Pine Bark, Hardwood Bark Compost, and Peat Amendment Effects on Development of *Phytophthora* spp. and Lupine Root Rot

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ABSTRACT

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The use of bark and peat media for suppressing Phytophthora root rot was evaluated in the greenhouse and laboratory. Development of root rot of *Lupinus angustifolius* (lupine), an assay plant highly susceptible to *Phytophthora cinnamomi*, was observed in media containing peat, hardwood bark compost (HBC), or pine bark (PB). With or without added sand, HBC was more effective in suppressing root rot of lupine than was PB. The development of disease was delayed and suppressed more in PB at pH 4.5 than in PB at pH 6.0. Sand and lime amendments to PB reduced the suppressive capacity to that of similarly treated peat. Mycelial growth and chlamydospore formation by *P. citricola* and *P. cinnamomi* was greater on cornmeal and/or water agar incorporated with water-soluble, filter-sterilized extracts of PB and peat at pH 6.5 than on agar incorporated with HBC extract. Sporangial production by *P. cinnamomi* at pH 6.0 was lower in sterile PB and HBC extracts amended with a stimulatory salt solution than in amended sterile water. Sporangial production by *P. citricola* was not similarly reduced. Sporangial production by both *Phytophthora* spp. was generally higher in nonsterile extracts than in sterile extracts. Sporangial production was generally lower in solutions at pH 4.0 than at pH 6.0 although nonsterile extract of PB from one source overcame this pH effect.

Additional key words: inoculum density, disease progress curve.

The use of hammermilled pine bark in the container production of woody ornamentals is widely practiced by nurserymen in the southeastern United States. Pine bark is lightweight, usually pathogen-free, well-drained, and is a satisfactory substitute for peat moss as the organic component in container media (18,28). Similarly, composted hardwood bark is used in container media in the Midwest with satisfactory results (8,20). Hardwood bark also suppresses plant parasitic nematodes (22) and soilborne plant pathogens (4,13,25), including *Phytophthora cinnamomi* Rands (15,16). *P. cinnamomi* is cosmopolitan and has a wide host range that includes azalea and rhododendron (6,32). *P. citricola* Sawada causes root rot and dieback on rhododendron (14), *Pieris japonica* (Thunb.) D. Don (9), and *Aucuba japonica* Thunb. (31). Although bark of Australian radiata pine suppressed Phytophthora root rot of eucalyptus (10,11) bark of pine species grown in the southeastern USA was never tested.

The present study reported here is an examination of the relative suppression of *P. cinnamomi* root rot in bark and peat media using lupine as a highly susceptible assay plant (3,19), and the effects of water-soluble extracts of bark and peat moss on mycelial growth, chlamydospore formation, and/or sporangial formation by *P. cinnamomi* and *P. citricola*.

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MATERIALS AND METHODS

Bark sources and extract preparation. Pine bark (PB) of undetermined age was obtained from Holt Lake Nursery, Smithfield, NC 27577 (PB1 [source I], pH 3.8), and Coulbourn Lumber Co., Windsor, NC 27983 (PB [source II], pH 4.5). Hardwood bark compost (HBC, pH 6.7) was obtained from H. A. J. Hoitink, Ohio Agricultural Research and Development Center, Wooster, OH 44691, for comparison with PB. Pine bark and HBC had cation exchange capacities of 10–15 meq/100 g, bulk densities of 0.4 g/cm^3, and base saturation percentages of 34 and 95%, respectively. The P, K, Ca, Mg, and Mn concentrations were three to five times higher in HBC than in PB; however, nutrients are added to HBC prior to composting (16). Water-soluble extracts of barks and peat moss (pH 3.7) were prepared by soaking 2,000 cm^3 of each medium with 1 L of sterile distilled water (SDW) for 15–24 hr at 22–24 C. Filtrates were collected through eight layers of sterile cheesecloth. Particles in the filtrates were removed by centrifugation at 4,000 *g* for 5 min followed by filtration through sterile Whatman No. 1 filter paper. These extracts were designated nonsterile extracts (NS). The pH was adjusted with 1N HCl or NaOH in certain experiments. Filter-sterilized extracts (FS) were prepared by centrifuging NS extracts an additional 20 min at 16,000 *g* and filtering through a sterile Millipore filter (0.22- or 0.45-μm pore size). To confirm sterility of FS solutions, 1-ml samples were placed on nutrient agar plates and observed at 2 days for evidence of bacterial or fungal growth. The pellet obtained in the centrifugation procedure to obtain FS extracts was resuspended in some experiments in SDW equal in volume to that of the original extract. Extracts and resuspended pellet solutions were used immediately.

