Nonphytotoxic Aluminum-Peat Complexes Suppress *Phytophthora parasitica*

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ABSTRACT

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Amendment of peat-based potting media with $\text{Al}_2(\text{SO}_4)_3$ suppresses damping-off of Vinca (*Catharanthus roseus*) caused by *Phytophthora parasitica*. The species of aluminum (Al) responsible for disease suppression have not been identified. The objective of this study was to determine the effects of amount and pH of $\text{Al}_2(\text{SO}_4)_3$ amendment solutions on survival of *P. parasitica*. In separate experiments, peat was amended with $\text{Al}_2(\text{SO}_4)_3$ solutions adjusted to pH 4 or 6 at either 0.0158 or 0.0079 g of Al per gram of peat. Amended peat was placed in Büchner funnels maintained at -2.5 kPa matric potential. Peat was infested with *P. parasitica* by placing zero, two, or five colonized Vinca leaf disks in each funnel, and 15 Vinca seeds were placed in each funnel. After 24 h, the matric

potential was brought to 0 kPa to induce zoospore release and returned to -2.5 kPa after 24 h. Pathogen populations and stand counts were assessed after 2-week incubation. Al amendment solutions at both pH 4 and 6 reduced pathogen populations at 0.0158 g of Al per gram of peat. Solutions at pH 4 reduced pathogen populations by more than 90% at both inoculum levels; amendment solutions at pH 6 reduced populations by 95% at the low inoculum level and 65% at the high inoculum level. The prevalence of $\text{Al}(\text{OH})_2^+$ in peat amended with $\text{Al}_2(\text{SO}_4)_3$ solution at pH 6 suggests that ions other than Al^{3+} may be responsible for pathogen suppression. Based on the difference in chemical conditions of Al-amended peat and suppressive mineral soils, the mechanism of Al-mediated suppression of plant pathogens is speculated to be different in the two systems. Peat containing Al-peat complexes was chemically suppressive to *P. parasitica* and may confer Al-mediated suppression of plant pathogens with a nonphytotoxic form of Al.

Abiotic suppression of plant pathogens by high levels of exchangeable aluminum (Al) has been described in numerous acid mineral soils. Examples of pathogens suppressed by Al include *Streptomyces scabies* (28), *Rhizoctonia solani* (20), *Fusarium solani* (14), *Verticillium albo-atrum* (30), *Thielaviopsis basicola* (25–27), *Aspergillus flavus* (13), *Neurospora tetrasperma* (21), and multiple *Phytophthora* spp. (2–4,29). Applications of this Al-mediated suppression have been limited, however, primarily because of potential phytotoxic effects of Al in mineral soil (32). Studies on disease suppression focused on levels of free ionic Al (Al^{3+}), the most prominent dissolved Al species at pH < 4.5. However, Al exists in soil as multiple chemical species, including the pH-dependent hydrolysis species $\text{Al}(\text{OH})_2^+$, $\text{Al}(\text{OH})_2^+$, $\text{Al}(\text{OH})_3^0$, and $\text{Al}(\text{OH})_4^-$, referred to as monomeric Al species (33), Al_{13} polymers (17), and organically complexed Al (5). Studies have quantified the toxicity of these Al species to plants (18,33,38), but the influence of Al species other than Al^{3+} on fungi is largely unknown.

Al-mediated pathogen suppression has also been observed in a peat-based potting medium (3), where the organic fraction controls the activity of dissolved Al (6). Suppression of *Phytophthora parasitica*, the causal agent of pre- and postemergence damping-off of Vinca (*Catharanthus roseus*), was observed at pH > 6, with low levels of exchangeable Al (3). In this pH range, the $\text{Al}(\text{OH})_2^+$ is the primary species in solution (23), and it preferentially binds to organic matter over the Al^{3+} species (6). The prevalence of organically complexed Al and Al hydrolysis species in this system suggests that Al^{3+} is not solely responsible for pathogen and disease suppression.

Addition of organic matter to acid soils decreases the phytotoxicity of Al by reducing the activity of Al in the soil solution (38). Because Al binds more strongly to soil organic matter than to the permanent charge sites in a mineral soil (6,8), it was thought to form chelation complexes with aromatic, carboxylate, and hydroxide groups of soil organic matter (37). Titration and electron spin resonance studies, however, suggest that metal ions, including Cu, Mn, and Al, do not form chelation complexes with functional groups on H-saturated peat and humic acid (5). Most metals, except Cu^{2+} (10), form outer-sphere (hydrated) complexes with the variable charge carboxylic acid sites of organic matter (5). Because these acid groups have a pH-dependent charge, the binding of Al varies directly with pH (5,15,16). Hydrolyzed Al ions bind more strongly than Al^{3+} to organic matter (6,16), and the relationship between pH and Al adsorption can be modeled with the assumption that 1 mol of Al is bound per mole of carboxyl groups (5).

