Sustenance of Microbial Activity in Potting Mixes and its Impact on Severity of Pythium Root Rot of Poinsettia

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ABSTRACT

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Potting mixes prepared with Canadian sphagnum peats varied in suppressiveness to Pythium root rot of poinsettia caused by *Pythium ultimum*. Root rot and population development of *P. ultimum* were highest in the most decomposed, dark (H_4 on the von Post decomposition scale) peat, intermediate in a slightly decomposed (H_3) peat, and suppressed in the least decomposed light (H_2) peat. Microbial activity, based on the rate of hydrolysis of fluorescein diacetate (FDA), was highest in the suppressive and lowest in the conducive potting mixes. In mixes prepared with the slightly (H_3) and most decomposed (H_4) peats, microbial activity declined with time, whereas the population density of *P. ultimum* increased, and root rot developed. In a mix prepared with the least decomposed (H_2) peat and in a composted pine bark-amended mix, microbial activity and suppression were sustained throughout the growth period. Populations of *P. ultimum* and Pythium root rot were suppressed as long as the rate of hydrolysis of FDA was sustained above a level of 3.2 $\mu g\ min^{-1}\ g^{-1}$ dry weight potting mix. Suppression was negated by heating, suggesting that the effect was biological in origin. Both the microflora in and the microbial carrying capacity of the peat contributed to sustained suppression.

Until recently, potting mixes prepared with sphagnum peat as the sole source of organic matter have been considered conducive to diseases caused by soilborne plant pathogens such as *Pythium* species (12). Addition of mature composts prepared from tree bark (2,8,11), municipal sewage sludges (13,22,29), separated cattle manure, and grape pomace (4,5,15,17,23,24) to peat mixes increases microbial activity and induces microbiostasis and suppression to Pythium root rot and damping-off (1,3,24). A number of microorganisms in compost-amended mixes may play a role in the suppression of Pythium root rot (20,34), as was described also for soil (9). Rhizosphere bacteria able to grow at high rates at both high and low nutrient concentrations (facultative oligotrophs) are most effective as seed inoculants for biological control of Pythium damping-off (34). "General suppression," as described by Cook and Baker (6), best explains this mechanism of biological control of damping-off caused by *Pythium* spp. in compost-amended substrates (1,3,24).

Slightly decomposed light-colored sphagnum peat, harvested from the surface of bogs, may be suppressive to damping-off and root rot caused by various soilborne plant pathogenic fungi, including *Pythium* spp. (35,40). The suppressive effect of these peats may last for up to 7 wk after potting.

In this paper, we examine interactions between sphagnum peat decomposition level, changes in microbial activity in the potting mix with time, and suppression of the population of *Pythium ultimum* Trow and of Pythium root rot during production of poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch 'Rochford'). Suppressiveness of potting mixes prepared with Canadian sphagnum peat differing in decomposition level is compared with that of a composted pine bark-amended mix consistently suppressive to the disease.

MATERIALS AND METHODS

Preparation of potting mixes. Four potting mixes that differed in suppressiveness to Pythium damping-off were used. Three mixes were prepared with Canadian sphagnum peat (Premier Peat Moss Ltd., Rivière-du-Loup, Québec, Canada) and perlite. The first of these mixes was prepared with a dark-colored, decomposed peat, classified as H_4 on the von Post decomposition scale (28), and the others with light-colored, slightly decomposed (H_2 and H_3) peats. These mixes were prepared by blending peat and coarse horticultural grade perlite (1:1, v/v) with 7.1 g of $CaCO_3$ (<0.15 mm), 1.1 g of superphosphate, 1.1 g of KNO_3 and 1.1 g of gypsum per liter. Water was added during mixing (3 min) in a cement mixer to raise the moisture level to 50% (w/w). Mixes were stored 14 days at 24 C. Acidity at the time of planting and throughout the growth period ranged from pH 5.5 to 6.2. The fourth mix, which was a composted pine bark-amended mix, contained composted pine bark (45%, v/v), Canadian sphagnum peat (H_3–H_4), vermiculite, and coarse horticultural grade perlite (Ball Seed Company, West Chicago, IL). The air capacity of all mixes was at least 15% (v/v) in a 10-cm tall pot. Percolation rates were greater than 2 cm/min.

