Comparisons Between P-Fertilized and Mycorrhizal Plants[1]

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ABSTRACT

In experimentation with vesicular-arbuscular mycorrhizal (VAM) fungi, the availability of non-VAM control plants of equal size to VAM plants is a fundamental requirement. The purpose of this work was to determine nutrient regimes needed to achieve growth equivalence between VAM and non-VAM plants. Soybean [*Glycine max* (L.) Merr.] cv. Amsoy 71 and sorghum [*Sorghum bicolor* (L.) Moench] cv. Bok 8 plants were grown under controlled conditions in a soil (Josephine silty clay loam, mesic Typic Haploxerult) low in plant-available P. Soybeans were inoculated with one of four species and sorghum with one of two species of VAM fungi. Non-inoculated control plants received nutrient solutions that contained 0.0, 0.2, 0.4, or 1.0 m*M* P. While the growth of P-supplemented controls may be equivalent to VAM plants, an important question remains: Are these plants also equivalent in terms of such functional parameters as leaf development, dry matter partitioning, and nutrient assimilation? The objective of this experiment was to answer these questions. The response to VAM colonization was similar in both hosts, although less extensive colonization was observed in sorghum. Dry weight, leaf area, and P content increased exponentially with nutrient solution P level. Plants colonized with VAM fungi grew 3 to 6 times larger than the P-free controls but attained only 35 to 65% of maximum growth possible with high fertilizer P input. Host response to VAM colonization was equivalent to that of plants receiving between 0.12 and 0.22 m*M* P for phytomass, leaf area, and N content. Mycorrhizal plants contained less P, Mn, and root Fe but more Zn and Cu than comparable plants fertilized with P. It was concluded that P-treated, non-VAM plants differed physiologically and anatomically from VAM plants of equivalent size grown under P stress. It may therefore be necessary to establish the comparability of VAM plants and of "VAM-equivalent controls" separately for each plant parameter of interest. Even then, differential growth responses in VAM-host associations may prevent complete comparability between VAM and P-fertilized plants.

Additional index words: Glomus, Micronutrient, Phosphorus nutrition, Sorghum, Soybean.

PLANTS exhibit a wide range of host responses to vesicular-arbuscular mycorrhizal (VAM) colonization under different environmental conditions (32). External conditions affecting P (3, 28) and carbohydrate (7) availability to the symbiotic partners influence the magnitude of host-plant growth. The nutritional status the non-VAM plants used as controls affects the interpretation of mycorrhizal effects (31). In all comparisons of VAM and non-VAM plants, a fundamental problem is to obtain plants of similar size and development. Non-VAM plants supplied with additional P to compensate for enhanced P uptake by VAM fungi have been used experimentally in an attempt to obtain comparable controls (25, 26, 31). While apparent growth of such controls may be equivalent to VAM plants, an important question remains: Are these plants also equivalent in terms of such functional parameters as leaf development, dry matter partitioning, and nutrient assimilation? The objectives of this study were: i) to measure the growth response of soybean [*Glycine max* (L.) Merr.] and sorghum [*Sorghum bicolor* (L.) Moench] to P fertilization or VAM colonization, ii) to determine the P input needed by non-VAM plants to produce growth equivalent to that of VAM plants, and iii) to compare some morphological characteristics and nutrient content of VAM plants with those of non-VAM plants.

MATERIALS AND METHODS

Biological Materials

Soybean (cv. Amsoy 71) plants were inoculated with one of four species of VAM fungi or remained non-inoculated and received one of four P-amended nutrient solutions. Three species of VAM fungi, *Glomus epigaeum* Daniels and Trappe (12), *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe (14), and an undescribed *Glomus* species, used in the study were collected from the Anzo-Borrego Desert State Park, California (6). The fourth species, the Gerdemann isolate of *Glomus fasciculatum* (Thaxter *sensu* Gerd.) Gerd. and Trappe was obtained from Abbott Laboratories (Long Grove, IL 60047)[3]. All fungi were cultured for 6 months on sorghum (cv. G766) grown in a sand/perlite (2/1,v/v) medium. Spores of each species were collected by wet sieving. Approximately 100 ± 7 spores of each VAM isolate were used as inoculum for plants grown in this experiment.