Cultures and inoculum. *P. cinnamomi* isolates 101 (from *Rhododendron* sp.) and 137 (from *A. japonica*), and *P. citricola* isolate 614 (from *A. japonica*) were tested. Isolates were maintained on V-8 juice agar at 20 C. Mycelial agar disks (7 mm in diameter) were cut from the edge of 4-day-old cultures growing on cornmeal agar (CMA) at 25 C in continuous fluorescent light, and used as indicated in the various procedures. Mycelial mats were grown from agar disks of the fungi in 25 ml of 5% lima bean extract (LBE; 50 g of frozen lima beans per liter, filtered). All laboratory tests were done at 22–25 C.

Lupine root rot development in various container media. Lupine seeds (*Lupinus angustifolius* L., obtained from H. D. Wells, Coastal Plain Experimental Station, Tifton, GA 31794) were surface sterilized in 0.1% NaOCl for 2 min and placed on moistened sterile paper towels in plastic containers for 2 days in the dark at 24 C to induce germination. Inoculum was prepared by adding three agar disks of *P. cinnamomi* to 150 cm^3 of sterile, moist, cornmeal:sand medium (1:49, w/w) in 250-ml flasks and incubating for 6–10 wk at 25 C and continuous light. Chlamydospore density was determined by diluting the inoculum on CMA and counting the resulting colonies. Inoculum was diluted with sand so that resulting chlamydospore density was 0.1, 1, or 10 per cubic centimeter of medium when 50 g of the sand mixture was added to 400 cm^3 (in 600-cm^3 containers) of each of the following test media. PB, pH 4.5 or pH 6.0; HBC, pH 6.5; peat:sand (1:1, v/v), pH 6.5; PB:sand (1:1, v/v), pH 6.0; and HBC:sand (1:1, v/v) pH 6.5. The pH of PB and peat was increased with agricultural grade lime 2 days prior to introduction of inoculum. Final pH determinations were made prior to addition of inoculum. Controls received 50 g of sand. The percent volume airspace (after drainage for 2 hr, at container capacity) of media with and without sand was 16–17% and 32–44%, respectively. Prior to transferring five germinated seeds to each container, 50 cm^3 of sand was placed evenly over the surface of the test medium. Lupines were covered with 100 cm^3 of sand, watered, and the containers then covered with a plastic film to conserve moisture. The film was removed 2 days later at emergence and the seedlings watered daily. Lupine emergence and disease incidence were determined at 2-day intervals 5–29 days after transplanting. Disease symptoms included damping-off, wilting, and/or necrosis at the base of the lupine stem. Diseased plants were removed and placed on a modified pimaricin-penicillin-polymixin selective medium (7) containing 10 mg/L pimaricin instead of 100 mg/L to assay for *P. cinnamomi*. Disease progress curves were plotted as mean percent mortality or mean proportion mortality corrected for multiple infections $\log_e (1/[1-y])$ (in which y = mean proportion mortality) vs time for each medium by inoculum level.

Effect of extracts on mycelial growth. The effect of sterile medium extracts on mycelial growth of *P. cinnamomi* and *P. citricola* was studied by mixing an equal volume of filter-sterilized extract of either PB, peat, or HBC, as well as SDW, (all at pH 6.0–6.5) to either CMA or water agar (WA) (prepared in half the regular amount of water) that had cooled almost to solidification. The resulting media was 2% agar by weight, and approximately 1:1, SDW:sterile extract (or SDW) by volume, and was dispensed at a rate of 20 ml per petri plate. Mycelial agar disks of each isolate were placed in the center of the extract-incorporated agar plate (five replicates). Fungal growth was measured at 5, 8, and 11 days, and expressed as mean linear growth.

Effect of extracts on chlamydospore formation. Filter-sterilized extracts of either PB, peat, or HBC, as well as SDW (all at pH 5.8–6.5) were incorporated into WA as described previously. An agar disk of *P. cinnamomi* was placed in the center of each agar plate. At 10 days, chlamydospores were counted in four 0.5-cm^2 areas near the agar disk and averaged to obtain one determination per plate (four plates per treatment). Chlamydospore formation in liquid culture was induced by placing a 2-day-old mycelial mat of *P. cinnamomi* in a petri plate with 25 ml of one of the above sterile extracts (four replicates). SDW, 5% LBE, and 0.5% LBE were also tested. After 3 days, the chlamydospores in each of four edge areas (0.5 cm^2) per mat were counted and averaged to get one determination per plate.