Preparation of inocula. Isolate 211 of *P. ultimum*, which was originally isolated from poinsettia (33) was used throughout this study. Two procedures were used to prepare inoculum. Inoculum referred to hereafter as "soil inoculum" was prepared as described previously (2) using Ko and Hora's chopped potato soil medium (18). Inoculum referred to as "peat inoculum" was prepared by planting cucumber (*Cucumis sativus* L. 'Straight Eight', 90% germination) seeds in a sterilized sphagnum peat (H_4) mix infested with *P. ultimum* soil inoculum (1.0 g/L). Pots were irrigated daily and incubated 10 days at a constant temperature of 20 C with 16 h of illumination (225 $\mu E\ m^{-2}\ s^{-1}$) per day. Cucumber seedlings that survived were removed, and a second crop was planted. Cucumber plant residues were removed, and the infested mix was air-dried overnight and ground with a mortar

and pestle. Particles were sieved, and 1- to 2-mm particles were used as peat inoculum.

Cucumber bioassay. Potting mixes were placed into plastic bags, amended with 2.5 g of slow release fertilizer (Osmocote 14-14-14, Grace-Sierra Chemical Co., Milpitas, CA) and infested with 0.5 g/L of *P. ultimum* soil inoculum as described previously (2). Controls included autoclaved (1 h, 121 C) mixes with and without *P. inoculum*. Bags were shaken vigorously to ensure uniform distribution of the inoculum and fertilizer. Infested mixes were distributed into five disposable styrofoam pots (400 ml per pot) that had perforated bases to allow adequate drainage. Eight cucumber seeds were planted 1 cm deep in each of the pots. The pots were then placed randomly into a growth chamber set to provide identical conditions as those described above. Disease severity was rated 10 days after planting according to the following scale: 1 = symptomless; 2 = emerged but wilted, chlorotic, or with visible lesions on hypocotyl; 3 = postemergent damping-off; and 4 = pre-emergent damping-off. A mean disease severity of eight seedlings per pot was calculated to represent one treatment replication (five replicates per treatment). Diseased seedlings and nongerminated seeds were surface-sterilized in 1% sodium hypochlorite (30 s), rinsed twice in sterile distilled water, and placed on semi-selective sucrose asparagine-pentachloronitrobenzene benomyl neomycin sulfate chloramphenicol (SA-PBNC) agar for reisolation of the pathogen (30). Randomly selected hyphal tips were transferred to lima bean agar (Difco Laboratories, Detroit, MI) to verify pathogen identity. Middleton's description of *P. ultimum* was used to identify isolates (25).

Poinsettia root rot bioassay. Poinsettia cuttings rooted in Oasis cubes (Smithers Oasis, Kent, OH) were planted in 1.2-L plastic pots. Before planting, all potting mixes were infested with 0.15 g/L of peat inoculum. Control treatments were not infested. Each pot was filled with potting mix diagonally from the bottom in one side to the top of the other side to approximately 66% of the pot's capacity. Next a double layer of nylon fabric (0.3-mm mesh) was placed on the surface of the potting mix. This fabric prevented the root system from completely ramifying the potting mix. During planting, a small volume of noninfested mix (50 ml) was added immediately around each rooted cutting. This prevented direct contact of inoculum with root tips damaged during transplanting. The remaining volume of the pot was then filled.

