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Effect of Container Plant Growth Medium and Fertilizer Phosphorus on Establishment and Host Growth Response to Vesicular–Arbuscular Mycorrhizae

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Abstract. **The establishment and performance of vesicular–arbuscular mycorrhizae (VAM) formed by *Glomus fasciculatum* (Thaxter) Gerd. & Trappe were studied on geranium (*Pelargonium* X *hortorum* L.H. Bailey) and subterranean clover (*Trifolium subterraneum* L.) in various growth media at 2 P fertility levels. Colonization by *G. fasciculatum* was not extensive and shoot dry weight and P uptake consequently were not increased by VAM in soilless media such as peat, bark, perlite, and vermiculite. In media containing soil and fertilized at the low P level, roots were colonized extensively by *G. fasciculatum*, and host shoot growth and P concentrations were increased by VAM. Host growth enhancement by VAM was not observed at the higher P fertility level. Differences in colonization and mycorrhizal response in different fertilized growth media were correlated negatively with the logarithm of the equilibrium solution P concentration. Colonization, growth response, and P uptake by geranium inoculated with *G. mosseae* (Nic. & Gerd.) Gerd. & Trappe or *Acaulospora spinosa* Walker & Trappe were affected by growth medium and P fertilizer in the same way as plants inoculated with *G. fasciculatum*. Peat mosses from different sources varied considerably in their effects on mycorrhiza formation by *G. fasciculatum*, and on growth response of geranium when the peat was diluted with different amounts of soil. These differences appeared to be related to the equilibrium solution P concentration of the fertilized peats, and not to extractable P of the unfertilized peats. Use of rock phosphate or bonemeal instead of NaH_2PO_4 as a source of P did not improve the establishment of VAM and host growth response in soil, peat, or vermiculite. Addition of 5–10% Turface, bentonite, silt loam soil, or clay subsoil to peat or vermiculite resulted in increased colonization of host roots and significant mycorrhizal growth response, whereas amendment with liquid sludge inhibited formation of mycorrhizae.**

Vesicular–arbuscular mycorrhizal (VAM) fungi have potential for commercial application on container-grown plants since they have been shown to increase host plant uptake of water and mineral nutrients (15), reduce disease caused by soil-borne pathogens (8, 15), and increase transplant survival and growth (2, 5, 7).

Soil factors are known to influence the establishment and performance of VAM (11, 12, 17). Menge et al. (16) found that growth response of Troyer citrange (x *Citroncirus webberi* Ing. & Moore) to mycorrhizal colonization in various mineral soils was correlated inversely with percentage of organic matter, cation exchange capacity, and P, Cu, Mn, and Zn content. In general, colonization by mycorrhizal fungi and host growth response decrease as soil fertility increases, and application of available P has often been cited as a factor reducing colonization and host growth enhancement by VAM (11, 12, 17).

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In the last few decades, growers of containerized plants have, to a large extent, replaced mineral soils in growth media with soilless components such as sphagnum peat, perlite, vermiculite, and shredded or milled bark. Little is known about effects of these substrates on VAM. Peuss (20) found that addition of peat to soil reduced plant colonization and growth enhancement by VAM. Gaunt (10) obtained growth enhancement of onion and tomato by VAM in mineral soil and in 75% soil/25% vermiculite (v/v) but not 50% soil/50% vermiculite.

The experiments described here were undertaken to: 1) determine whether VAM could be established and enhance plant growth in various commercially used growth media fertilized with soluble P, and how individual media components and equilibrium P level of the medium affected VAM; 2) determine whether peats from different sources varied in their effect on development of VAM and host plant response, and if they did, to discover what properties of the peat were related to inhibitory effects on mycorrhizae; 3) test different fertilizer P sources and levels for their effect on VAM on plants growing in various media; and 4) study the effects of adding various amendments to peat or vermiculite on formation of VAM and plant growth response to inoculation.

Materials and Methods

Seeds of 'Sprinter Scarlet' geranium and 'Mt. Barker' sub-

hypochlorite, placed under running tap water for 15 hr, then germinated on water agar plates for 48 hr in darkness at 21°C. Seedlings were then planted individually in 50-ml plastic growth tubes. The subterranean clover seedlings were dipped in a suspension of about 10^8 cells/ml of *Rhizobium trifolii* prior to planting.

Peat, bark, sand, and soil used in these experiments were pasteurized with aerated steam for 30 min at 60°C. Powdered lime was used to adjust media to the following pH (after 2 days equilibration, aqueous paste): Expt. 1 (5.8–7.3); expt. 2 and 3 (5.5–6.5); expt. 4 (5.7–6.2); expt. 5 (6.0–6.5); and expt. 6 (5.6–6.2). The exception was the pH of vermiculite, which ranged from 7.6 to 8.5 without lime. Media pH in each treatment were measured again when experiments were terminated, and were similar to initial pH.

Plants were watered as needed and maintained in a greenhouse at 16°/20° to 22°C (night/day) temperature. High-pressure sodium vapor lamps provided supplemental lighting with an intensity of 200 $\mu E/m^2$ at plant level from 6:00 AM to 10:00 PM daily.

All experiments were completely randomized and had 10 single plant replications of each treatment. Expt. 1 and 2 were terminated and measurements taken 5 weeks after planting; expt. 3-6 were terminated after 6 weeks. Root and shoot fresh weights were measured in expt. 1 and 2 and used to calculate root-to-shoot ratios. In all experiments, shoot dry weights (70°C for 48 hr) were determined.

Plant growth response was defined as the ratio of the dry weight of shoots of mycorrhizal plants to that of nonmycorrhizal plants. Roots of all plants were cleared and stained (21), and colonization by the endophyte was measured as percentage of root length with mycorrhizae (4). P content of shoots was determined colorimetrically (1) by the Oregon State Univ. Dept. of Soil Science Plant Analysis Lab., after combining all 10 plants in each treatment.

Media, media components, and soluble phosphorus. Whether *G. fasciculatum* could be established and enhance plant growth was determined in various media fertilized with soluble P. Effects of individual media components and equlibrium solution P level of the medium on VAM were also determined. Media used in expt. 1 (subterranean clover) were Canadian sphagnum peat (2 μg/g P), coarse perlite (2 μg/g P), medium-grade horticultural vermiculite (2 μg/g P), shredded 1-cm sieved douglas-fir bark (13 μg/g P), silt loam soil (13 μg/g P), silty river sand (4 μg/g P), 1 soil : 1 bark, 1 peat : 1 vermiculite, and 1 soil : 1 peat : 1 perlite. The same media (except sand and perlite) were used in expt. 2 (subteranean clover and geranium); additional media in expt. 2 (geranium) were 3 soil : 1 peat, 1 soil : 1 peat, and 1 soil : 3 peat. Sodium bicarbonate extractable P (18) of components as listed above was determined by the Soil Testing Lab. at Oregon State Univ.

Inoculum mixed with the various media before planting consisted of washed and finely chopped roots colonized by *G. fasciculatum*, or roots of nonmycorrhizal plants which had been treated with 37-μm-sieved *G. fasciculatum* spore washings. About 0.2 g peppermint (*Menta piperita* L.) roots were used per plant in expt. 1, and 0.1 g cotton (*Gossypium hirsutum* L.) roots per plant in expt. 2.

Each plant was fertilized weekly with 10 ml Long Ashton nutrient solution (13) at full strength P (43 ppm P) or one-quarter strength P (11 ppm P) provided by monobasic sodium phosphate.