Effect of extracts on sporangium formation. Two-day-old mats of *P. cinnamomi* were rinsed twice for 30 min in SDW before incubation in one of the following extracts amended 3:1 by volume with a sporangial-stimulating salt solution (5,29) prepared at four times the normal concentration (Ca^{++}, 28 mM; K^+, 16 mM; Mg^{++}, 10 mM; $FeSO_4$, 0.3 mM, filter-sterilized and added to salt solution after autoclaving): nonsterile PB (pH 6.0), peat (pH 6.3), and HBC (pH 6.5); filter-sterilized PB (pH 6.0), peat (pH 6.4), and HBC (pH 6.5); and SDW (pH 4.0 and 6.0) (four replicates). Nonsterile and sterile extracts of pine bark from the Smithfield source (PB1) were used in earlier experiments. After incubation for 13–45 hr, sporangia were counted in the manner described for chlamydospores in liquid culture. Test solution pH was monitored before and after incubation. Stimulating properties of extracts towards sporangial formation of *P. cinnamomi* and *P. citricola* were studied by using similar procedures except the stimulating salt solution was not added, and extracts of PB and resuspended pellets of PB at pH 4.0 were included in the test (four replicates). After the last sporangial count, mats were chilled at 4 C for 15–30 min in either SDW or the original solution, and the sporangia were observed for zoospore release. The effect of HBC extract on formation of sporangia by *P. citricola* was not studied.

RESULTS

Lupine root rot development in various container media. Disease progress curves (Fig. 1) indicate that in a given media, disease generally developed sooner and more rapidly in media at 10 chlamydospore per cubic centimeter than in media at 0.1 or 1.0 chlamydospores per cubic centimeter. Generally, slope values of the transformed disease progress curves increased and T_{50} values (time until 50% of plants were killed) decreased with increasing inoculum density (Table 1). All regression lines had significant linear correlation coefficients ($P \leq 0.05$). Based on slope and T_{50} values at a given inoculum level, the media were generally ranked by suppressiveness from lowest to highest:peat:sand, pH 6.0; PB:sand, pH 6.0; PB, pH 6.0; PB, pH 4.5; HBC, pH 6.5; and HBC:sand, pH 6.5. The relative suppressive effect of PB at pH 4.5 and pH 6.0 was most apparent at inoculum densities of 0.1 and 1.0 chlamydospore per cubic centimeter, and the media only delayed the onset of disease.

Effect of extracts on mycelial growth. Linear growth of *P.*

cinnamomi was greater at each sampling date on WA incorporated with filter-sterilized PB and peat extracts than on WA incorporated with sterile water (Table 2). However, growth was less on WA incorporated with HBC extract. *P. citricola* did not grow on WA unless the agar was incorporated with sterile PB, peat, or HBC extract. When CMA was used as the medium, all extracts supported significantly greater growth of *P. cinnamomi* than did the control. Similarly, growth of *P. citricola* was greater on CMA incorporated with extracts of peat and PB, but not HBC.

Effect of extracts on chlamydospore formation. In general, *P. cinnamomi* formed more chlamydospores in liquid culture than in water agar culture (Table 3). Filter-sterilized PB and peat extracts increased the number of chlamydospores in either culture method. HBC extract increased chlamydospore number in water agar culture but not in liquid culture. Lima bean extract increased chlamydospore number but not to the same extent as PB and peat.

Effect of extracts on sporangium formation. Fewer sporangia formed in filter-sterilized bark extracts amended with sporangia-

TABLE 1. Linear regression equations for the incidence of lupine mortality (corrected for multiple infections) versus days after transplanting at three chlamydospore densities of *Phytophthora cinnamomi* in six potting media