In aqueous solution, the ability of an organic ligand to reduce Al phytotoxicity is related to the stability of Al-ligand complexes (7). Weak Al complexers, such as phenolics and catechol compounds, have no effect on Al toxicity to plants (7). Short-chained carboxylic acids, however, range from strong to weak in their ability to complex Al (7,18). Al toxicity to plants is reduced if Al is strongly bound to soil solids such as organic matter, or if dissolved organic ligands form stable complexes with dissolved Al. The effects of solid-phase and dissolved Al complexes on suppression of soilborne pathogens have not been quantified.

This research focused on the suppression of *P. parasitica* in peat with organically complexed Al. The objectives of this study were to (i) determine the Al binding capacity of peat, (ii) assess the efficacy of Al amendment solutions at pH 4 and 6 for control of *P. parasitica* in an organic medium, and (iii) characterize suppression of the pathogen due to physical factors of the peat matrix.

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MATERIALS AND METHODS

Peat preparation. A dark, commercial grade of Canadian sphagnum peatmoss (Fertiloam, Quebec, Canada) was passed through a sieve with 2 mm openings and stored dry for subsequent use in all experiments. The pH of the peat was 3.1 before liming.

Estimation of Al binding capacity. A titration procedure, based on that of Martin and Reeve (24), was used to estimate the number of acid functional groups in the peat that could potentially bind Al. One gram of peat was suspended in 100 ml of 0.05 M NaCl solution. Peat was solubilized by the addition of 0.1 M KOH to pH 11, and the suspension was titrated to pH 3 with the gradual addition of 0.05 M HCl. Nitrogen gas was bubbled through the suspension during the titration, and pH values were determined with a glass, Ross combination pH electrode attached to an Orion PerpHect LogR meter (Fisher Scientific Co., Norcross, GA). The background solution also was titrated in the absence of peat. The titration was repeated twice with similar results, and an average of the two titrations was used in subsequent calculations. Proton consumption by peat was calculated by subtracting the amount of H^+ entering solution in the titration of the background solution from the amount of acid added in the peat titration.

Inoculum production. An isolate of *P. parasitica* (isolate 2155, provided by D. M. Benson, North Carolina State University, Raleigh) obtained from diseased Vinca plants was used as inoculum in all experiments. Leaf disks (1-cm diameter) were cut from mature *C. roseus* cv. Little Bright Eyes plants with a cork borer, placed in a 250-ml beaker containing 100 ml of water and a drop of Tween 80 (Fisher, Norcross, GA), and autoclaved for 30 min on 2 consecutive days. The sterilized leaf disks were placed on cultures of *P. parasitica* on corn meal agar (Difco Laboratories, Detroit) and incubated for 5 days at room temperature. The colonized leaf disks were removed and used as inoculum. Inoculum levels were varied by adding different numbers of colonized leaf disks to peat contained in Büchner funnels.

Effects of Al amendment on pathogen populations. Two experiments were conducted to study the effect of Al on populations of *P. parasitica*. In the first experiment, a 0.05 M $Al_2(SO_4)_3$ solution was adjusted to pH 4, in which Al^{3+} is the dominant aqueous Al species (23). In the second experiment, a 0.05 M $Al_2(SO_4)_3$ solution was adjusted to pH 6, in which $Al(OH)_2^+$ is the dominant aqueous Al species (23). The pH adjustments were made by adding 1 N KOH. In both experiments, 140 g of sieved peat was placed in each of three plastic bags and mixed thoroughly with $Ca(OH)_2$ at a rate of 0.024 g g^{-1} air-dry peat. The addition of lime ensured that Ca would not be limiting in the system and raised the pH from 3.1 to 4.7. Limed peat was moistened and allowed to equilibrate for 2 days. Peat was amended with three levels of Al (0, 0.0079, or 0.0158 g of Al per gram of peat) by varying the amount of a 0.05 M $Al_2(SO_4)_3$ solution added to each bag of peat medium. Deionized water was added to achieve a uniform final volume of water (6.8 ml g^{-1} of peat) in each treatment. Each peat suspension was mixed in a separate plastic bag and incubated at room temperature for 2 days to allow complexation of Al.