Both experiments were designed as complete factorial combinations of [illegible] and P fertilizer levels.

To evaluate equilibrium concentration of P in solution in the root environment with various media and P fertilization rates, 500 ml of each of the media used in expt. 1 and 2 was saturated with Long Ashton nutrient solution with either 43 or 11 ppm P (only the lower level was used for the soil/peat dilutions). The media were covered to prevent evaporation and allowed to equilibrate 24 hr, after which concentration of P remaining in the decanted solution was determined colorimetrically (1). Equilibrium solution P concentrations of the various fertilized media are shown in Table 1.

Regression and correlation analysis were used to determine the relationship between equilibrium solution P of the various fertilized media and VAM development (percentage of root length colonized), shoot dry weight (proportion of nonmycorrhizal control), and shoot P concentration (proportion of nonmycorrhizal control). Planned statistical comparisons (F tests) were made between soilless media and media containing soil, between P fertilizer levels, and between mycorrhizal and nonmycorrhizal plants.

Endophyte species. Whether different endophyte species are affected by growth media in the same way as *G. fasciculatum* was determined. Expt. 3 was similar to expt. 1 and 2 except that geranium plants were inoculated with 0.2 g per plant of subterranean clover roots colonized (40–60% of length) by *Gigaspora margarita, Glomus mosseae, Glomus fasciculatum, Acaulospora spinosa*, or roots of nonmycorrhizal plants treated with combined spore washings passed through a 37-μm sieve. Plants were grown in either soil, peat, vermiculite, river sand, or a mixture of soil, peat, and perlite. Each plant was fertilized weekly at a high or low P level as described above. Expt. 3 was analyzed as a complete factorial of endophyte species, media, and P fertilizer levels.

Type of peat. The effect of type of peat on formation of VAM, geranium growth response, and relative shoot P concentration was determined in expt. 4. One hypnum peat and 4 Canadian sphagnum peats (2 shipments from each of 2 sources) were each diluted with 0%, 10%, 25%, or 50% (v/v) silt loam soil, or plants were grown in 100% soil. Geranium plants were fertilized weekly with 10 ml per plant Long Ashton nutrient solution (13) with P at full strength (43 ppm P) or one-quarter strength (11 ppm P). Media were inoculated with 0.15 g/plant mycorrhizal (*G. fasciculatum*) or nonmycorrhizal subterranean clover roots. The design was a complete factorial of media, inocula, and P fertility levels. Sodium bicarbonate extractable P of unfertilized peats and equilibrium solution P of fertilized peats were measured as described for expt. 1 and 2, and are

Table 1. Equilibrium solution P concentration of growth media fertilized at 2 soluble P concentrations.

	Equilibrium P concn (ppm)	
	Soluble P concn	
Growth medium	11 ppm	43 ppm
Fertilizer control	9.6	42.5
Soil	<0.25	<0.25
Soil/bark	3.1	8.5
Soil/peat/perlite	1.7	21.0
Sand	<0.25	10.6
Peat	6.3	26.4
Bark	11.0	37.5
Vermiculite	6.3	32.9
Perlite	8.5	40.8
Peat/vermiculite	7.8	32.9

shown in Table 2. Relationship of these parameters to mycorrhizal growth enhancement (averaged over the soil dilutions) was determined by regression and correlation analysis. The relationship between proportion of soil and colonization of roots, host growth response, and relative shoot P concentration were similarly determined.

P fertilizer source. The effect of P fertilizer source on formation of VAM, geranium growth response, and relative shoot P concentration was determined in expt. 5. Relationship of equilibrium solution P concentration of fertilized media to these parameters was also determined. Plants were grown in silt loam soil, Canadian sphagnum peat, or medium-grade vermiculite and fertilized weekly with 10 ml per plant Long Ashton nutrient solution at 0, 11,or 43 ppm P. In other fertilization treatments, bonemeal was mixed with each medium at 20 or 80 g/liter, or C-grade rock phosphate was incorporated at 12, 50, or 200 g/liter. Plants in these treatments were fertilized with nutrient solution as for the soluble P fertilizer treatments, but P was omitted. Inoculum treatments were as in expt. 4.

Complete factorial combinations of the 3 media, 8 P fertilizer treatments, and 2 inocula were used. Equilibrium solution P concentrations of the fertilized media were measured as described for expt. 1 and 2, and are shown in Table 3. The relationship between equilibrium solution P of the fertilized media and plant growth enhancement was determined by regression and correlation analysis. Relationship between host growth response in the various P treatments and growth of nonmycorrhizal plants, formation of mycorrhizae, and shoot P concentrations were similarly determined for each medium.

Media amendments. The effects of adding amendments to peat or vermiculite on equilibrium solution P concentration, formation of VAM, and geranium growth response and relative shoot P concentration were determined in expt. 6. Sphagnum peat or medium-grade vermiculite were unamended or amended with 10%, 25%, or 50% (v/v) baked montmorillonite clay (Turface); 10%, 25%, or 50% silt loam soil; 10%, 25%, or 50% clay subsoil; 5% or 10% dry granular bentonite clay; 25% or 50% digested liquid sewage sludge (2.7% w/v solids); 20 or 80 g/l (104 or 416 meq/liter) Bio-Rad analytical-grade cation-exchange resin; or 30 or 120 g/liter (105 or 415 meq/liter) Bio-Rad analytical-grade anion-exchange resin. Plants in all growth media were fertilized weekly with 10 ml per plant Long Ashton nutrient solution with P at one-quarter strength (11 ppm P). VAM inoculation was as in expt. 4. The design was a complete factorial of original media (peat or vermiculite), amendments and inocula.

Relationships between relative shoot P concentration of VAM plants and host VAM growth response were determined by regression and correlation analysis.

Equilibrium solution P of the fertilized amended media was measured as described for expt. 1 and 2.

Table 2. Extractable P concentration of unfertilized peats and equilibrium solution P concentration of peats fertilized at 2 soluble P concentrations.

Type of peat	Extractable P concn (ppm)	Equilibrium P concn (ppm)	
		Soluble P concn	
		11 ppm	43 ppm
Hypnum	3	0.97	11.7
Sphagnum A	17	6.34	26.4
B	34	8.14	33.6
C	32	5.63	23.2
D	16	5.60	21.9

Table 3. Equilibrium solution P concentration of various media containing different types and sources of fertilizer P.

Fertilizer P source and level	Equilibrium solution P concn (ppm)		
	Soil	Peat	Vermiculite
No P fertilizer	<0.28	<0.28	<0.28
NaH_2PO_4 (11 ppm)	<0.28	5.22	6.28
(43 ppm)	<0.28	21.9	32.0
Bonemeal (20 g/liter)	<0.28	22.5	<0.28
(80 g/liter)	<0.28	26.7	<0.28
Rock phosphate (12 g/liter)	<0.28	0.63	<0.28
(50 g/liter)	<0.28	3.8	<0.28
(200 g/liter)	<0.28	2.4	<0.28

Results

Media, media components, and soluble phosphorus. Colonization by mycorrhizal fungi was generally lower in soilless media than in those containing mineral soil or in sand. Application of P at the higher rate reduced or had no effect on colonization of geranium or subterranean clover by *Glomus fasciculatum*, except on subterranean clover in the peat/vermiculite medium where colonization was low at both P levels (Table 4). Increasing fertilizer P reduced colonization of geranium to a greater degree in the media without soil (Table 4). Development of VAM on geranium in peat, bark, and peat/vermiculite was sparse and limited mostly to the outer cortical cells. In media containing soil, VAM development within colonized areas was more extensive and included the entire cortex. The control plants did not have VAM.