Medium	Inoculum density (cpc)[a]	Linear regression equation[b]	R[c]	T_{50}[d]
Peat:sand	0.1	$Y = 0.024\ X - 0.24$	0.93 ***	40
pH 6.0	1.0	$Y = 0.157\ X - 1.43$	0.94 ***	14
	10.0	$Y = 0.141\ X - 0.73$	0.94 ***	10
Pine bark:sand	0.1	$Y = 0.019\ X - 0.20$	0.92 ***	47
pH 6.0	1.0	$Y = 0.106\ X - 0.89$	0.96 ***	15
	10.0	$Y = 0.101\ X - 0.53$	0.97 ***	12
Pine bark	0.1	$Y = 0.015\ X - 0.19$	0.66 **	59
pH 6.0	1.0	$Y = 0.054\ X - 0.52$	0.95 ***	22
	10.0	$Y = 0.147\ X - 1.15$	0.97 ***	13
Pine bark	0.1	$Y = 0.011\ X - 0.13$	0.64 **	78
pH 4.5	1.0	$Y = 0.031\ X - 0.35$	0.89 ***	33
	10.0	$Y = 0.116\ X - 1.02$	0.95 ***	15
Hardwood bark	0.1	$Y = 0.002\ X - 0.02$	0.42 *	479
compost pH 6.5	1.0	$Y = 0.013\ X - 0.11$	0.90 ***	63
	10.0	$Y = 0.045\ X - 0.32$	0.97 ***	23
Hardwook bark	0.1	...[e]	...	...
compost:sand	1.0	$Y = 0.011\ X - 0.06$	0.90 ***	71
pH 6.5	10.0	$Y = 0.035\ X - 0.02$	0.83 ***	21

[a] cpc = Chlamydospores per cubic centimeter of medium.
[b] Linear regression equations of $\log_e (1/[1-y])$ (in which y = proportion diseased plants) versus time (days after transplanting from day 8 through 29).
[c] The linear correlation coefficient (R) was significant at $P \leq 0.05$ (*) $P \leq 0.01$ (**) or $P = 0.001$ (***).
[d] T_{50} = days required for 50% of plants to develop aboveground symptoms.
[e] No mortality on any day.

TABLE 2. Average linear growth of *Phytophthora cinnamomi* and *Phytophthora citricola* on water and cornmeal agar amended with sterile peat or bark extracts

Fungus isolate	Test solution[y]	Average linear growth (mm)[z] On water agar (at 11 days)	On cornmeal agar (at 8 days)
Phytophthora cinnamomi	Pine bark	32 c	42 b
	Hardwood bark compost	19 a	42 b
	Peat	34 c	42 b
	Water	27 b	37 a
Phytophthora citricola	Pine bark	11 c	26 b
	Hardwood bark compost	7 b	18 a
	Peat	14 d	34 c
	Water	0 a	21 a

[y] All extracts were filter-sterilized and adjusted to pH 6.0–6.5 before incorporation into agar.
[z] Means in the same column for a given species followed by the same letter do not differ significantly, $P = 0.05$, according to Duncan's multiple range test.