Each experiment was a complete factorial with three Al levels (0, 0.0079, and 0.0158 g of Al per gram of peat) and three inoculum levels (0, 2, or 5 infested leaf disks) in a completely randomized design with four replicate funnels of each treatment. Water-saturated, amended peat was placed in 150-ml fritted-glass Büchner funnels (Fisher Scientific) and was allowed to drain to -2.5 kPa matric potential (ψ_m), with respect to the peat surface, by use of hanging water columns. Peat was packed to an average bulk density (D_b) of 0.12 g cm^{-3} , resulting in a 3 cm depth of peat in each funnel. After draining for 6 h, the top 1 cm of peat was removed from each funnel to obtain samples for chemical analysis, and infested leaf disks and 15 Vinca seeds were placed in each funnel. Inoculum and seed were then covered with the remainder of the previously removed peat, and funnels were covered with

plastic bags to prevent evaporation. After incubating seed for 24 h, zoospore release was induced by raising the free-water surface to achieve a ψ_m of 0 kPa (flooding) with respect to the peat surface (22). The water saturation of peat was maintained for 24 h, and the peat was returned to $\psi_m -2.5$ kPa for the duration of the experiment.

Two weeks after planting, stand counts and pathogen populations were assessed. The contents of each funnel were placed in individual plastic bags, mixed thoroughly, and a 1-g sample of peat was taken from each bag and suspended in 25 ml of deionized water. Each suspension was spread over five plates of PARP selective medium (19) containing 50 $\mu g/ml$ of hymexazol (Sankyo Co., Tokyo) and incubated in the dark for 2 days. Plates were then rinsed with deionized water and the colonies of *P. parasitica* were counted. Data were analyzed using the general linear models procedure, and treatment differences were determined with a Waller-Duncan K-ratio test ($K = 100$) (SAS Institute, Cary, NC). Each experiment was run twice.

Exchangeable Al and pH determination. Peat samples, 3 g each, were removed from each funnel at the time of planting (initial) and 2 weeks after planting (final). Two samples, one for exchangeable Al analysis and one for pH determination, were taken from each funnel. KCl-exchangeable Al was determined with a modified acid-base titration procedure (39). Each peat sample was suspended in 25 ml of a 1 M KCl solution for 2 h, filtered through Q5 filter paper (Fisher Scientific), and rinsed three times with 25 ml of 1 M KCl. Ten drops of phenolphthalein solution was added to each extract, and extracts were titrated with 0.1 M NaOH to a pale pink endpoint. A drop of 0.1 M HCl was added to return solution to colorless, and then 10 ml of 4% NaF was added. In the presence of Al, a stable fluoaluminate complex forms and the pink color returns. Extracts were titrated to a clear endpoint with 0.1 M HCl. Three moles of H^+ titrate 1 mol of exchangeable Al (39). The pH was determined in a 1:2 (wt/vol) suspension of peat in 0.01 M $CaCl_2$ solution (35). A two-tailed t test was used to compare initial and final values for both exchangeable Al and pH within each Al treatment.

Effect of counter anion on pathogen population. A complete factorial treatment design with two sources of Al, 0.05 M $AlCl_3$ and 0.05 M $Al_2(SO_4)_3$ amendment solutions, adjusted to pH 4 and 6, was used to determine the effect of Cl^- and SO_4^{2-} on pathogen population. Peat was amended with 0.0158 g of Al per gram of peat, and two infested Vinca leaf disks were placed in each funnel. Each treatment contained four replicates in a completely random design, and the experiment was run twice. The activities of Al^{3+} and monomeric Al species in each amendment solution were predicted using GEOCHEM-PC (31), a chemical speciation program. The above procedures for peat amendment, chemical analysis, pathogen population assessment, and data analysis were repeated in this experiment. Correlation between exchangeable Al and pH was determined by linear regression analysis.