In all media containing soil, but in none of the media without soil, *G. fasciculatum* increased shoot dry weight of geranium and subterranean clover at the low P level (Table 5). At the higher P level, shoot dry weight was not increased significantly in any medium. Shoot dry weight was decreased in some cases when plants were inoculated with the endophyte, especially in soilless media (Table 5). Growth of both mycorrhizal and nonmycorrhizal plants varied considerably in different media and at different P fertility levels (Table 5).

Table 4. Effect of growth medium and fertilizer P level on colonization of geranium and subterranean clover roots by *Glomus fasciculatum* (5 weeks after germination).

Growth medium	Root length with VAM (%)			
	Subterranean clover (Expt. 1)		Geranium (Expt. 2)	
	11 ppm P	43 ppm P	11 ppm P	43 ppm P
Soil	59.5 f[z]	53.8 b	87.1 i	80.9 hi
Soil/bark	4.4 c	1.8 c	78.0 h	79.4 h
Soil/peat/perlite	61.0 e	25.3 e	85.2 hi	69.0 g
Sand	55.5 f	29.1 e	---	---
Vermiculite	6.2 c	1.4 b	37.6 de	7.9 a
Peat	7.6 c	0.1 a	52.4 f	18.7 b
Bark	1.0 ab	0.2 a	43.5 e	27.8 c
Perlite	3.7 c	0.6 ab	---	---
Peat/vermiculite	0.2 a	18.9 c	79.3 c	31.8 cd

[z]Mean separation for plant species by Duncan's multiple range test.

Table 5. Effect of growth medium and fertilizer P level on mycorrhizal growth response of geranium and subterranean clover inoculated with *Glomus fasciculatum* (5 weeks after germination).

Growth medium	Subterranean clover (Expt. 1)		Geranium (Expt. 2)	
	11 ppm P	43 ppm P	11 ppm P	43 ppm P
Soil	101/68 = 1.48**	110/100 = 1.10^{NS}	138/79 = 1.75**	172/173 = 0.99^{NS}
Soil/bark	61/47 = 1.29*	54/58 = 0.92^{NS}	168/91 = 1.85**	158/175 = 0.90^{NS}
Soil/peat/perlite	84/71 = 1.18*	104/114 = 0.92^{NS}	161/116 = 1.39**	193/245 = 0.79*
Sand	67/62 = 1.08^{NS}	88/99 = 0.89^{NS}	---	---
Vermiculite	61/64 = 0.96^{NS}	55/63 = 0.87^{NS}	94/135 = 0.69**	192/236 = 0.81*
Peat	72/91 = 0.79*	95/108 = 0.88^{NS}	137/151 = 0.91^{NS}	195/213 = 0.92^{NS}
Bark	40/52 = 0.77*	44/52 = 0.84^{NS}	142/156 = 0.91^{NS}	147/160 = 0.92^{NS}
Perlite	70/73 = 0.96^{NS}	70/80 = 0.87^{NS}	---	---
Peat/vermiculite	67/72 = 0.93^{NS}	83/98 = 0.84*	112/129 = 0.87^{NS}	243/239 = 1.02^{NS}

NS, *, **Nonsignificant (NS) or significantly different from nonmycorrhizal controls at 5% (*) or 1% (**) levels (*t* test).

The shoot P concentration of mycorrhizal plants relative to controls was highest in media with soil and in sand, and was generally not strongly affected by fertilizer P.

At the low P level, the root-to-shoot ratio was decreased by mycorrhizae in media containing soil, but this effect was not observed at the high P level (Table 6). The root-to-shoot ratio was not as strongly affected by VAM in soilless media, although it was decreased on subterranean clover grown in vermiculite and perlite at the low P level (Table 6).

Addition of peat to soil at 25%, 50%, or 75% did not decrease mycorrhizal growth response of geranium at either P level (Fig. 1). Colonization at both P levels was only reduced in 100% peat (Fig. 2). The P content of mycorrhizal plants relative to controls decreased with increasing proportion of peat at both P levels (Fig. 3). The solution P concentration of fertilized media after equilibration increased with increasing amounts of peat (Fig. 4).

Results with subterranean clover in expt. 2 were similar to those of expt. 1, except that colonization in the soil/bark mix was equivalent to that in other mixes containing soil.

The P content of fertilizer solutions equilibrated with media containing soil or sand was lower than that of all of the soilless media (F test, $P < 1\%$). Nutrient solutions equilibrated with soilless media (vermiculite, perlite, bark, or peat) contained

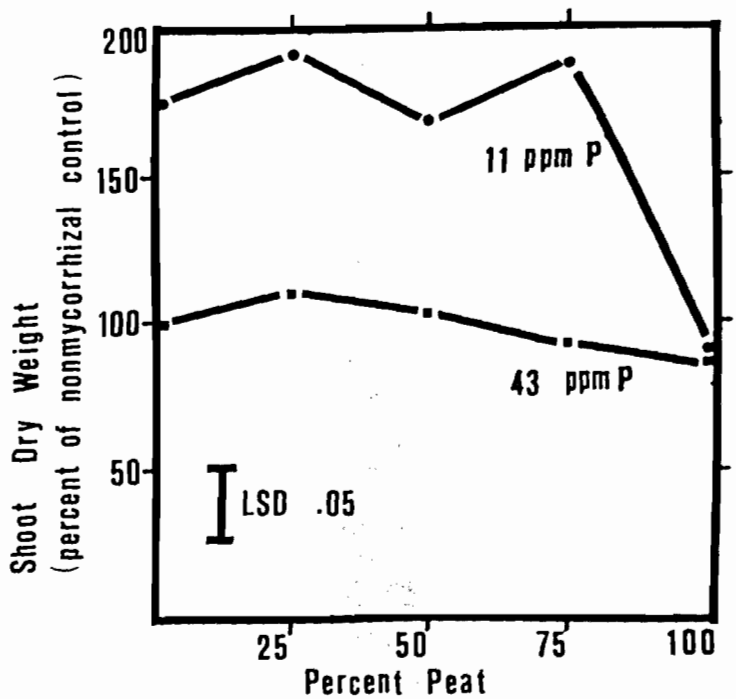

Fig. 1. Effect of proportion of soil in a soil peat medium and of fertilizer P level on growth response of geranium inoculated with *Glomus fasciculatum*.

Table 6. Effect of growth medium and fertilizer P level on root-to-shoot ratio of geranium and subterranean clover inoculated with *Glomus fasciculatum* (5 weeks after germination).

Growth medium	Root-to-shoot ratio (proportion of nonmycorrhizal controls)			
	Subterranean clover (Expt. 1)		Geranium (Expt. 2)	
	11 ppm P	43 ppm P	11 ppm P	43 ppm P
Soil	0.70**	1.20*	0.73**	0.77^{NS}
Soil/bark	0.85*	1.18^{NS}	0.72**	0.92^{NS}
Soil/peat/perlite	0.71**	1.02^{NS}	0.86^{NS}	0.96^{NS}
Sand	0.71**	1.11^{NS}	---	---
Vermiculite	0.79*	0.87^{NS}	1.07^{NS}	0.97^{NS}
Peat	1.09^{NS}	1.08^{NS}	1.07^{NS}	1.00^{NS}
Bark	1.24^{NS}	0.99^{NS}	0.94^{NS}	0.97^{NS}
Perlite	0.85*	1.13^{NS}	---	---
Peat/vermiculite	0.95^{NS}	0.87^{NS}	0.94^{NS}	1.04^{NS}

NS, *, **Nonsignificant (NS) or significantly different from nonmycor-

levels of soluble phosphorus similar to that in the original nutrient solution (F test, NS).