Soybean seeds (0.5 to 0.6 g) were surface sterilized successively in 0.7 L L^{-1} ethanol (1 min), 1.0 g L^{-1} $HgCl_2$ (10 min), and 0.01 *N* HCl (10 min); rinsed with sterile, distilled water; and germinated for 2 days at 27°C. Three seedlings were planted in 1.5 L pots and were initially treated with a leachate of the original VAM cultures free of VAM propagules to establish similar biota in VAM and control treatments. The two smallest plants per pot were removed after 1 week. Each treatment was replicated six times in a randomized-block design. Plants were harvested after 9 weeks.

Sorghum (cv. Bok 8) was tested for response to *G. fasciculatum* and *G. mosseae* only. For each pot, six seeds (0.15 to 0.25 g) were surface sterilized using the procedure described for soybean, planted, and thinned to three plants per pot after 1 week. Each treatment was replicated five times in a randomized-block design. Plants were grown for 9 weeks.

Soil

Soil used was a moderately acid (pH 5.7) Josephine silty clay loam (fine-loamy, mixed, mesic Typic Haploxerult), obtained from the University of California Field Station at Hopland, CA, and collected from 0 to 100 mm depth. Soil tests showed 4 μg g^{-1} Olsen-available P, 0.31 mg g^{-1} total P, 0.95 g P retained g^{-1} P added, 12.8 μg g^{-1} NH_4^+-N, 4.2 μg g^{-1} NO_3^--N, 1.5 mg g^{-1} Kjeldahl-N, and 27 mg g^{-1} organic matter. Chelate extraction (20) yielded 21 μg g^{-1} Fe, 110 μg g^{-1} Mn, and 0.6 μg g^{-1} Cu. Soil was sieved (10-

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[3] Reference to a company and/or product named by the department is only for purposes of information and does not imply approval or recommendation of the product to the exclusion of others which may also be suitable.

mm mesh), sterilized with ethylene oxide (12 h, 45°C), incubated for 3 weeks after sterilization, and limed (10g $CaCO_3$ kg^{-1} soil) according to Peech (27) to alleviate Mn toxicity (final pH 7.1). Each 1.5 L pot received 1.25 kg of soil, which was covered with a 20-mm layer of perlite.

Nutrient Solutions

The nutrient solution was equivalent to one-quarter strength Johnson's solution (18), except in P. Micronutrients were supplied as described previously (7). Phosphorus was added as either 0.0, 0.2, 0.4, or 1.0 m*M* KH_2PO_4. The pH of each solution was adjusted to 6.9 with 0.01 *N* KOH. Pots inoculated with VAM fungi received the same solution as the 0.0 m*M* P treatment (-P control). All pots were watered to field capacity with the appropriate nutrient solution 3 times a week for 6 weeks and 5 times a week for the last 3 weeks of the experiment. Once each week pots were flushed with 0.5 L deionized water. Phosphorus input into the plant-soil system was calculated from the mean volume of nutrient solution retained per pot at field capacity, the schedule of application, and the solution-P concentration. During the last 4 weeks leachate was collected from P-fertilized pots and analyzed for soluble P after watering with nutrient solution (23). The highest concentration of P in the leachate (0.05 m*M*) was from the pots receiving 1.0 m*M* P.

Growth Conditions

Soybean plants were grown in a greenhouse in Albany, CA from April to June 1982, with temperature and relative humidity varying within the maximum day/minimum night ranges of 32/19°C and 50/90%, respectively. Average photosynthetic photon flux density (PPFD) was 900 μmol m^{-2} s^{-1} at 1200 h on sunny days or 250 μmol m^{-2} s^{-1} on overcast days. Sylvania 1000 W metal halide lamps mounted vertically in parabolic reflectors provided supplementary PPFD of 500 μmol m^{-2} s^{-1} at plant emergence level during the light period of the 16/8 h day/night cycle. Sorghum plants were grown in a growth chamber (Sherer model CEL 36-10, Marshall, MI 49068) with day/night temperatures of 30/25°C and RH of 45/85%. The light/dark period was 16/8 h, and PPFD varied from 550 to 450 μmol m^{-2} s^{-1} from the center to the edge of the growth platform. Plants were rotated daily within blocks to avoid positional effects.