Plants were grown in a greenhouse with naturally occurring photoperiods and were irrigated daily. Fertilizer (200 mg/L of Peters 20-20-20, Grace-Sierra Chemical Co., Milpitas, CA) was applied twice weekly. Five plants from each treatment were harvested at various times throughout the growth period. During harvesting, potting mix associated with the root system was dissociated gently with the pot label. Root segments suspected of being infected with *P. ultimum* were removed for reisolation of the pathogen. The root ball was then gently submerged into tap water to remove additional potting mix residues, and plants were rated for root rot severity as described below. Pathogen identity was verified as described for the cucumber bioassay.

Three poinsettia root rot bioassays were performed. The first two were similar. The same batches of light peat (H_3), dark peat (H_4), and composted pine bark-amended potting mix were used in each. Both bioassays were conducted during the late summer and fall when potting mix temperatures ranged from 18 to 25 C. Poinsettia plants were harvested at 4, 14, 35, 63, and 88 days after planting during bioassay 1, and at 4, 14, 28, 35, 42, 63, and 77 days after planting during bioassay 2. In both bioassays, root rot severity was rated using a scale in which 1 = symptomless; 2 = mild root rot; 3 = severe root rot; 4 = severe root rot and crown infection; and 5 = dead plant.

The third poinsettia bioassay was performed between March and June, when potting mix temperatures ranged from 19 to 27 C. The least decomposed source of light peat (H_2), the dark peat (H_4) mix, and a different batch of composted pine bark-amended potting mix were used. Although the peat potting mixes were prepared as those described in the first two bioassays, the moisture contents of the mixes were not as high (40%, w/w). Plants were harvested at 4, 10, 17, 24, 45, 63, and 77 days after planting. Root rot severity was rated using a revised scale in which 1 = symptomless; 2 = mild root rot (<one-third of roots rotted); 3 = intermediate root rot (between one-third and two-thirds of roots rotted); 4 = severe root rot (>two-thirds of roots rotted); 5 = severe root rot and crown infection; and 6 = dead plant. This experiment was repeated once.

***P. ultimum* population density.** The population density of *P. ultimum* was determined on SA-PBNC agar using a soil surface dilution plating technique (30). A 2.0-g sample of each of the mixes was added to 20 ml of dilute water agar (0.4%) and homogenized for 1 min using a Waring blender. Successive 10-fold dilutions were made, and 0.2-ml aliquots of each dilution were plated in triplicate on SA-PBNC medium. Plates were incubated 48 h at 25 C and rinsed gently with tap water to remove any remaining potting mix residues. The number of colony-forming units (cfu) of *P. ultimum* per gram dry weight mix was recorded. This procedure was replicated three times for each potting mix sample.

Microbial activity. Microbial activity was monitored by measuring the rate of hydrolysis of fluorescein diacetate (FDA, Sigma Chemical Co., St. Louis, MO) (14,31). FDA was dissolved in acetone and stored as a stock solution (2.0 mg/ml) at −20 C. Potting mix samples were collected at each harvest date from just beyond (approximately 2 cm) the growing root systems, below the nylon fabric, or the bottom 5 cm of the pot during the late stages of plant growth. All visible root segments were removed from potting mix samples. Five-gram samples of each potting mix were placed into 250-ml Erlenmyer flasks, and 20.0 ml of 60 mM potassium phosphate buffer, pH 7.6 (8.7 g of KH_2PO_4 and 1.3 g of K_2HPO_4 per liter distilled water) was added. The reaction (FDA hydrolysis) was started by adding 0.2 ml of FDA (400 μg) from the stock solution to the flask. Each treatment was replicated four times with a control to which FDA had not been added. Reaction flasks were incubated for 20 min on a rotary shaker (90 rpm) at 25 C. FDA hydrolysis was halted by addition of 20 ml of acetone to each of the reaction flasks. Potting mix residues were removed from the mixture by filtration through filter paper (Whatman No. 1). The filtrate was collected in a test tube, covered with Parafilm (American Can Co., Greenwich, CT), and placed into an ice bath to reduce volatilization of the acetone. The concentration of free fluorescein was determined spectrophotometrically with an HP 8452A Diode-Array Spectrophotometer (Hewlett-Packard Co., Palo Alto, CA) and by comparing absorbancies (490 nm) against a standard curve. Background absorbance was corrected for each treatment with the control sample.