Colonization of roots, host growth response, and relative shoot P concentration of mycorrhizal plants were correlated negatively with the logarithm of the equilibrium solution P concentration when data from both hosts in all media and fertilizer treatments were examined (Fig. 5–7). Significant growth enhancement by mycorrhizae did not occur in fertilized media with equilibrium solution P concentrations greater than 4 ppm (Fig. 5). Relative shoot P concentration and colonization by the endophyte were affected most strongly by equilibrium solution P between 0 and 5 ppm, although shoot P concentration was enhanced by mycorrhizae at solution P concentrations up to 25 ppm (Fig. 6 and 7).

Endophyte species. *Glomus mosseae* and *Acaulospora spinosa* were inhibited in soilless media in the same way as *Glomus fasciculatum*, but colonized host roots extensively and promoted host growth and P uptake in media containing soil or sand.

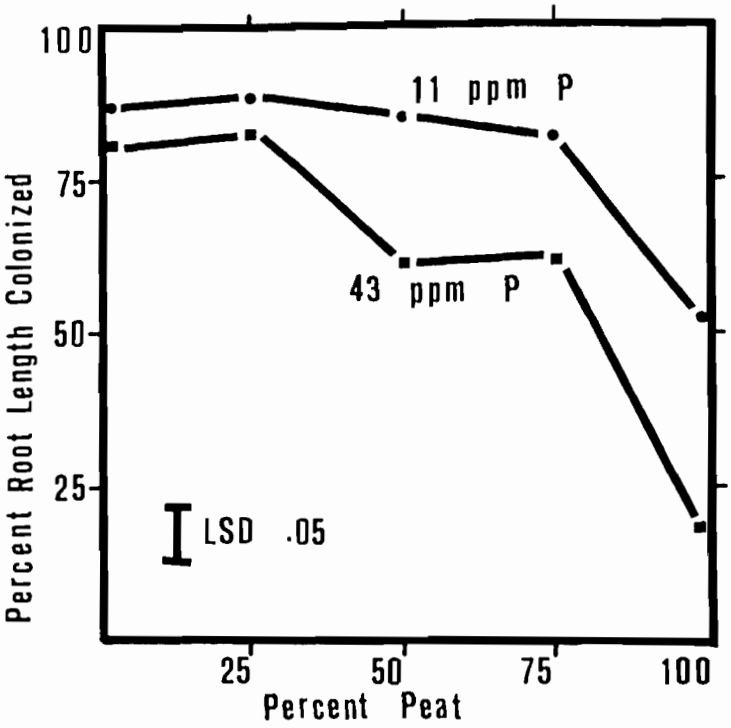

Fig. 2. Effect of proportion of soil in a soil/peat medium and of fertilizer P level on colonization of geranium inoculated with *Glomus fasciculatum*.

Gigaspora margarita did not colonize roots or affect the host in any treatment.

Type of peat. The type of peat had very little effect on the amount of colonization of geranium roots by *G. fasciculatum* when the medium contained 10%, 25%, or 50% soil (Table 7). With no soil in the medium at the lower fertilizer P level, the amount of colonization was higher in the hypnum peat than in the 4 sphagnums. For all peats and soil/peat dilutions, the application of fertilizer P at the higher level reduced formation of VAM significantly. All peats tested had an inhibitory effect on development of VAM compared to soil, since colonization of roots increased with increasing proportion of soil.

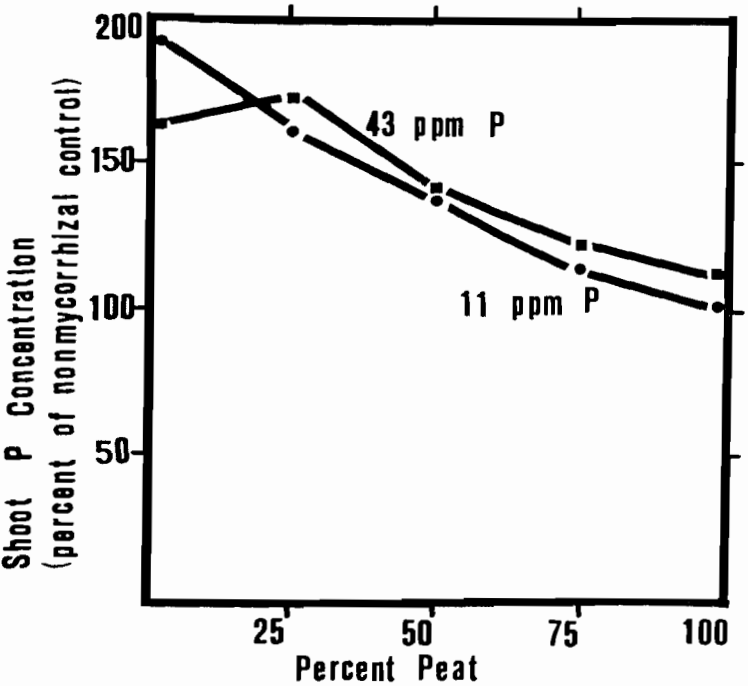

Fig. 3. Effect of proportion of soil in a soil/peat medium and of fertilizer P level on shoot P concentration of geranium inoculated with *Glomus fasciculatum*.

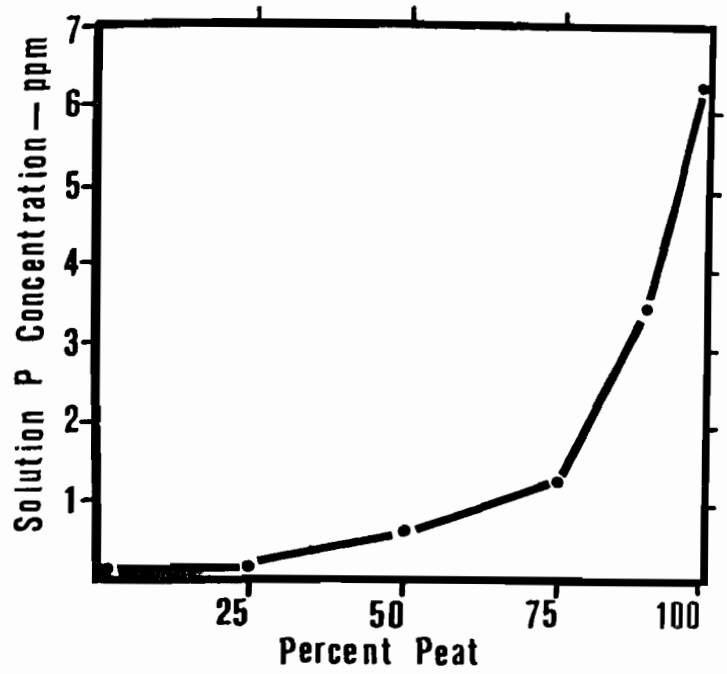

Fig. 4. Effect of proportion of soil in a soil/peat medium on equilibrium solution P concentration.

