −1.0 kPa immediately after irrigation to about −3.0 kPa after 48 h. Matric water potentials for the pine bark media on the sampling dates in trial 1 ranged from −1.0 kPa after irrigation to −8.0 kPa

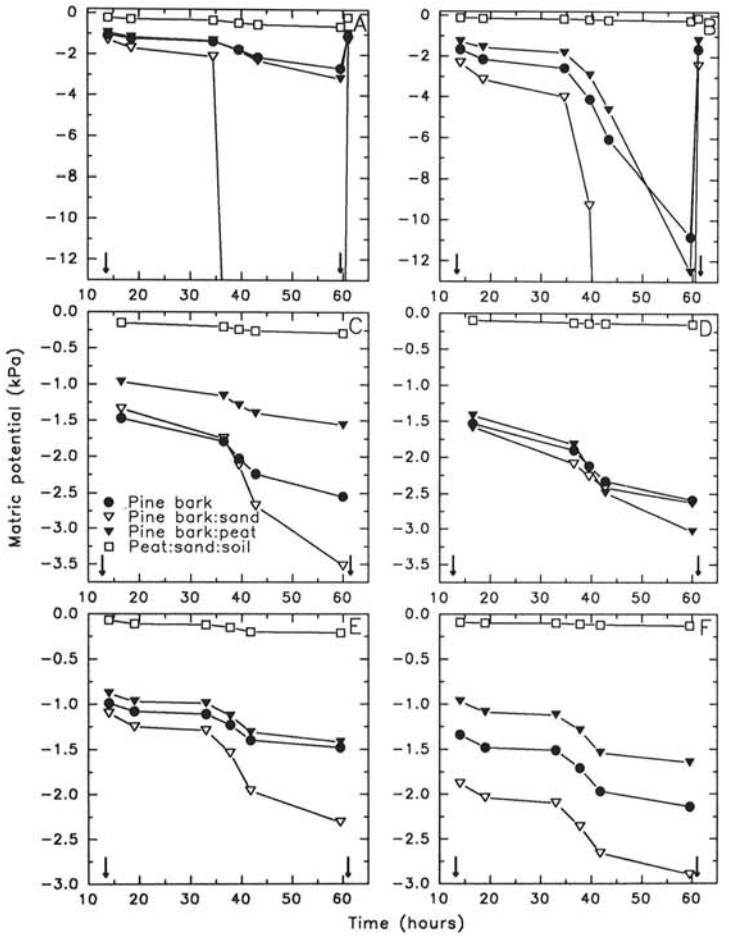


**Fig. 4.** Matric water potentials of four container media at various times after irrigating containers potted with rhododendron. Irrigation (arrows) was by two trickle rings around each plant at 1100–1130 hour every other day. Sampling periods were at 30, 79, and 91 days for plants in the uninfested media (**A,C,E**) and media infested with nine oat grains of *Phytophthora cinnamomi* (**B,D,F**), respectively.

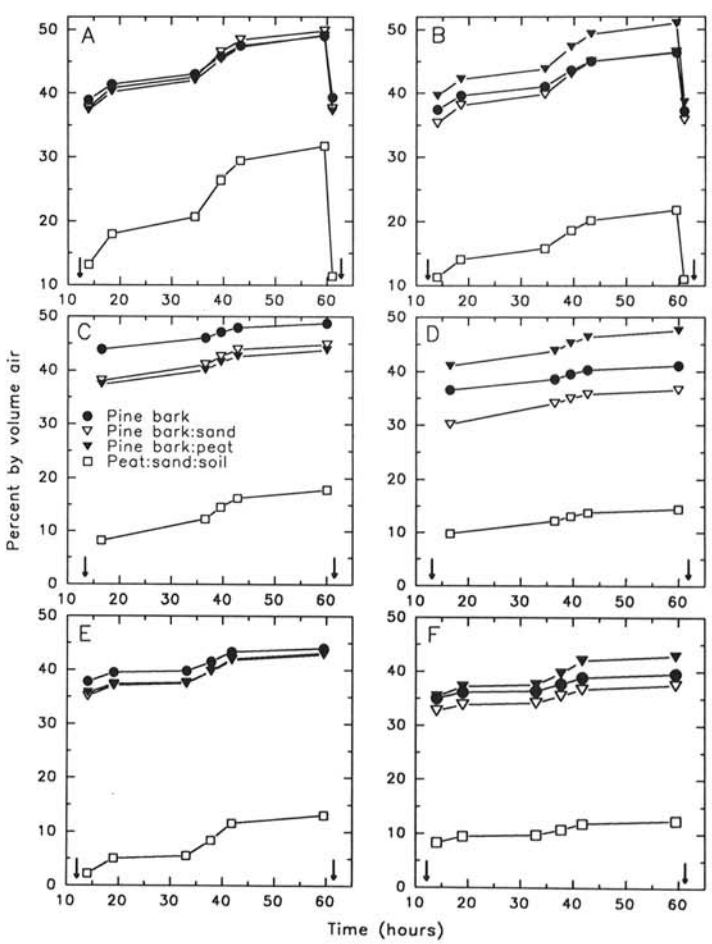


**Fig. 5.** Air-filled porosity of four container media at various times after irrigating containers potted with rhododendron. Irrigation (arrows) was by two trickle rings around each plant at 1100–1130 hour every other day. Sampling periods were at 30, 79, and 91 days for plants in the uninfested media (**A,C,E**) and media infested with nine oat grains of *Phytophthora cinnamomi* (**B,D,F**), respectively.