Standard curves were prepared in duplicate for each treatment at each harvest date to avoid serious errors caused by adsorption of fluorescein to organic matter, particularly in the more decomposed (H_4) peat mixes (14). Various quantities of FDA (0, 100, 200, 300, and 400 μg in the stock solution) were added to 5.0 ml of phosphate buffer in screw-cap tubes. Tubes were capped tightly and incubated for 60 min in boiling water to hydrolyze the FDA. Cooled fluorescein was then added to 250-ml Erlenmyer flasks containing 5.0 g samples of the various potting mixes. An additional 15.0 ml of phosphate buffer was used to wash the fluorescein from the tubes into the samples. Flasks were then shaken 20 min on a rotary shaker (90 rpm) at 25 C, after which 20 ml of acetone was added. Finally, the samples were filtered and processed as described above.

Experimental designs and statistical analyses. Completely randomized designs were used in all cucumber bioassays. Each treatment was replicated five times (five pots per treatment). Randomized complete block designs were used in all poinsettia bioassays. Treatments were replicated five times (five pots per treatment) per harvest date. One-way analyses of variance (ANOVA) were preformed with Minitab statistical software (Minitab Inc., State College, PA). Separations of means were based on the least significant difference (LSD, $P = 0.05$).

Overall relationships between root rot severity, pathogen densities, and microbial activity were assessed using ordinary least squares regression. Regression analyses also were performed with Minitab statistical software. Standardized residuals of data used in regression analyses were plotted to check for normality of the data and to ensure that errors were randomly, independently, and normally distributed with a common variance.

RESULTS

Variability in suppressiveness of Canadian sphagnum peat to Pythium damping-off of cucumber. Pythium damping-off was suppressed consistently in three cucumber bioassays that were conducted with the least decomposed light peat (H_2) mix. Disease severity values in this mix ranged from 1.4 to 1.7. Disease severity values in the dark peat (H_4) mix ranged from 2.7 to 3.2, which is significantly higher ($LSD_{0.05} = 0.8$). The disease severity values in the noninfested and infested controls were 1.1 and 3.7, respectively.