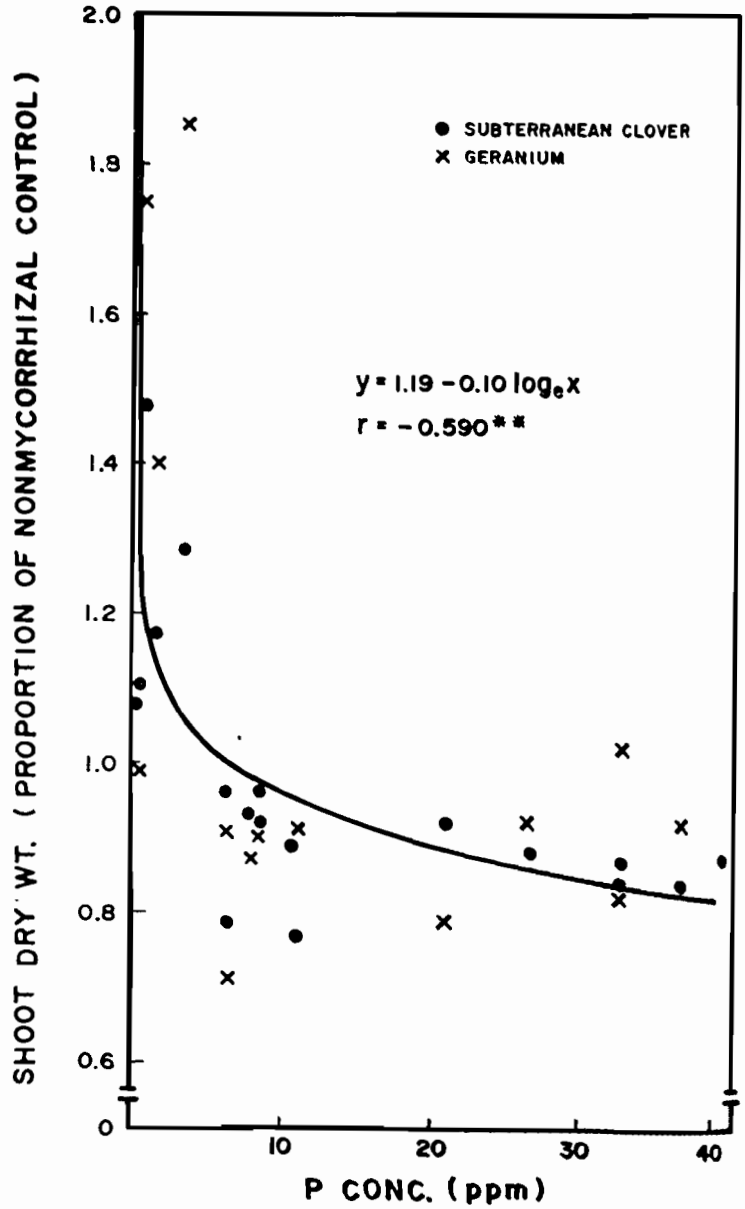

Fig. 5. Relationship between mycorrhizal growth response and equilibrium solution P concentration.

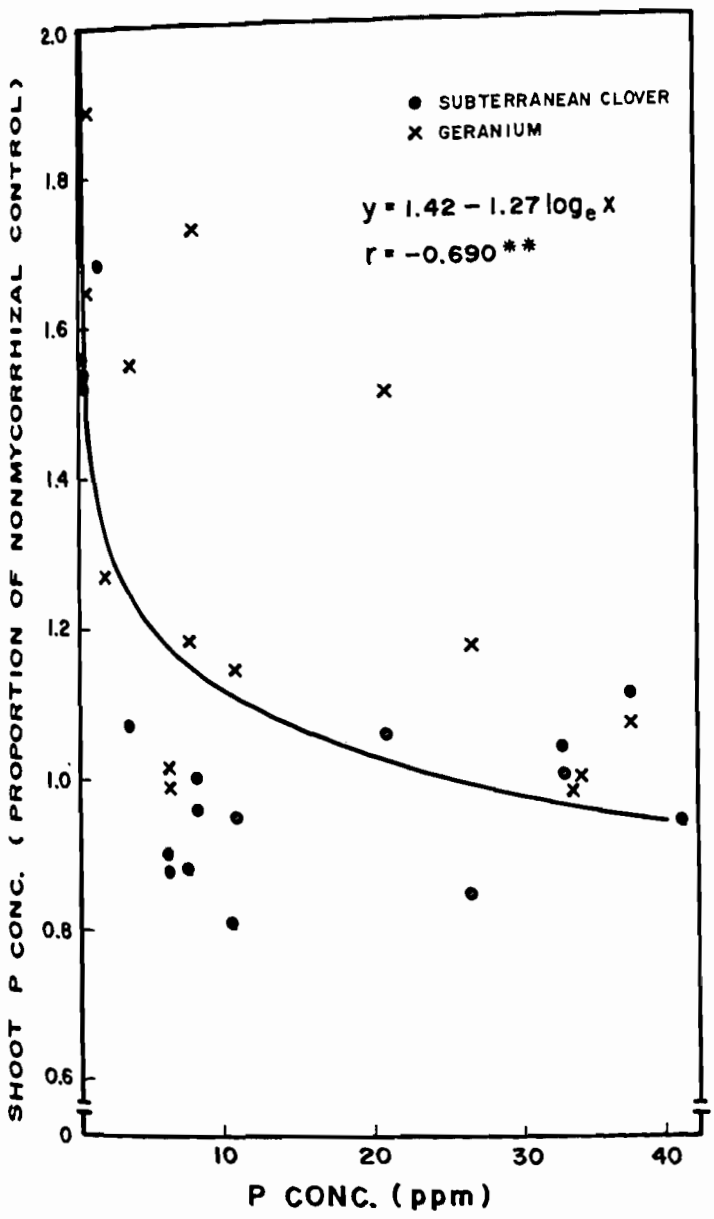

Fig. 6. Relationship between relative shoot P concentration of mycorrhizal plants and equilibrium solution P concentration.

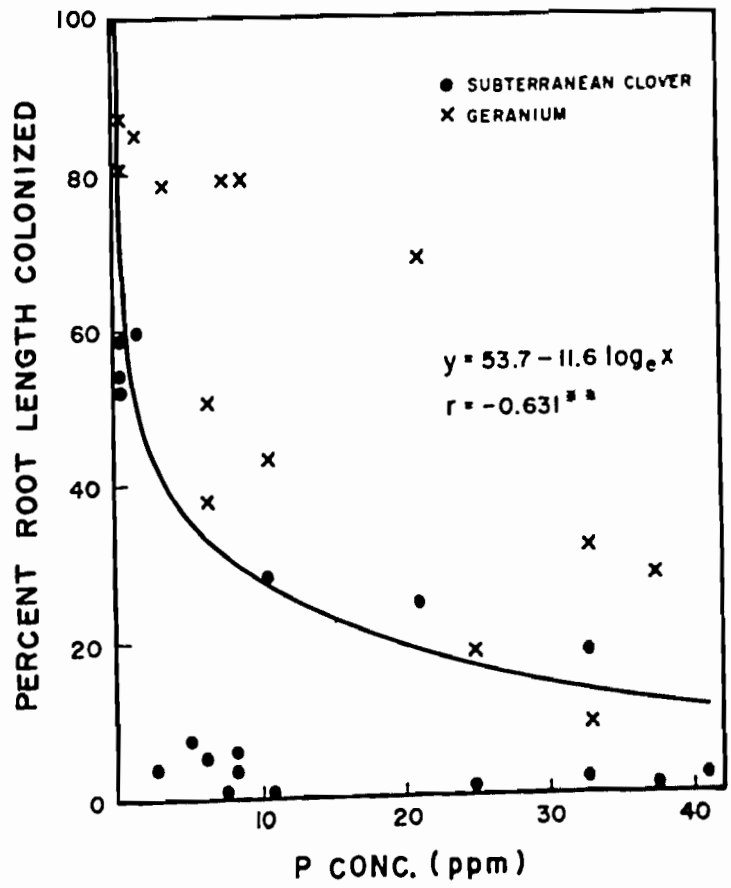

Fig. 7. Relationship between colonization of host roots by the endophyte and equilibrium solution P concentration.