Zoospore movement. The horizontal movement of zoospores through peat was investigated. Peat was saturated with deionized water and placed in Büchner funnels at -2.5 kPa ψ_m . After 6 h, the sieved peat was packed to an average D_b of 0.12 g cm^{-3} to approximate the conditions of Al amendment experiments. The top 0.5 cm of peat was removed from the surface of each funnel, and one infested Vinca leaf disk was placed in the center of each funnel. Two-centimeter long stem segments from greenhouse-grown Vinca plants were used as bait for zoospores. Five bait segments were inserted vertically around the inoculum at either 0.5 or 1.0 cm from the perimeter of the infested leaf tissue. A layer of moist peat was placed over the inoculum, but stem segments were allowed to protrude through the surface for easy removal. Funnels were incubated at -2.5 kPa ψ_m for 24 h, and the ψ_m was increased to 0 kPa to induce zoospore release. After either 24 or 60 h of saturation, funnels were returned to -2.5 kPa ψ_m , and stem segment baits were removed and placed on PARP selective medium

for 4 days in the dark. The number of baits infected with *P. parasitica* from each funnel was determined. The treatment design was a complete factorial with two radial distances, 0.5 and 1.0 cm, and two flood durations, 24 and 60 h. Each treatment had four replicates in a completely random design, and the experiment was con-

Fig. 1. Titration curve of exchangeable acidity for 1 g of peat. The proton consumption was calculated as 1.41 mmol/g of peat in a titration from pH 11 to 3.

Fig. 2. Assays of *Phytophthora parasitica* populations were conducted 2 weeks after planting 15 Vinca seeds in peat amended with $\text{Al}_2(\text{SO}_4)_3$ solutions at pH 4 and infesting peat with either two or five colonized Vinca leaf disks in A and B, two separate experiments. Different letters above bars designate significant differences based on the Waller-Duncan K-ratio test ($K = 100$).

ducted twice. The general linear models procedure was used for data analysis, and treatment differences were determined with a Waller-Duncan K-ratio test ($K = 100$).

Pore-size distribution analysis. A pore-size distribution analysis was conducted to determine whether the largest water-filled pores at various ψ_m values could accommodate zoospore movement in the peat system. Moist peat was placed in Büchner funnels and packed to a D_b of approximately 0.12 g cm^{-3} . Plastic bags were placed over each funnel to prevent evaporation. Funnels were brought to saturation for 24 h, equilibrated at either 0, -1.0 , -2.5 , -5.0 , or $-10.0 \text{ kPa } \psi_m$ with respect to the peat surface using hanging water columns, and allowed to equilibrate for 2 days. One peat sample was removed from each of four replicate funnels and weighed on an analytical balance. Samples were oven dried for 48 h at 105°C , and dry weight was recorded. A soil moisture characteristic was developed by plotting volumetric water content (cm^3/cm^3) versus ψ_m .

A pore-size distribution was calculated by a standard equation (9), with surface tension and density of water taken at 30°C . The water-filled volume fraction of total pore space was plotted against pore diameter (micrometer).

RESULTS

Estimation of Al binding capacity. Proton consumption by peat, determined by titrating with 0.05 M HCl , resulted in two pH-buffering regions (Fig. 1). Adsorption of H^+ was pronounced between pH 11 and 8 and between pH 5 and 3. The proton consumption was calculated as 1.41 mmol g^{-1} of peat between pH 11 and 3. Most H^+ adsorption occurred between pH 5 and 3, with

TABLE 1. Exchangeable aluminum (Al) and pH measurements in peat amended with $\text{Al}_2(\text{SO}_4)_3$ at pH 4 or 6

Soln. pH ^w	Al level (g of $\text{Al}_2(\text{SO}_4)_3$ /g of peat) ^x	Initial exchangeable Al (mmol/g of peat) ^y	Final exchangeable Al (mmol/g of peat) ^y	pH ^z
4.0	0.0079	0.0094	0.0079	4.61
4.0	0.0158	0.0615	0.0586	4.35
6.0	0.0079	0.0003	0.0027*	5.18
6.0	0.0158	0.0010	0.0010	5.39

^w $\text{Al}_2(\text{SO}_4)_3$ solution was speciated at pH 4.0 or 6.0 with 1.0 N KOH .

^x Al levels were determined by the amount of $0.05 \text{ M Al}_2(\text{SO}_4)_3$ added to peat.

^y Levels of exchangeable Al measured by an extraction with 1.0 M KCl followed by titration of exchangeable Al according to the method of Yuan (39). * indicates significant difference ($P \leq 0.05$) between initial and final level of exchangeable Al determined by Student's *t* test.

^z Average pH; measured in 1:2 (wt/vol) suspension of peat in 0.01 M CaCl_2 (35).