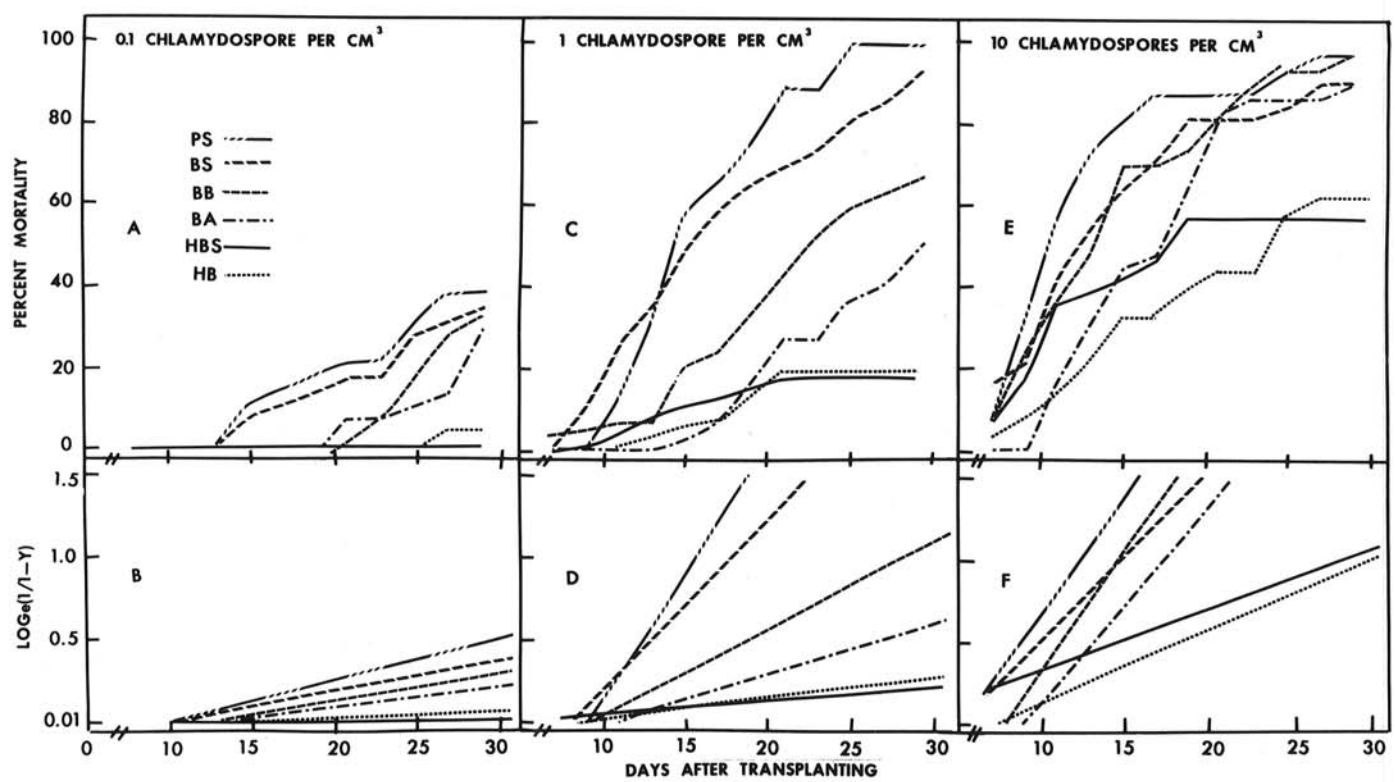

Fig. 1. A–F, Disease progress curves for mortality of lupine seedlings caused by *Phytophthora cinnamomi* at three chlamydospore densities as affected by six potting media. **A and B,** arithmetic and transformed ($\log_e 1/[1-y]$) data for 0.1 chlamydospore per cubic centimeter, **C and D,** one chlamydospore per cubic centimeter and **E and F,** 10 chlamydospores per cubic centimeter. PS = peat:sand, pH 6.5; BS = pine bark:sand, pH 6.0; BB = pine bark, pH 6.0; BA = pine bark, pH 4.5; HBS = hardwood bark compost:sand, pH 6.5; and HBC = hardwood bark compost, pH 6.5.

stimulating salts than in the SDW control (Table 4). Low pH (4.0) also depressed sporangial number. The depressing effect of NS extracts decreased with time and was eventually overcome in all but nonsterile PB extract. Sporangial numbers in nonsterile PB1 extract were similar to the control.

Nonamended nonsterile extracts and resuspended pellet solutions increased sporangial production by *P. cinnamomi* (Table 5). Sporangial production was greater with nonamended nonsterile PB1 extract (source I) than with nonamended nonsterile PB extract (source II). Nonamended nonsterile extracts and pellet solutions of PB1 at pH 4.0 increased numbers of sporangia formed while similar solutions of PB did not. Number of *P. citricola* sporangia was not different at pH 6.0–6.5 in any NS or FS extract as compared to SDW (Table 5). However, at 48 hr more sporangia of *P. citricola* were found in NS extracts than in SDW and FS extracts. Fewer sporangia of *P. citricola* formed in SDW and FS extracts at pH 4.0 than at pH 6.0. However, at pH 4.0, more sporangia formed in NS extracts than in FS extracts.

DISCUSSION

Physical properties of media resulting in better drainage help to explain lower root rot disease severity, especially at inoculum densities of less than one chlamydospore per cubic centimeter. However, both HBC:sand and HBC media were more suppressive to lupine root rot than were other media with similar physical characteristics at all inoculum densities, which supports the results of Hoitink (16). In our test, pine bark only delayed development of lupine root rot; this may reflect either a gradual increase of pH in the medium during the experiment or a change in the susceptibility of the host. We have observed that PB and HBC are equally effective in inhibiting Phytophthora root rot of *A. japonica* in roots that were evaluated 10 days after inoculation (31). A longer incubation period may have resulted in differences in suppression between media as was observed in the present study with lupine. Lupine and aucuba may differ in their susceptibility to *Phytophthora* spp. Pine bark at pH 4.5 was more suppressive than pine bark at pH 6.0, although differences were not statistically significant. Use of pine bark with a low pH could be of value in the control of root rot disease of plants tolerant to low pH (eg, azaleas) under proper fertilizer regimes. Pegg (27) previously reported the value of low pH in suppression of Phytophthora root rot. The low pH may be inhibiting the pathogen or bacteria that stimulate the fungus to produce sporangia, or stimulating the growth of antagonistic microorganisms. The buffering capacity of bark may be important in this pH effect; we have observed that the pH of pine bark:sand medium can change from 4.7 to 5.3 in 20 days with daily watering.