Shoot growth increased significantly due to inoculation with *G. fasciculatum* only at the lower P fertility level, where growth response to VAM was correlated positively with addition of soil to all types of peat (Table 8). Significant mycorrhizal enhancement of host plant growth occurred in the hypnum peat when only 10% soil was added, in sphagnum D with only 25% added, and in sphagnum C only when 50% was added; it did not occur in sphagnums A or B at any soil dilution level tested.

The shoot P concentratioan was generally increased by *G. fasciculatum* when plants were grown at the low P fertility (F test, $P < 1\%$), but was unaffected by inoculation when plants were grown at the high P fertility level (F test, NS). Increasing the proportion of soil generally increased the shoot P of mycorrhizal plants relative to control plants at both fertilizer P levels ($r = 0.912$, $P < 1\%$ at 11 ppm P; $r = 0.960$, $P < 1\%$ at 43 ppm P).

The extractable P concentration of the various peats was not related to the average mycorrhizal growth enhancement in peat over the various soil dilutions ($r = -0.808$, NS). However, the equilibrium solution P concentration of peats after fertilizing

Table 7. Effect of type of peat, proportion of soil in the medium, and fertilizer P level on colonization of geranium roots by *Glomus fasciculatum* (6 weeks after germination).

Type of peat	Fertilizer P level (ppm)	Root length mycorrhizal (%)				Correlation between mycorrhizal development and proportion of soil
		0% soil	10% soil	25% soil	50% soil	
Hypnum	11	55.8 d[z]	65.0 c	73.7 e	71.0 c	$r = 0.770$, $P < 1\%$
Sphagnum A	11	18.9 bc	62.5 c	65.7 de	73.6 c	$r = 0.783$, $P < 1\%$
B	11	15.3 b	61.0 c	61.5 d	74.2 c	$r = 0.801$, $P < 1\%$
C	11	26.2 c	61.5 c	68.6 de	74.8 c	$r = 0.817$, $P < 1\%$
D	11	17.1 b	60.8 c	62.6 d	73.0 c	$r = 0.796$, $P < 1\%$
Hypnum	43	2.2 a	13.4 a	23.9 ab	40.7 a	$r = 0.994$, $P < 1\%$
Sphagnum A	43	2.0 a	25.4 b	37.2 c	58.4 b	$r = 0.990$, $P < 1\%$
B	43	2.2 a	14.6 a	30.4 b	37.2 a	$r = 0.946$, $P < 1\%$
C	43	3.6 a	15.0 a	24.6 ab	61.4 b	$r = 0.988$, $P < 1\%$
D	43	3.0 a	13.9 a	22.3 a	46.2 a	$r = 0.995$, $P < 1\%$

[z]Mean separation within columns by Duncan's multiple range test, 5% level.

Table 8. Effect of type of peat, proportion of soil in the medium, and fertilizer P level on growth response of geranium inoculated with *Glomus fasciculatum* (6 weeks after germination).

Type of peat	Fertilizer P level (ppm)	Mycorrhizal growth response [proportion of nonmycorrhizal control shoot dry wt (mg)] 0% soil	10% soil	25% soil	50% soil	Correlation between mycorrhizal growth response and proportion of soil
Hypnum	11	195/193 = 1.01^{NS}	237/145 = 1.63**	244/161 = 1.52**	290/181 = 1.60**	$r = 0.628$, $P < 1\%$
Sphagnum A	11	387/370 = 1.04^{NS}	320/362 = 0.88^{NS}	276/321 = 0.86^{NS}	324/283 = 1.14^{NS}	$r = 0.459$, $P < 1\%$
B	11	262/320 = 0.80*	264/297 = 0.89^{NS}	242/289 = 0.84^{NS}	182/175 = 1.04^{NS}	$r = 0.881$, $P < 1\%$
C	11	398/397 = 1.00^{NS}	335/359 = 0.93^{NS}	321/303 = 1.06^{NS}	308/231 = 1.33**	$r = 0.920$, $P < 1\%$
D	11	316/306 = 1.03^{NS}	331/400 = 0.83^{NS}	368/291 = 1.26*	369/282 = 1.31**	$r = 0.772$, $P < 1\%$
Hypnum	43	305/308 = 0.99^{NS}	410/375 = 1.09^{NS}	413/357 = 1.16^{NS}	377/430 = 0.88^{NS}	$r = -0.459$, $P < 1\%$
Sphagnum A	43	409/361 = 1.13^{NS}	405/472 = 0.86^{NS}	401/473 = 0.85^{NS}	359/471 = 0.76^{NS}	$r = -0.830$, $P < 1\%$
B	43	314/299 = 1.05^{NS}	329/338 = 0.97^{NS}	382/411 = 0.93^{NS}	277/304 = 0.91^{NS}	$r = -0.885$, $P < 1\%$
C	43	487/415 = 1.10^{NS}	407/504 = 0.81^{NS}	383/432 = 0.89^{NS}	378/383 = 0.99^{NS}	$r = -0.084$, ^{NS}
D	43	392/400 = 0.98^{NS}	390/501 = 0.89^{NS}	508/446 = 1.14^{NS}	435/502 = 0.87^{NS}	$r = -0.031$, ^{NS}

^{NS}, *, **Nonsignificant (NS) or significantly different from nonmycorrhizal controls at 5% (*) or 1% (**) levels (*t* test).

with either 11 or 43 ppm P was correlated negatively with average host growth enhancement ($r = -0.992$, $P < 1\%$ for equilibrium solution P concentration after fertilizing with 11 ppm P; $r = -0.977$, $P < 1\%$ for 43 ppm P).

Phosphorus fertilizer source. No growth enhancement from VAM occurred in treatments in peat or vermiculite regardless of P source or level, but host growth depression occurred with some fertilizer treatments in vermiculite (Table 9). Significant host growth enhancement occurred in soil in treatments with no fertilizer, NaH_2PO_4 at the lower level, or rock phosphate at the lowest level. Data are not reported for plants in vermiculite fertilized with bonemeal at the higher level since those plants died.

Percentage of root length with VAM was highest in unfertilized soil and peat media fertilized with the lower level of P in nutrient solution, or media fertilized with rock phosphate at the 2 lower levels (Table 9). Colonization of roots followed a similar pattern in vermiculite, except that there was very little colonization when no fertilizer P was added.

Host plant growth response to inoculation with *G. fasciculatum* decreased when compared with increasing shoot dry weight of nonmycorrhizal plants grown in soil or peat and fertilized

Table 9. Effect of growth medium and fertilizer P source and level on establishment of mycorrhizae and VAM growth response of geranium inoculated with *Glomus fasciculatum* (6 weeks after germination).