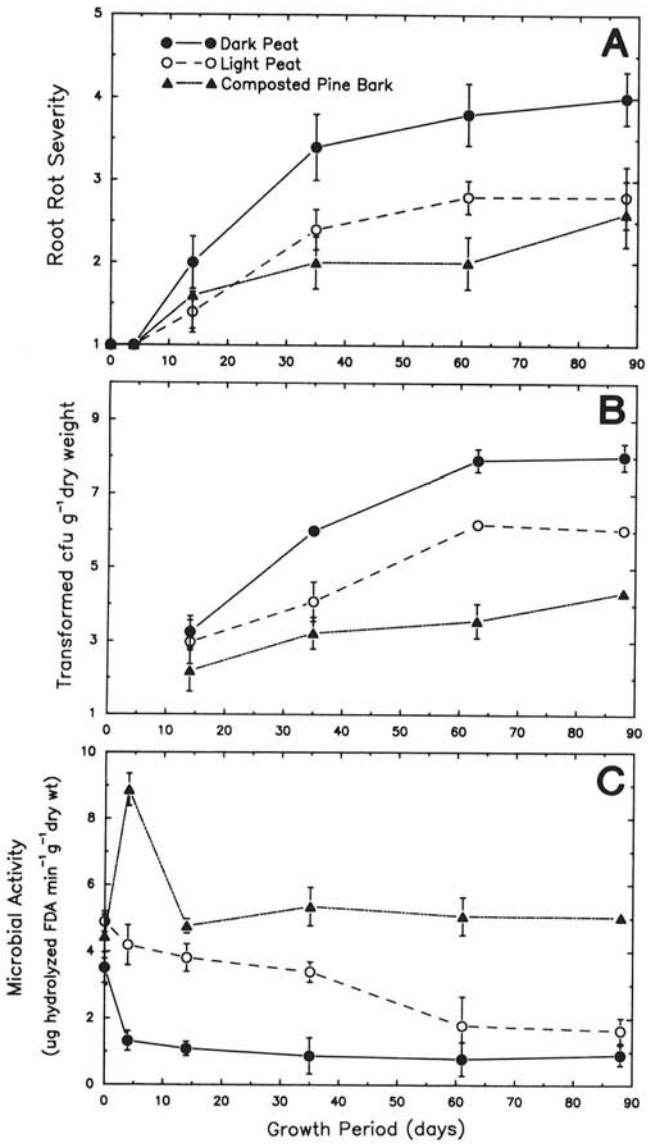

Fig. 1. Comparison of Pythium root rot severity, population density of *Pythium ultimum*, and microbial activity in a light (H_3) and a dark (H_4) peat mix and a composted pine bark-amended potting mix. **A,** root rot severity; 1 = symptomless, 2 = mild root rot, 3 = severe root rot, 4 = severe root rot and crown infection, and 5 = dead plant. Vertical bars represent standard errors ($n = 5$). **B,** population density of *P. ultimum*. Population density data was transformed using Taylor's power law ($b = 0.76$). Vertical bars represent standard errors ($n = 3$). **C,** microbial activity based on the rate of hydrolysis of fluorescein diacetate. Vertical bars represent standard errors ($n = 4$).

Poinsettia root rot bioassays 1 and 2. *Root rot severity.* In the first bioassay, symptoms of Pythium root rot were evident 14 days after potting in all infested treatments. Root rot severity (mean = 2.0) did not differ significantly ($P = 0.05$) among the potting mixes at this time (Fig. 1A). By 35 days after planting, roots in the dark peat (H_4) mix had a higher level of rot (mean = 3.4) than those in either the light peat (H_3) (mean = 2.4) or the composted pine bark-amended mix (mean = 2.0), respectively. Plants in the dark peat (H_4) mix had higher levels of root rot for the remainder of the growth period. Root rot on plants in the light peat (H_3) mix was intermediate with a maximum mean root rot severity of 2.8. Root rot severity in the composted pine bark-amended mix reached a maximum mean value of 2.6 at the final harvest date. The only significant ($P = 0.05$) differences in root rot severity between plants grown in the light peat (H_3) and compost-amended mixes occurred 63 days after planting, when mean root rot severities were 2.8 and 2.0, respectively.

P. ultimum population density. During the first bioassay, the population density of *P. ultimum* in the mixes did not differ significantly ($P = 0.05$) 14 days after planting (Fig. 1B). Thereafter, the densities in all mixes differed significantly. The population density of *P. ultimum* in the light peat (H_3) mix were significantly ($P = 0.05$) lower than those in the dark peat (H_4) mix. In the composted pine bark-amended mix it was low throughout the duration of the growth period.

Microbial activity. During the first bioassay, microbial activity in the dark peat (H_4) mix at planting was sufficient to hydrolyze 3.52 μg FDA min^{-1} g^{-1} dry weight mix (FDA units) (Fig. 1C). By the fourth day after planting, it had declined significantly ($P = 0.05$) to 1.32 FDA units and remained at this low level for the remainder of the growth period. Microbial activity in the light peat (H_3) and in the composted pine bark-amended mix did not differ initially (4.65 FDA units). By the fourth day after planting, significant differences ($P = 0.05$) were apparent. The relatively high level of microbial activity in the light peat (H_3) mix was sustained during the initial 35 days of the growth period. However, between the 35th and 63rd day of the growth period, a significant decline ($P = 0.05$) occurred. Thereafter, microbial activity in this mix remained at this low level.