Evaluations and Assays

All plants were harvested at 9 weeks after planting. For soybeans, in most cases, this corresponded to beginning bloom (R1) or full bloom (R2) stage (13). Leaf area was determined for soybean plants using a Li-Cor L-1500 leaf area meter (Lincoln, NE 68504). Sorghum leaf area was not determined. Leaf, stem, and root dry weights were measured after drying for 2 days at 70°C. Plant N content was measured with an ERBA (Turin, IT.) model 1400 autoanalyzer and plant P content by the method of Allen (1). The method of analysis for ash, Fe, Mn, Cu, and Zn was according to Chapman and Pratt (10). Percent colonization of roots by VAM fungi was evaluated visually (8).

The chitin (poly-β-1,4-N-acetylglucosamine) content of 20 mg of roots from VAM-inoculated plants was determined spectrophotometrically (8). Six replicates from the 0.2 m*M* P treatment were subjected to chitin analyses as were the VAM roots, and the mean absorbance was subtracted from each VAM-root absorbance value to account for contamination by chitin-containing organisms other than VAM fungi. An estimate of the intraradical VAM-fungal biomass was calculated from the chitin content of the extraradical mycelium (88.5 μg chitin mg^{-1} VAM fungus) of *G. fasciculatum* (4) and that of VAM roots. Percent VAM-fungal biomass was calculated from total fungal and root biomass. Determination of extraradical VAM-fungal biomass contained in the soil by the chitin assay (24) was not feasible due to high levels of interfering substances (490 μg hexosamine g^{-1} soil). Soil analyses after harvest were performed to determine the pH (21), available P (34), and total P (30). Plant and soil data were subjected to an analysis of variance, and a Duncan's Multiple Range Test was performed on data for VAM plants and fungal biomass. Plant response as a function of P fertilization was analyzed by curve fitting ($y = a[1 - b \exp(-cx)]$) using the procedures of the Statistical Analysis Systems (2). Means and variances for VAM plants were projected onto these growth curves to determine the equivalent P input and to establish confidence intervals for comparisons of VAM hosts with P-fertilized plants.

RESULTS

Phytomass

Total plant dry weight increased with increasing concentrations of solution P according to the negative exponential function that describes growth relative to nutrient supply (29). For soybean the function was [$y = 31.4 - 28.5 \exp(-2.4x)$] and sorghum [$y = 29.4 - 25.7 \exp(-2.9x)$]. Non-fertilized plants inoculated with one of the four VAM-fungal species weighed 3.5 to 6 times more than the -P control (Table 1). Dry weights of plants inoculated with VAM fungi were comparable and showed no significant differences by regression analysis from those of the 0.2 m*M* P treatment. The pattern of shoot and root increase was different for the two host plants [soybean shoot: $y = 24.7 - 22.9 \exp(-2.4x)$ and sorghum shoot: $y = 17.3 - 15.4 \exp(-2.9x)$], although the total dry weight increase was similar. The increase in shoot to root ratios with P fertilization (Table 1) was more pronounced in soybean than in sorghum. Shoot to root ratios for VAM plants were equivalent to soybeans that received from 0.18 to 0.32 m*M* P by regression analysis, while in sorghum the ratios were higher than those of the 1.0 m*M* P treatment.

Table 1. Dry weights and shoot/root ratios of sorghum and soybean plants inoculated with VAM fungi or fertilized with P.

Treatment	Dry weight		Shoot/root ratio	
	Sorghum	Soybean	Sorghum	Soybean
P concentration (m*M*)† in nutrient solution	g			
0.0	3.55	2.94	1.03	1.82
0.2	15.76	13.88	1.37	2.97
0.4	20.94	20.29	1.41	3.56
1.0	28.16	28.86	1.45	3.81
VAM Fungi				
Glomus sp. nov.	-	9.94**	-	2.94a
G. epigaeum	-	10.00b	-	3.38b
G. fasciculatum	13.35a	12.15b	1.76a	3.10a
G. mosseae	14.25a	17.52c	1.76a	2.88a

* Values having common letters within a column are not significantly different at the 0.05 level (Duncan's).