48 h later, with the exception of pine bark/sand at 58 days when matric water potential was <−30 kPa 48 h after irrigation (*unpublished*). Thus, in only two of six sampling dates over two experiments, matric water potential was <−10 kPa in only one (pine bark/sand) of three pine bark media.

Results of this study are similar to a previous report of development of Phytophthora root rot at controlled matric water potentials (30). Root rot of avocado caused by *P. cinnamomi* was most severe with chlamydospore inoculum in soils at a constant matric water potential of zero, followed by −5.0 and −10.0 kPa. Root rot severity was least at −25.0 kPa (30).

The influence of matric water potential on development of Phytophthora root rot may be due primarily to effects on reproduction and survival of the pathogen. Release, motility, and chemotaxis of zoospores are affected by matric water potential. MacDonald and Duniway (18) reported that release of zoospores by *P. cryptogea* and *P. megasperma* was optimal at 0, impaired at −0.5, restricted at −1.0, and fully prevented at −2.5 kPa. Zoospores swim readily in surface waters of flooded soils or at matric water potentials from 0 to −0.1 kPa, but movement is greatly reduced at −1.0 kPa (8). Thus, severity and more rapid rate of development of root rot of plants in peat/sand/soil may be related to optimal conditions for zoospore release, movement, and chemoattraction. The pattern of matric water potential found within the peat/sand/soil medium is consistent with known effects of matric water potential on zoospore release and movement in soils in relation to disease development (9,10,14). In contrast, the observation that drainage occurred rapidly in pine bark media is an indication that conditions for zoospore discharge and dispersal were seldom favorable (18). Zoospores that were discharged may have been carried out of the container with the irrigation water.

Sporangium production by *P. cinnamomi* in vitro occurred primarily from −1.5 to −7.5 kPa in pine bark and a clay loam (2). Ideally, less conducive media should undergo a steep change in matric water potential within 12 h after irrigation, so that values lower than −10 kPa result in an environment not conducive to sporangium formation (2). Matric water potentials in this range were recorded only in pine bark/sand 30 days after initiation of the experiment. Nevertheless, root rot was less severe in pine bark based-media than in peat/sand/soil. Because matric water potential conditions in pine bark media were favorable for sporangium formation, restriction of release and movement of zoospores of *Phytophthora* was probably the primary factor in suppression of root rot in pine bark media.

Germination and survival of chlamydospores, the form of inoculum used in this study, also are affected by matric water potential. Sterne et al (31) reported the greatest germination of chlamydospores of *P. cinnamomi* at 0 kPa, decreasing at −0.5 and −1.0 kPa, and greatly diminished at −25.0 kPa. Additionally, survival of pathogen inoculum may be affected by antagonistic activity of indigenous soil microorganisms, particularly bacteria, that are active at high matric water potentials (14). Bacteria antagonistic to *P. cinnamomi* have been isolated from pine bark (27).

It is possible that the three sampling dates for matric water potential were not representative of water relations in the containers over the experiment. However, the major differences in matric water potentials between peat/sand/soil and the pine bark media were evident at all sampling dates in both trials.

Differences in the use of midpoint values versus a gradient of matric water potential values from the bottom to top of the container in explaining severity of Phytophthora root rot in a given medium are probably minimal. Additionally, although the method of matric water potential determination may lack precision, it is adequate to show the large differences that exist between pine bark-based media and peat/sand/soil. This method was devised because previous attempts to use a tensiometer in coarse pine bark were unsuccessful. Large pores in the medium did not facilitate formation of an adequate seal between the ceramic cup of the tensiometer and pine bark particles. Other methods of determining matric water potential, such as the neutron probe and gamma ray attenuation, were not practical for containerized media in the nursery.

Survival of infected plants in medium with matric water potentials in a range that favors root rot development also may be due to adequate water content for plant growth despite impaired root function and to sufficient oxygen in the medium to enable the host to compensate for root necrosis and generate new roots. Air-filled porosity clearly distinguished the pine bark media from the peat/sand/soil medium. In all pine bark media at all sampling dates, air-filled porosities consistently fluctuated from near 40% 1–2 h after irrigation to near 45% 48 h later. In contrast, air-filled porosity in peat/sand/soil was much less, fluctuating from less than 5–10% 1–2 h after irrigation to 10–20% 48 h later. The apparent differences between air-filled porosity of pine bark media and peat/sand/soil are consistent with differences in water matric potential, total porosity (20), and air space (20). The low air-filled porosity determined in the conducive peat/sand/soil medium may enhance disease severity by impairing generation and growth of new roots (4,32).

Our study provides evidence that container media of pine bark are less conducive to development of Phytophthora root rot due, in part, to physical properties of the media that affect water relations. Alteration of air-filled porosity and matric water potential by manipulating particle size distribution and irrigation schedules may be used to improve disease suppression by pine bark media.

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