Fig. 3. Assays of *Phytophthora parasitica* populations were conducted 2 weeks after planting 15 Vinca seeds in peat amended with $\text{Al}_2(\text{SO}_4)_3$ solutions at pH 6 and infesting peat with either two or five colonized Vinca leaf disks.

approximately 1.11 mmol H⁺ binding per gram of peat in this region of the curve.

Effects of Al amendment on pathogen populations. Amendment of peat with 0.0158 g of Al per gram of peat, applied as Al₂(SO₄)₃ solution at pH 4, suppressed pathogen populations in both runs of the experiment, but because inoculum densities differed between runs, results of each test are presented separately (Fig. 2A and B). Analysis of variance (ANOVA) results from the first run of the experiment indicated a significant inoculum level by peat interaction ($P \leq 0.01$) effect, whereas ANOVA results of the second experiment indicated both an Al level ($P \leq 0.01$) and an inoculum level ($P \leq 0.01$) effect with no interaction. Peat amended with the high level of Al reduced pathogen populations by >98% at the low inoculum level and >86% at the high inoculum level compared with the control (Fig. 2A and B). Addition of Al₂(SO₄)₃ solution at pH 4 lowered the average pH from 4.7 (unamended with Al) to 4.61 and 4.35 at the low and high Al levels, respectively (Table 1). No significant differences between initial and final pH were observed. Peat amended with Al₂(SO₄)₃ solution at pH 4 contained an average of 0.0601 mmol exchangeable Al per gram of peat (Table 1). No statistical differences in stand counts were observed between treatments, and the pathogen was not detected in the uninoculated control treatments.

P. parasitica populations were also reduced in peat amended with Al₂(SO₄)₃ solution at pH 6 compared with the nonamended control (Fig. 3). There was a significant Al level effect ($P \leq 0.01$), but an inoculum level effect was not observed. The high Al level (0.0158 g of Al per gram of peat) reduced pathogen populations by 95 and 65% at the low and high inoculum levels, respectively. The low Al level (0.0079 g of Al per gram of peat) reduced the populations by 55% at the high inoculum level, but populations were similar to the controls at the low inoculum level (Fig. 3). Amendment of peat with Al₂(SO₄)₃ solution at pH 6 raised the pH from 4.7 to 5.18 and 5.39 at the low and high Al levels, respectively (Table 1). No significant differences between initial and final pH were observed. Peat contained an average of 0.0015 and 0.001 mmol exchangeable Al per gram of peat after amendment with the low and high Al levels, respectively (Table 1). No statistical differences in stand counts were observed between treatments, and propagules of *P. parasitica* were not detected in the uninoculated control treatments.

Effect of counter anion. Similar levels of pathogen suppression were observed in the presence of Cl⁻ and SO₄²⁻ at each amendment solution pH (Table 2). The amendment solution pH, however, had a significant effect on pathogen populations ($P \leq 0.05$). Exchangeable Al levels and pH differed with the AlCl₃ and Al₂(SO₄)₃ treatments; AlCl₃ treatments at pH 4 resulted in higher levels of exchangeable Al than Al₂(SO₄)₃ treatments (Table 2). Peat amended with AlCl₃ and Al₂(SO₄)₃ solutions at pH 6 contained similar levels of exchangeable Al (Table 2). The initial and

final levels of exchangeable Al were negatively correlated with average pH ($R^2 = 0.86$). For example, the AlCl₃ treatment at pH 4 resulted in the lowest pH (3.62) and the highest level of exchangeable Al (0.1825 mmol g⁻¹ of peat). The 0.05 M AlCl₃ amendment solution also contained the highest Al³⁺ activity as predicted by the chemical speciation program GEOCHEM-PC (Table 3) (31). This treatment also was toxic to *C. roseus*, resulting in almost total inhibition of seed germination (Table 2). In contrast, peat amended with Al₂(SO₄)₃ solution at pH 4 equilibrated at a pH of 4.12, resulting in an average exchangeable Al level of 0.0505 mmol g⁻¹, and seed germination was 75%. Amendment with AlCl₃ solution at pH 6 elevated the pH to 5.64, with an average of 0.0020 mmol exchangeable Al per gram of peat. Similarly, amendment with Al₂(SO₄)₃ solution at pH 6 increased the pH to 5.34, with an average exchangeable Al level of 0.0045 mmol g⁻¹ of peat.