The relative differences between sterile extracts of pine bark and hardwood bark compost in stimulating chlamydospore formation and mycelial growth, and in inhibiting sporangial formation of *P. cinnamomi* may help to explain differences in disease suppression between media observed in the host infection study. However, observations under axenic conditions may not be directly applicable to those under nonsterile conditions, where sporangia form sooner and in more abundance than chlamydospores. An inverse relationship between sporangia and chlamydospore formation was noted by other workers (2) and was observed consistently throughout our study.

The barks, especially HBC, are high in nutrients and organic substances, which may account for the inhibition of sporangia formation by *P. cinnamomi* observed with filter-sterilized extracts even though amended with sporangia-stimulating salts. Ayers and Zentmyer (1) observed that the inhibition of sporangial formation due to glucose or nutrients in the culture medium was eventually overridden under nonsterile conditions. We observed that bacteria could override the inhibition due to extracts and the inhibition due to low pH (4.0). If a chemical inhibitor rather than excess nutrients is responsible for inhibition of sporangial formation in *P. cinnamomi*, bark medium may not be inhibitory to formation by other *Phytophthora* spp. Sporangial formation by *P. citricola*, which readily produces sporangia in water as well as in high nutrient solutions (30), was not inhibited by pine bark extracts relative to SDW. The lack of stimulation of chlamydospore formation by HBC extracts in liquid culture does not appear to be

TABLE 3. Stimulation of chlamydospore formation in *Phytophthora cinnamomi* by sterile bark and peat extracts in liquid culture or incorporated into water agar

Test solution[w]	Number of chlamydospores per 0.5 cm[2y]	
	Agar culture[x]	Liquid culture[z]
FS Pine bark	46 c	328 c
FS Peat	33 c	250 c
FS Hardwood bark compost	12 b	13 a
Sterile distilled water	5 a	1 a
5% Lima bean extract	···	134 b
0.5% Lima bean extract	···	27 a

[w] FS = filter-sterilized extract. The pH values of all solutions were adjusted to 5.8–6.5 before use.

[x] Determinations were made at 10 days on the oldest growth near the agar disk. ··· = Not determined.

[y] Means in the same column followed by the same letter do not differ significantly, $P = 0.05$, according to Duncan's multiple range test).

[z] Determinations were made at 3 days on the newest growth at the edge of mycelial mats.

TABLE 4. Inhibition of sporangial formation on mycelial mats of *Phytophthora cinnamomi* in bark and peat extracts amended with sporangia-stimulating salt solution

Test solutions[y]	Average number of sporangia produced per 0.5 cm[2] edge area during the specified time of incubation in test solutions[z]			
	Source I		Source II	
	24 hr	45 hr	13 hr	36 hr
NS Pine bark	113 (110%) b	653 (250%) c	7 (10%) a	48 (30%) ab
FS Pine bark	9 (10%)a	13 (10%)a	11 (10%) a	17(10%) ab
NS Hardwood bark compost	···	···	3 (0%) a	230 (130%) d
FS Hardwood bark compost	···	···	0 (0%) a	5 (0%) a
NS Peat	···	···	77 (80%) c	190 (110%) cd
FS Peat	···	···	45 (50%) b	62 (40%) b
Sterile water, pH 5.8	99 (100%) ab	260 (100%) b	95 (100%) d	173 (100%) c
Sterile water, pH 4.0	0 (0%) a	0 (0%) a	0 (0%) a	0 (0%) a

[y] The pH values of all extracts were between 5.8 and 6.5 after mixing with salt solution. NS = nonsterile extract; FS = filter-sterilized extract. All test solutions were amended with the sporangial-stimulating salt solution.