Fertilizer P source and level	Mycorrhizal growth response [proportion of nonmycorrhizal control shoot dry wt (mg)] Soil	Peat	Vermiculite	Root length mycorrhizal (%) Soil	Peat	Vermiculite
No P added	190/88 = 2.16**	68/60 = 1.13^{NS}	43/41 = 1.04^{NS}	82.8 c[z]	51.0 f	0.8 a
NaH_2PO_4 (11 ppm)	220/148 = 1.49**	309/282 = 1.10^{NS}	154/170 = 0.90^{NS}	78.9 c	32.8 e	10.5 b
NaH_2PO_4 (43 ppm)	294/260 = 1.13^{NS}	422/447 = 0.88^{NS}	213/225 = 0.95^{NS}	53.0 b	5.2 b	0.3 a
Bonemeal (20 g/liter)	263/337 = 0.78^{NS}	332/348 = 0.95^{NS}	173/199 = 0.87^{NS}	42.2 ab	1.1 a	1.4 a
Bonemeal (80 g/liter)	179/236 = 0.76^{NS}	119/86 = 1.38^{NS}	---	26.9 a	0.4 a	---
Rock phosphate (12 g/liter)	222/153 = 1.45*	418/393 = 1.06^{NS}	90/127 = 0.71*	79.6 c	20.3 d	36.9 d
Rock phosphate (50 g/liter)	270/237 = 1.14^{NS}	407/394 = 1.03^{NS}	178/255 = 0.70*	73.4 c	14.0 cd	30.7 d
Rock phosphate (200 g/liter)	314/307 = 1.02^{NS}	412/399 = 1.03^{NS}	252/310 = 0.81^{NS}	58.0 b	9.2 bc	20.2 c

[z]Mean separation within columns by Duncan's multiple range test, 5% level.

^{NS}, *, **Nonsignificant (NS) or significantly different from nonmycorrhizal controls at 5% (*) or 1% (**) levels (*t* test).

with the various P treatments ($r = -0.883$, $P < 1\%$ for soil; $r = -0.799$, $P < 1\%$ for peat). Host growth response to *G. fasciculatum* in soil was correlated positively with formation of mycorrhizae ($r = 0.827$, $P < 1\%$); in peat there was no correlation ($r = 0.105$); and a negative correlation existed for plants grown in vermiculite ($r = -0.911$). Host plant growth response in soil was correlated negatively with shoot P concentration of mycorrhizal plants ($r = -0.768$, $P < 1\%$ and correlated positively with the P concentration of mycorrhizal plants relative to nonmycorrhizal controls ($r = 0.545$, $P < 5\%$). These 2 variables were not related to host growth response when plants were grown in peat or vermiculite ($P < 5\%$).

Equilibrium solution P concentrations were uniformly low in soil, and in vermiculite when bonemeal or rock phosphate was used (Table 3), and thus could not be tested for correlation with host growth response. When soluble P was applied, appreciable amounts were in solution in peat and vermiculite at equilibrium. Smaller amounts were found in solution in peat when rock phosphate was used as a P source, but fertilization with bonemeal resulted in the highest solution P concentrations. There was no significant correlation between host plant growth enhancement in peat treated with the various P fertilizers and equilibrium solution P concentration ($r = 0.115$, NS).

Media amendments. Colonization of geranium roots by *G. fasciculatum* was increased when Turface, silt loam soil, bentonite clay, or anion-exchange resin were added to either peat or vermiculite at all levels tested (Table 10). The addition of clay subsoil at 10%, 25%, or 50% increased formation of VAM on plants grown in peat, but only increased formation of VAM on those grown in vermiculite when used at the lowest level (10%). Adding cation-exchange resin or liquid sludge reduced fungal colonization of host roots (Table 10). Growth of both VAM and nonmycorrhizal plants varied considerably in the different amended media (Table 10).

Turface, silt loam soil, clay subsoil, bentonite clay, and liquid sludge all resulted in a significant mycorrhizal growth response of plants grown in either peat or vermiculite amended with these substances at nearly all levels tested. Host growth was unaffected by inoculation with *G. fasciculatum* in either medium unamended or amended with cation-exchange or anion-exchange resins. No data are reported for plants grown in peat amended with cation-exchange resin at 80 g/liter because these plants died. Increase in shoot P concentration in plants with VAM was not significantly correlated with host plant growth response to VAM in this experiment ($r = 0.405$ for peat treatments, $r = -0.150$ for vermiculite treatments).

The equilibrium solution P concentration of either peat or vermiculite was reduced when Turface, silt loam soil, clay subsoil, or anion-exchange resin were added (Table 11). Cation-exchange resin did not affect the solution P concentration strongly, but liquid sludge increased it.

Discussion

In these experiments, host growth enhancement by VAM only occurred in media containing soil or sand, and VAM growth enhancement was suppressed by increasing the fertilizer P level.

Table 10. Effect of various amendments added to sphagnum peat or vermiculite on establishment of mycorrhizae and VAM growth response of geranium inoculated with *Glomus fasciculatum*.

Amendment	Root length mycorrhizal (%)		Mycorrhizal growth response [proportion of nonmycorrhizal control shoot dry wt (mg)]	
	Peat	Vermiculite	Peat	Vermiculite
Turface (100%)	41.1 cde[z]	62.7 fg	280/296 = 0.95^{NS}	185/115 = 1.61 **
(25%)	58.7 def	55.9 def	337/187 = 1.80**	198/99 = 2.00**
(50%)	58.3 de	63.5 fg	275/122 = 2.25**	142/71 = 2.00**
Silt loam soil (10%)	61.7 ef	58.7 ef	327/295 = 1.11^{NS}	168/145 = 1.16 *
(25%)	62.9 ef	63.8 fg	314/200 = 1.57**	239/133 = 1.80**
(50%)	64.9 ef	73.3 g	294/195 = 1.51**	273/127 = 2.15**
Clay subsoil (10%)	68.4 f	51.4 cdef	173/78 = 2.22**	75/46 = 1.63**
(25%)	61.4 def	33.4 b	110/62 = 1.77**	52/44 = 1.18^{NS}
(50%)	44.7 cde	39.4 bc	70/40 = 1.75**	41/43 = 0.95^{NS}
Bentonite clay (5%)	62.0 ef	70.1 g	221/132 = 1.67**	212/169 = 1.25*
(10%)	67.0 ef	53.1 def	214/101 = 2.12**	200/224 = 0.89^{NS}
Cation-exchange resin (20 g/liter)	9.4 b	6.7 a	339/340 = 1.00^{NS}	40/46 = 0.87^{NS}
(80 g/liter)	---	0.0 a	---	47/52 = 0.90^{NS}
Anion-exchange resin (30 g/liter)	54.0 de	47.4 cde	287/334 = 0.86^{NS}	103/112 = 0.92^{NS}
(120 g/liter)	60.6 def	50.3 cdef	235/266 = 0.88^{NS}	105/122 = 0.86^{NS}
Liquid sludge (25%)	1.1 a	1.2 a	548/410 = 1.34*	430/327 = 1.31*
(50%)	1.2 a	1.1 a	418/290 = 1.44*	542/523 = 1.04^{NS}
Unamended control	33.2 c	29.5 b	251/265 = 0.91^{NS}	147/156 = 0.94^{NS}

[z]Mean separation within a column by Duncan's multiple range test, 5% level.

NS, *, **Nonsignificant (NS) or significantly different from nonmycorrhizal controls at 5% (*) or 1% (**) levels (*t* test).

Table 11. Equilibrium solution P concentration of sphagnum peat or vermiculite containing various amendments after saturation with fertilizer solution containing 11 ppm P.