Zoospore movement. The distance between inoculum source and bait affected infection of baits. Twenty-four percent of bait segments were infected at the 0.5-cm distance, but no infection was detected in baits 1.0 cm from the inoculum source. The duration of flood had no effect on infection of baits.

Soil moisture characteristic/pore-size distribution. Peat had a volumetric water content of 0.97 cm³ cm⁻³ at saturation, and 0.58 cm³ cm⁻³ upon equilibration at -2.5 kPa ψ_m . The pore-size distribution of the peat medium indicated that at -2.5 kPa ψ_m , 60% of the total pore space was filled with water (Fig. 4). Therefore, approximately 40% of the pores are greater than 116 μ m in diameter, which allows for zoospore motility.

DISCUSSION

Assuming that Al binds to carboxylic acid functional groups on peat, the titration of exchangeable acidity of the peat-based medium used in this study provided a quantitative estimation of the

TABLE 3. Activity of Al³⁺ and sum activity of monomeric Al species in solutions used to amend peat, as predicted by GEOCHEM-PC^v

Amendment solution ^w	pH ^x	-log (Al ³⁺) ^y	-log (Σ mono) ^z
0.05 M Al ₂ (SO ₄) ₃	4.0	6.07	6.03
0.05 M Al ₂ (SO ₄) ₃	6.0	9.90	7.80
0.05 M AlCl ₃	4.0	3.90	4.86
0.05 M AlCl ₃	6.0	9.90	7.80

^v Al amendment levels were determined by varying the amount of Al₂(SO₄)₃ and AlCl₃ solutions added to peat.

^w Peat was amended with either an Al₂(SO₄)₃ or AlCl₃ solution. Al levels were determined by varying the amount of solution added to peat.

^x The pH of each solution was adjusted to either 4.0 or 6.0 with the addition of 1.0 N KOH.

^y -log (Al³⁺) in each solution was predicted by GEOCHEM-PC.

^z Σ mono = (Al³⁺) + (AlOH²⁺) + (Al(OH)₂⁺) + (Al(OH)₃⁰) + (Al(OH)₄⁻). Activities of each species were predicted by GEOCHEM-PC.

TABLE 2. Exchangeable aluminum (Al) levels and pH of peat amended with Al₂(SO₄)₃ and AlCl₃ solutions and effects on germination of Vinca and pathogen population

Al source ^a	Amendment solution pH ^v	Initial exchangeable Al (mmol/g of peat) ^w	Final exchangeable Al (mmol/g of peat) ^w	pH ^x	% Germination ^y	Propagules per gram of peat ^z
Al ₂ (SO ₄) ₃	4.0	0.0510	0.0500	4.12	75 a	0.75 a
Al ₂ (SO ₄) ₃	6.0	0.0035	0.0055	5.34	68 a	21 b
AlCl ₃	4.0	0.1865	0.1785	3.62	1.6 b	0 a
AlCl ₃	6.0	0.0035	0.0005*	5.64	68 a	29 b

^a Peat was amended with either 0.05 M Al₂(SO₄)₃ or AlCl₃ at 0.0158 g of Al per gram of peat.

^v Al₂(SO₄)₃ solution was adjusted to pH 4.0 or 6.0 with 1.0 N KOH.

^w Levels of exchangeable Al measured by an extraction with 1.0 M KCl followed by titration of exchangeable Al according to the method of Yuan (39).

*Significant difference ($P \leq 0.05$) between initial and final level of exchangeable Al determined by Student's *t* test.

^x Average pH; measured in 1:2 (wt/vol) suspension of peat in 0.01 M CaCl₂ (35).

^y Percent germination of 15 seeds in each funnel. Values within column followed by the same letter indicate significant differences in means ($P \leq 0.05$), determined by Waller-Duncan K-ratio test.

^z Average number of propagules per gram of peat. Values within column followed by the same letter indicate significant differences in means ($P \leq 0.05$), determined by Waller-Duncan K-ratio test.

peat's potential Al binding capacity (5). Titration of peat from pH 11 to 3 sequentially protonates these acid groups, first neutralizing the charge of phenolic groups (pK_a 8 to 11) and then the carboxylic acid groups (pK_a 3 to 6). The presence of specific acid functional groups can be determined by the location of buffer regions on the titration curve (36). The two buffer regions observed in our peat medium corresponded to the pK_a values of phenolic and carboxylic acids. Because Al binds preferentially to carboxylic acid groups (5), the Al binding capacity is closely related to the acidity titrated between pH 6 and 3. If Al complexation is best modeled by a 1:1 relationship, with 1 mol Al binding to 1 mol carboxyl groups (5), the expected Al binding capacity of peat would be 1.11 mmol g^{-1} of peat, which was the exchangeable acidity titrated between pH 6 and 3. In this study, the highest added Al level was 0.585 mmol Al per gram of peat or about one-half of the expected Al binding capacity of the peat medium.