† Represents 0, 50, 100, and 250 mg P pot^{-1} or 0, 0.22, 0.45 and 1.10 kg KH_2PO_4 m^{-3} soil, respectively.

Leaf Area

For soybean, the increase in primary [$y = 0.15 - 0.12 \exp(-3.0x)$] and secondary [$y = 0.26 - 0.25 \exp(-2.0x)$] leaf area with P fertilization was similar to that of plant dry weight (Table 2). In contrast, the proportion of the total leaf area contributed by the primary (main stem) trifoliates decreased with increasing P. Secondary (lateral branch) leaves accounted for only 25% of the total leaf area in the -P control, while at the highest P level 60% of the total leaf area was produced by the secondary leaves. The average area of primary leaflets [$y = 4020 - 2950 \exp(-2.8x)$] increased more with P input than the secondary leaflets [$y = 1660 - 1260 \exp(-4.3x)$], but total primary leaf area was limited by the fixed number of primary nodes. In VAM plants, developmental stages (13) and number of primary nodes were not significantly different from the 0.2 m*M* P plants. All VAM-plant leaf parameters were equivalent to those of soybeans given between 0.17 and 0.28 m*M* P (regression analysis), except for specific leaf area which corresponded to plants given from 0.0 to 0.11 m*M* P.

Elemental Composition

Soybean root and leaf P content increased markedly as fertilizer P increased, while in sorghum the increase was slight (Table 3). Soybean and sorghum leaves from VAM plants were similar in P content to the -P controls, but root P content was comparable to plants that received from 0.1 to 0.2 m*M* P. Total plant P increased linearly with solution P for soybean [$y = 96.0x - 2.2$, $r^2 = 0.79$, at 0.01 level] and sorghum [$y = 21.3x + 7.1$, $r^2 = 0.83$, at 0.01 level]. The 2 mg P in the seed accounted for nearly all the total plant P in the -P control. Total P in all VAM plants was equivalent to plants given between 0.08 and 0.17 m*M* P as determined by regression analysis. Mycorrhizal plants contained an average of 11 mg P plant^{-1}, 25% in excess of P initially available in the seed and soil. Nitrogen contents for most VAM-colonized soybean plants were similar to the 0.2 m*M* P plants and in sorghum equivalent to the 0.4 m*M* P treatment (Table 3). Total plant N increased exponentially with increases in phosphate fertilizer for soybean [$y = 472 - 380 \exp(-5.3x)$] and sorghum [$y = 300 - 242 \exp(-5.9x)$].

The uptake of micronutrients was significantly modified by VAM plants in comparison to non-VAM plants (Table 4). The Fe and Mn concentrations were lower in VAM plants, particularly in the roots, while the Zn and Cu concentrations were generally higher in VAM plants than in non-VAM plants. Micronutrient concentrations tended to decrease with increasing P addition.

Colonization by VAM Fungi

Soybean and sorghum showed about 50% colonization of root length with *G. fasciculatum* (Table 5). *Glomus mosseae* colonized sorghum roots least effectively and soybean roots most effectively. In soybean,

Table 2. Leaf area parameters and developmental stage for soybean inoculated with VAM fungi or fertilized with P.

Treatment	Developmental level (Stage)†	Developmental level (Nodes)	Primary leaf area	Secondary leaf area	Average area Primary leaflet	Average area Secondary leaflet	Specific leaf area
			m²		mm² leaf⁻¹		m² kg⁻¹
P concentration (m*M*)							
0.0	V12	12	0.03	0.005	1050	400	27.9
0.2	R1	14	0.08	0.079	2320	1120	31.3
0.4	R2	15	0.109	0.154	3060	1450	34.4
1.0	R2	15	0.140	0.224	3820	1640	34.1
VAM fungi							
Glomus sp. nov.	R1	13a*	0.053a	0.039a	1820a	840a	26.8a
G. epigaeum	R1	14a	0.064a	0.050a	1870a	1110bc	29.9bc
G. fasciculatum	R2	14a	0.066a	0.053a	2070ab	930ab	27.3ab
G. mosseae	R2	13a	0.080b	0.076b	2490c	980b	25.6a

* Values having common letters within a column are not significantly different at the 0.05 level (Duncan's).
† According to Fehr and Caviness (13).