A significant increase ($P = 0.05$) in microbial activity occurred in the composted pine bark-amended potting mix during the initial 4 days of the growth period. This high level of activity was transitory and had stabilized by day 14 at 4.77 FDA units. Microbial activity in the composted pine bark-amended mix was consistently higher than that in either of the peat mixes used in this bioassay. In the second poinsettia bioassay, trends in root rot severity, population density of *P. ultimum*, and microbial activity were essentially identical to those observed in the first (Fig. 1).

Poinsettia bioassay 3. In the third bioassay, trends in root rot severity (Fig. 2A), population density of *P. ultimum* (Fig. 2B), and microbial activity (Fig. 2C) in the light (H_2) peat mix were different from those in poinsettia bioassays 1 and 2. Trends in the dark peat (H_4) and the composted pine bark-amended mixes were similar to those observed in the first two bioassays (Fig. 1). In this batch of light peat (H_2) mix, microbial activity was sustained, root rot severity remained mild, and population density of *P. ultimum* remained low throughout the growth period. An increase of microbial activity in this peat (H_2) mix was detected early after planting. This activity was similar to, although significantly lower ($P = 0.05$) in intensity, than that observed in the composted pine bark-amended potting mix.

Relationships between root rot severity, population density of *P. ultimum*, and microbial activity during the production of a poinsettia crop. Increases in root rot severity and population density of *P. ultimum* were observed 28 days after planting and thereafter were negatively correlated with microbial activity (Fig. 3A,B).

DISCUSSION

Microbial activity at planting in both compost-amended and sphagnum peat potting mixes have been used to predict damping-off severity of cucumber caused by *P. ultimum* (1,14). A similar relationship has been described for suppression of damping-off of cucumber caused by *Pythium aphanidermatum* (Edson) Fitzp. (23). The results of this work indicate that microbial activity over time also predicts potting mix suppressiveness to Pythium root rot of poinsettia. A decrease in microbial activity during the production of the crop was accompanied by an increase in the population density of *P. ultimum* and root rot severity. At low levels of microbial activity, the concentration of water-soluble root exudates apparently was sufficient to stimulate germination of *P. ultimum* propagules, infection of roots, and development of root rot (3,9,23,32).