The lower levels of exchangeable Al detected in peat amended with $Al_2(SO_4)_3$ solutions at pH 6 than those at pH 4 may be related to the Al species distribution and the pH-dependent Al binding capacity of peat. The Al species distributions are different in Al solutions at pH 4 and 6. At pH 4, over 95% of total Al in solution is expected to be in the Al^{3+} form, but at pH 6, approximately 80% is expected in the $Al(OH)_2^+$ form (23). Bloom and McBride (5) suggest that the hydrolysis species bind more strongly to organic ligands than Al^{3+} . The prevalence of $Al(OH)_2^+$ and its strong association with carboxylic acid groups may account for the lower levels of exchangeable Al in treatments amended with Al solutions at pH 6. The pH-dependent formation of an $Al(OH)_3$ precipitate may also explain the lower levels of exchangeable Al in peat amended with Al solutions at pH 6. In pH 4 amendment solutions, the amount of total soluble Al in equilibrium with gibbsite was approximately 10^{-3} M, whereas at pH 6, the total soluble Al was approximately $10^{-6.3}$ M, as predicted by thermodynamics (23). The pH 4 solution was 10^2 times supersaturated with respect to gibbsite, and the pH 6 solution was $10^{5.3}$ times supersaturated with respect to gibbsite. The toxicity of gibbsite to fungi is unknown. Furthermore, peat amended with Al solutions at pH 6 equilibrated at a higher pH than peat amended with Al solutions at pH 4. The higher pH may increase the negative surface charge on peat, consequently increasing the Al binding capacity of the medium.

Benson (3) observed suppression of *P. parasitica* in an organic potting medium composed of peat and vermiculite, but unlike

suppression of soilborne fungi in mineral soils (21,26,27,29), the reduction of pathogen populations occurred with low levels of exchangeable Al. The low levels of exchangeable Al in Benson's system suggest that much of the Al was complexed with the peat fraction rather than in the exchanger phase of the vermiculite. In our system, the mineral component was excluded to eliminate the cation exchange capacity offered by the vermiculite. Consequently, this work documents suppression of *P. parasitica* in medium containing very low levels of exchangeable Al. Peat amended with 0.0158 g of Al per gram of peat as an $Al_2(SO_4)_3$ solution at pH 6, reduced populations of *P. parasitica* by more than 90% with only 0.0010 mmol exchangeable Al per gram of peat. The amount of KCl exchangeable Al in the peat system is approximately three times lower than levels suppressive to *T. basicola* (26,27) and *P. infestans* (2), and 11 times lower than levels suppressive to *P. capsici* (29) on a volume basis. Studies of Al toxicity to these fungi were conducted either in vitro or in mineral soils, and suppression was directly related to the level of exchangeable Al or Al in solution. In contrast, the low level of KCl exchangeable Al in the peat system suggests that either solid phase or dissolved complexes of Al ions may be responsible for suppression of *P. parasitica*.

Suppression of pathogens in mineral soils generally occurs at pH 5.2 and below, whereas suppression of *P. parasitica* was observed in Al-amended peat with a pH > 5.2. Less than 1% of the summed total activity of monomeric Al species was contributed by Al^{3+} activity in both amendment solutions ($AlCl_3$ and $Al_2(SO_4)_3$) at pH 6, as predicted by GEOCHEM-PC (31). Peat amended with the high level of Al, added at pH 6, equilibrated at pH > 5.3. Assuming that surface hydrolysis and hydrolysis of dissolved Al are the same at a given pH, approximately 90% of monomeric Al is expected in the $Al(OH)_2^+$ species at pH 5.3 (23). The prevalence of $Al(OH)_2^+$ in the system suggests that ions other than Al^{3+} were responsible for pathogen suppression. GEOCHEM-PC was not used to model speciation of Al in the peat system because the predictions do not account for Al complexes with the soluble organic ligands that would be expected to form in the peat. The relative toxicity of each Al hydrolysis species to fungi is unknown; however, recent studies indicate that phytotoxicity is correlated with the sum of the activities of monomeric Al species rather than the activity of Al^{3+} alone (18,33).