Amendment	Equilibrium solution P conc (ppm)	
	Peat	Vermiculite
Turface (10%)	2.93	4.16
(25%)	1.55	2.05
(50%)	1.21	1.34
Silt loam soil (10%)	2.05	2.05
(25%)	1.34	<0.28
(50%)	<0.28	<0.28
Clay subsoil (10%)	<0.28	<0.28
(25%)	<0.28	<0.28
(50%)	<0.28	<0.28
Cation-exchange resin (20 g/liter)	---	7.34
(80 g/liter)	---	8.91
Anion-exchange resin (30 g/liter)	4.16	2.05
(120 g/liter)	2.05	1.34
Liquid sludge (25%)	52.20	21.10
(50%)	127.00	28.10
Unamended control	5.22	6.28

In soilless media, mycorrhizal fungi did not colonize plants as extensively and did not increase host P concentration. This phenomenon occurred with both host species and all 3 fungus species used in these experiments, indicating that the phenomenon probably is applicable to most VAM associations. Schultz et al. (23) found that spore production followed a similar pattern, with the greatest sporulation occurring in media containing soil, and the least in artificial, soilless media. Our results support the conclusion of Gaunt (10) that adding vermiculite to soil decreased mycorrhizal development and dependency by diluting the beneficial effects of the soil.

Host growth response to mycorrhizae and amount of colonization generally were related in these experiments, although growth enhancement of subterranean clover occurred when as little as 4.4% of the root length was colonized in soil/bark (Tables 1 and 2). Shoot growth increased by VAM were associated frequently with decreased root-to-shoot ratios. Likewise, adverse effects of VAM on shoot growth in some cases could be partially explained by slight increased in the root-to-shoot ratio.

Zak and Parkinson (24) found that the addition of sphagnum peat to mine spoils increased formation of VAM on slender wheatgrass. This was attributed to the presence of propagules of mycorrhizal fungi in the peat, rather than to the conduciveness of peat as a medium for VAM formation. None of the peats tested by us was as favorable a medium as silt loam soil for development of VAM and host plant growth response. However, we found no evidence that low concentrations of soluble substances found in peat inhibit the establishment and functioning of VAM, as observed by Peuss (20). It is possible that VAM-suppressive microorganisms caused effects observed by Peuss (20), and were eliminated by pasteurization in our experiments. Biological components of certain soils have been shown to inhibit VAM development (22). The degree of plant growth enhancement by mycorrhizae varied considerably between different peats diluted with soil, and this appeared to be related to the equilibrium solution P concentration of the fertilized peats (but not extractable P of unfertilized peats). This parameter could be used to predict the extent of inhibition of VAM by any given peat in formulating growth media or soil amendments for production of mycorrhizal plants.

Use of rock phosphate or bonemeal instead of NaH_2PO_4 did not improve establishment of VAM = (VAM) fungi and host growth response in any medium. Our results using various forms of fertilizer P support the conclusion of Pairunan et al. (19) that VAM increase host growth and P content of shoots at low or intermediate rates of P application, regardless of the solubility of the P source. Thus, host plant growth response to inoculation of soil with *G. fasciculatum* decreased when phosphate was apparently more available to nonmycorrhizal plants, as reflected in their higher shoot dry weight and P concentration.

The increase in colonization of roots and host growth response to *G. fasciculatum* obtained by adding Turface, bentonite, silt loam soil, and clay subsoil to peat or vermiculite could make these amendments practical for container-grown VAM plants. Small amounts (5–10%) of these amendments were effective. Turface was first found to be an effective medium for fungal colonization of roots and spore production by vesicular–arbuscular fungi by Furlan and Fortin (9).

The virtual absence of mycorrhizae on plants grown in media amended with liquid sewage sludge agrees with the lack of VAM in sludge-amended mine spoils observed by Zak and Parkinson (24), and with the lack of growth enhancement by VAM when sludge was added to a soil/peat/sand medium (14). The high equilibrium solution P level in sludge-amended media and high P level in shoots of plants grown in media containing sludge explain the low colonization level. We cannot, however, explain the growth enhancement from mycorrhizal inoculation which we observed in sludge-amended media in the absence of root colonization.

It is likely that the higher levels of phosphate which we detected in the ambient solution in fertilized media which did not contain soil or clay reduced VAM development and enhancement of host growth and P uptake. This is consistent with the effects of P application observed by us and by others (11, 12, 17, 19). VAM development and enhancement of host growth and P uptake were correlated negatively with the logarithm of the ambient solution P concentration of the various fertilized media (Fig. 5–7). Media amendments, such as soil and Turface, which removed applied P from solution, increased VAM development and enhancement of host growth in peat or vermiculite. Bentonite had a similar effect, and likewise absorbs appreciable amounts of P (Biermann, unpublished data). Anion-exchange resin also removed soluble P and increased VAM colonization of roots.

The maximum solution P concentration at which we observed a mycorrhizal growth response (4 ppm; Fig. 5) is similar to that in data of Bethlenfalvay and Yoder (3) for mycorrhizal soybean. Significant growth enhancement occurred in their experiments at solution P concentration of 0.1, 0.6, and 3.1 μg/g P, but not at 15.5 μg/g. Colonization and relative P uptake by VAM are also reduced greatly when plants are grown in media with solution P concentration greater than approximately 5 ppm (Fig. 6 and 7). Thus, it appears that about 4–5 ppm is the critical level at which the solution P concentration to which roots are exposed affects mycorrhizal development and function. For some soils this may correspond to the 34 ppm Olsen extractable P which was used by Menge et al. (16) as a guideline in predicting mycorrhizal dependency of Troyer citrange.

Even at relatively low fertilizer P levels, with correspondingly reduced solution P levels, growth enhancement by *G. fasciculatum* in peat or vermiculite was not significant; growth enhancement occurred only in soil. Although the P concentration of the ambient solution strongly affects the development of VAM and host growth response (3), other properties of the medium must also be involved. Effects of soil and clay on VAM could be due to matric effects on P diffusion rates. The net result would be more efficient uptake of P by the fungal hyphal network than by host roots. Another possibility is that clay-bound phosphate may be more available to mycorrhizal than to nonmycorrhizal roots.

The initial P content of some media may inhibit VAM fungi, although our data indicate that soluble P after fertilization may be a better indicator of potential effectiveness of mycorrhizal inoculation.

Differences between media may also be due to microbial factors. Bolton (6) found that Pythium root rot was more severe in soilless mixes than in those containing soil and attributed this to a lack of antagonistic microorganisms. The presence of organisms antagonistic to VAM fungi—or the absence of organisms which interact with VAM to provide growth enhancement—could cause the effects observed in soilless media. However, the mycorrhizal growth enhancement with relatively sterile substances (Turface and bentonite) indicates that the effect was due to physical or chemical rather than biological properties of the amendments.

Although soilless media in this study were not as favorable to development of VAM as those with soil, it may still be beneficial to inoculate plants grown in these media to take advantage of VAM to alleviate stresses if they are to be transplanted into soil later. Also, when plants are grown for longer periods than the 5 weeks we used here, mycorrhizae may be more useful in soilless media, although they still probably would not give as much host growth response as in soil (5). It may be possible to improve establishment of VAM and host growth response in soilless media by incorporating substances into the medium which remove P from solution or by using only very low levels of soluble P fertilizer.

For economic production of mycorrhizal plants, rapid plant growth is essential, as well as development of VAM. Use of P-adsorbing amendments may be the most practical solution, since they retain P in a form which is apparently available to VAM plants, but may not be as inhibitory as ambient solution P. P levels adequate for rapid growth of VAM plants could then be maintained.

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