[z] Means in the same column followed by the same letter are not significantly different, $P = 0.05$, according to Duncan's multiple range test. The initial pH of pine bark used from Source I was 3.8; from Source II, 4.5 (see text). Percentage values in parentheses were calculated based on the sterile-water-plus-salts control. ··· = not determined.

TABLE 5. Stimulation of sporangium formation on mycelial mats of *Phytophthora cinnamomi* and *Phytophthora citricola* in bark and peat extracts at pH 6.0 and 4.0

pH of solutions	Test solutions[z]	Average number of sporangia produced per 0.5 cm² edge area during the specified time of incubation in test solutions[y]									
		P. cinnamomi					*P. citricola*				
		Source I		Source II			Source I		Source II		
		24 hr	72 hr	13 hr	48 hr	72 hr	24 hr	72 hr	24 hr	48 hr	72 hr
6.0—6.5	NS Pine bark	85 b	510 b	0 a	54 ab	102 ab	···	···	···	1,775 b	···
	PEL Pine bark	27 a	118 a	10 a	3 ab	11 ab	···	···	···	···	···
	FS Pine bark	0 a	0 a	0 a	0 a	0 a	···	···	···	449 a	···
	NS Hardwood bark	···	···	0 a	377 c	907 d	···	···	···	···	···
	PEL Hardwood bark	···	···	7 a	35 ab	170 b	···	···	···	···	···
	FS Hardwood bark	···	···	0 a	0 a	0 a	···	···	···	···	···
	NS Peat	···	···	0 a	106 b	617 c	···	···	···	1,875 b	···
	PEL Peat	···	···	21 a	26 ab	87 ab	···	···	···	···	···
	FS Peat	···	···	0 a	0 a	0 a	···	···	···	433 a	···
	Sterile water	0 a	0 a	0 a	0 a	0 a	···	···	···	313 a	···
4.0	NS Pine bark	36 b	468 b	0 a	0 a	···	473 b	1,067 b	12 ab	···	98 b
	PEL Pine bark	9 a	135 ab	0 a	0 a	···	···	···	···	···	···
	FS Pine bark	0 a	0 a	···	···	···	0 a	6 a	1 a	···	5 a
	Sterile water	0 a	0 a	0 a	0 a	···	0 a	0 a	0 a	···	0

[y] Means in the same column followed by the same letter are not significantly different, $P = 0.05$, according to Duncan's multiple range test. The initial pH of pine bark used in source I was 3.8; in source II, 4.5 (see text). ··· = not determined.
[z] NS = nonsterile extract; PEL = pellet of NS extract resuspended in sterile distilled water; FS = Millipore-filter-sterilized extract.

due to excess nutrients, as 5% lima bean extract, a high nutrient solution, could stimulate formation. Bark may affect some other aspect of the fungus life cycle (eg, movement, survival, or encystment of zoospores; germination of chlamydospores; or growth under nonsterile conditions) that may be more important than those we studied in explaining disease suppression with bark media. Physical characteristics of media not defined in our study also may be involved in suppression. For example, matric potential, which involves more than simple drainage and aeration porosity, is a major influence in sporangial formation and zoospore release (21).

It is important to obtain a full description and background information on the bark used as a medium in host infection and laboratory studies, but this information is not often available. PB from Windsor, NC, was used exclusively in the present study except when pine bark from both sources was tested for sporangial formation. Small wood fragments were mixed in with the bark. Hoitink (13) and others have observed loss of root rot suppression in bark with attached wood. The two pine bark sources (PB and PB1) differed in pH values (4.5 and 3.8, respectively). Wood has a higher pH than bark (24) and would tend to raise the overall pH. Differences in pH may also indicate differences in pine species makeup (24), age of the tree (23), height of the tree where bark was collected (17,24), or length of aging time after collection (12). Although PB1 and PB were similar in the chemical or nutrient components responsible for inhibition of sporangium formation by *P. cinnamomi* (eg, 90% inhibition in sterile extracts of either), they differed in their ability to induce sporangia under nonsterile conditions, suggesting that they differed biologically. *Pseudomonas* spp. have been implicated in stimulating sporangial production by *P. cinnamomi* (1). Soils also differ in capacity to induce sporangial production; seasonal differences with the same soil have been observed (3,26). Hoitink (16) found that batches of HBC vary in suppression. A new line of study is suggested by the possibility that the variables that affect pH can result in differences in disease suppression among pine bark sources.

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