The type of counter anion present (Cl^- or SO_4^{2-}) in each Al source did not alter suppression of *P. parasitica*. Similarly, Al source, $AlCl_3$ or $Al_2(SO_4)_3$, has no effect on sporangia production of *P. infestans* (2), and multiple stages in the life cycle of *T. basicola* (27). Although both $AlCl_3$ and $Al_2(SO_4)_3$ were effective at reducing populations of *P. parasitica*, amendment of peat with $AlCl_3$ inhibited germination of *C. roseus*; consequently, this source of Al should not be used to amend peat for pathogen suppression. The phytotoxicity observed in peat amended with $AlCl_3$ may be related to the elevated activity of Al^{3+} and monomeric Al hydrolysis species in the amendment solution. Sulfate reduces the activities of Al hydrolysis species by formation of soluble complexes, such as $Al(SO_4)^+$ and $Al(SO_4)_2^-$ (32,33).

Damping-off was not observed in unamended, infested control treatments. Because the same isolate of the pathogen caused damping-off of *C. roseus* in coarse sand (E. J. Fichtner, unpublished data), it was hypothesized that the physical properties of peat may inhibit movement of zoospores from the inoculum to the seed. The low level of infection in stem segments placed 0.5 cm from inoculum, and the lack of infection at the 1.0-cm distance suggest that zoospore movement was limited in the peat system.

Zoospore motility is limited by pore size, low ψ_m , and lack of continuity of pores (11). Sporangia tend to discharge zoospores within 2 h of saturation (22), and zoospores remain motile for only a few hours before encysting (12). Because flood duration had no effect on infection of bait segments, the 24-h-saturation period in experiments should have induced zoospore release and provided

Fig. 4. Pore-size distribution for peat packed to a bulk density of 0.12 g/cm^3 at 30°C at selected matric potential values.

enough time for zoospore movement. Shew (34) reported that duration of saturation had little effect on disease of tobacco caused by *P. parasitica* var. *nicotianae*, with 100% infection occurring after only 0.5 h of saturation.

The pore-size distribution was used to determine whether pore size was a factor limiting zoospore motility in peat. Because zoospores of *P. cinnamomi* swim in a helical pattern with a radius of approximately 110 μm (1), an estimated 25% of the pores in the sieved peat have a diameter large enough to accommodate zoospore movement, assuming that zoospores of *P. parasitica* have a swim radius similar to that of *P. cinnamomi*. Both the prevalence of large pores ($\geq 220\text{-}\mu\text{m}$ diameter) and long duration of saturation suggest that zoospore movement was most likely limited by a lack of continuity of large pores in the peat matrix.

Al suppresses plant pathogens in both mineral soils and peat-based potting media; however, the chemical conditions in these systems are very different. In soils high in organic matter, soluble complexation reactions between organic ligands and Al reduce the activity of Al in solution. In the peat system, only 0.17% of the Al added as $\text{Al}_2(\text{SO}_4)_3$ solution at pH 6 (0.0158 g of Al per gram of peat) was extractable with KCl. The high Al binding capacity of peat and the strong association between Al hydrolysis species and organic ligands, and the predicted presence of an $\text{Al}(\text{OH})_3$ precipitate, all suggest that much of the Al in the peat system was either tightly bound to the organic fraction or in a precipitate of gibbsite. Furthermore, suppression of *P. parasitica* was observed in Al-amended peat at pH > 5.3, indicating that the species distribution of Al in the peat system was different than that in suppressive mineral soils (pH < 5.2). The prevalence of $\text{Al}(\text{OH})_2^+$ in peat amended with $\text{Al}_2(\text{SO}_4)_3$ and AlCl_3 solutions at pH 6 suggests that ions other than Al^{3+} may be responsible for pathogen suppression. Based on the difference in chemical conditions of Al-amended peat and suppressive mineral soils, we speculate that the mechanism of Al-mediated suppression of plant pathogens may be different in the two systems. Future studies, however, will be designed to study the mechanisms of suppression in both mineral and organic media. The low levels of exchangeable Al in the peat system may enable its integration into disease management programs as a suppressive component in potting media for plant container culture. Future studies also are planned to determine the role of organically complexed Al and monomeric Al hydrolysis species in the suppression of *P. parasitica*.

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