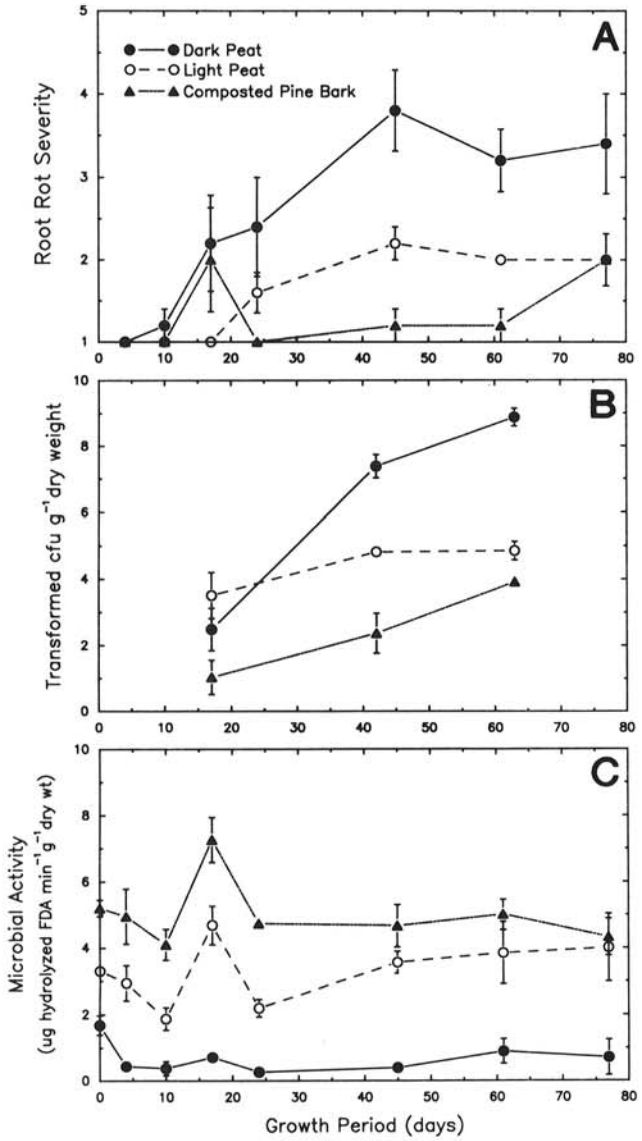

Fig. 2. Comparison of Pythium root rot severity, population density of *Pythium ultimum*, and microbial activity in a light (H_2) and a dark (H_4) peat mix and a composted pine bark-amended potting mix. **A,** root rot severity; 1 = symptomless, 2 = mild root rot (<one-third of roots rotted), 3 = intermediate root rot (between one-third and two-thirds of roots rotted), 4 = severe root rot (>two-thirds of roots rotted), 5 = severe root rot and crown infection, and 6 = dead plant. Vertical bars represent standard errors ($n = 5$). **B,** population density of *P. ultimum*. Population density data was transformed using Taylor's power law ($b = 0.76$). Vertical bars represent standard errors ($n = 3$). **C,** microbial activity based on the rate of hydrolysis of fluorescein diacetate. Vertical bars represent standard errors ($n = 4$).

The most suppressive mixes were prepared with the least decomposed sources of organic matter (i.e., composted pine bark-amended or the H_2 decomposition level sphagnum peat mixes). The highest populations of *P. ultimum* and root rot developed in the mixes prepared with the most decomposed (H_4) peat. In the mix prepared with the H_3 decomposition level peat, a shift from suppressiveness to conduciveness was observed. Therefore, organic matter decomposition level was inversely related to microbial activity and directly related to root rot severity. Finally, populations of *P. ultimum* and Pythium root rot were suppressed as long as the rate of hydrolysis of FDA was sustained above a level of 3.2 $\mu g\ min^{-1}\ g^{-1}$ dry weight potting mix.

Sphagnum peats harvested from increasing depths in bogs increase in decomposition level and decrease in ability to support growth of heterotrophic microorganisms (38). Kuster concluded in 1963, that "the more decomposed, humified, and carbonized the carbon material in peat, the smaller the content of utilizable compounds, and the less available they become for microbes" (19). The term "microbial carrying capacity" best describes this effect. The microbial carrying capacity of a potting mix depends on the decomposition level of the organic components used in the potting mix. During the past two decades, this property of potting mixes and field soils has eluded scientists interested in biological control. For diseases caused by exogenously nutrient-dependent plant pathogens, such as *P. ultimum*, that are suppressed through microbiostasis (3,23), this lack of knowledge is unfortunate. It has not been possible so far, to quantify the energy availability in or the carrying capacity of soil organic matter.

Recent breakthroughs in direct spectroscopy, utilizing cross-polarized magic angle spinning Carbon-13 nuclear magnetic resonance, have permitted nondestructive analysis of the decomposition of carbohydrates in composts (16,26), sphagnum peat (10,27,39), and other sources of soil organic matter. As a result, direct relationships among organic matter decomposition

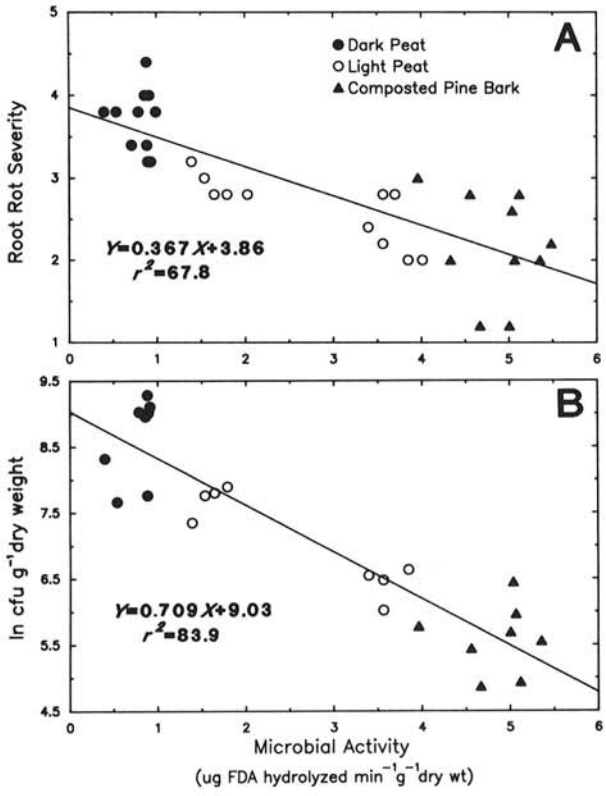

Fig. 3. Relationships between root rot severity, population density of *Pythium ultimum*, and microbial activity during the production of a poinsettia crop. **A,** root rot severity versus microbial activity. **B,** population density of *P. ultimum* versus microbial activity. Population density data was transformed to natural logarithm.

level, microbial carrying capacity, microbial activity, microbial biomass, the nutritional status of the microflora, and disease severity can now be developed. Potting mixes prepared with slightly decomposed (H_3) sphagnum peat offer unique opportunities to explore these fundamental interactions.

The population density of *P. ultimum* did not decline with time in any of the suppressive mixes used in these studies, which is consistent with earlier observations (3,23). Eradication, therefore, may not have played a major role in the suppressive effect in these mixes, although *Pythium* populations may have produced several generations so that rates of regrowth approximately equaled rates of eradication. Disregarding this possibility, we propose that microbiostasis resulting from nutrient competition was the principal mechanism of biological control involved in the suppressive sphagnum peat and composted pine bark-amended potting mixes, as was described previously for other compost-amended mixes (3,23).

Quantitative information on the contributions of specific biocontrol agents in suppression of Pythium root rot in peat mixes is sparse. Suppressiveness was destroyed by heating and restored after the addition of small amounts of light-colored peat, which suggests that the effect is biological. Addition of 25% (v/v) suppressive light (H_2) to conducive, dark (H_4) peat does not induce suppression to damping-off caused by *P. ultimum* (21). The conducive nature of the decomposed dark peat (H_4), therefore, is not due to the absence of biocontrol agents. During harvesting, peat routinely is stored in large piles or windrows, where temperatures within the piles, due to self-heating, are often high enough to kill mesophilic microorganisms. The microflora in processed peat, therefore, is influenced not only by the decomposition level but also by the procedures employed during processing (7). *Trichoderma viride* Pers. ex Fr., *Penicillium* spp., *Chrysosporium* spp., and *Streptomyces* spp. have been proposed as biocontrol agents involved in suppression of Pythium damping-off in Scandinavian sources of light-colored sphagnum peat (35,36,37,40,41). The acidity of sphagnum peat at harvest is too great (pH 3.0–4.7) to support growth of most bacteria. During the formulation of peat mixes, when the acidity is decreased to pH 5.5–6.2, and bacterial growth is no longer inhibited, a mild biological vacuum is created. Changes in microbial populations in peat that occur after formulation have been poorly described. The greatest potential for population development is in mixes prepared with the least decomposed peats, because these peats have the greatest microbial carrying capacity. The short-duration peaks in microbial activity observed in this work within days after planting in the least decomposed light (H_2) peat and the composted pine bark-amended mix support this observation. In conclusion, variability in suppressiveness reported for sphagnum peat in the past probably is attributable to both the composition of the microflora and the carrying capacity (decomposition level) of the peat.

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