Table 3. Concentration of P and N in soybean or sorghum plants inoculated with fungi or fertilized with P.

Treatment	Soybean P content Leaf	Soybean P content Root	Soybean N content Leaf	Soybean N content Root	Sorghum P content Shoot	Sorghum P content Root	Sorghum N content Shoot	Sorghum N content Root
	mg g⁻¹							
P concentration (m*M*)								
0.0	2.0	0.7	60.9	41.0	1.0	0.7	20.3	11.9
0.2	3.0	1.1	50.2	23.7	1.1	0.7	18.0	9.4
0.4	4.2	2.4	44.4	18.0	1.1	0.6	16.7	8.6
1.0	4.9	7.0	35.2	16.8	1.2	0.8	12.5	8.0
VAM Fungi								
Glomus sp. nov.	2.0b*	1.0ab	52.8a	29.1a	–	–	–	–
G. epigaeum	2.2b	1.1bc	54.7a	29.6a	–	–	–	–
G. fasciculatum	2.1b	1.0ab	51.6b	26.1b	0.9a	0.6a	16.5a	8.6a
G. mosseae	1.6a	0.8a	35.8c	26.6b	0.9a	0.6a	15.9a	8.2a

* Values having common letters within a column are not significantly different at the 0.05 level (Duncan's).

Table 4. Micronutrient concentration in soybean or sorghum plants inoculated with VAM fungi or fertilized with P.

Treatment	Fe		Mn		Zn		Cu	
	Leaf	Root	Leaf	Root	Leaf	Root	Leaf	Root
	$\mu g\ g^{-1}$							
Soybean								
P concentration (m*M*)								
0.0	135	661	183	116	36	39	10.3	18.7
0.2	115	788	229	158	23	33	6.2	10.8
0.4	120	610	233	153	23	38	6.1	10.0
1.0	126	806	218	185	22	45	5.9	10.8
VAM fungi								
Glomus sp. nov.	111bc*	453a	170b	87a	79a	136a	11.7ab	30.4a
G. epigaeum	119b	406a	189a	90a	53a	125a	12.2a	33.1a
G. fasciculatum	137a	455a	169b	86a	26c	96b	10.6b	25.2b
G. mosseae	103c	417a	176b	88a	35b	110b	8.5c	19.8c
Sorghum								
P concentration (m*M*)								
0.0	78	543	75	423	47	42	6.8	15.7
0.2	67	610	58	553	29	26	4.3	13.4
0.4	64	311	54	313	31	43	4.5	9.7
1.0	57	441	45	324	26	19	3.5	8.6
VAM fungi								
G. fasciculatum	54z	502x	52z	378y	58w	56z	9.2z	16.2z
G. mosseae	59z	400y	46z	296z	38y	46z	9.5z	15.1z

* Values with common letters within a column are not significantly different at the 0.05 level (Duncan's).

there was a twofold difference in colonization between *G. mosseae* and the new *Glomus* sp. but a sevenfold difference in VAM fungal biomass. Intraradical VAM biomass varied more widely with VAM species than did colonization. The percent fungal biomass was closely correlated with plant dry weight (r = 0.98; at the 0.01 level), total leaf area (r = 0.99; at the 0.01 level), and total plant P (r = 0.86; at 0.01 level). Percent colonization of root length was correlated with dry weight (r = 0.70; at 0.05 level), total P (r = 0.72; at 0.05 level), and total leaf area (r = 0.88; at 0.01 level). In soybean, the percentage of *G. fasciculatum* biomass was twice that found in sorghum. For *G. mosseae*, this difference was fourfold.

Plant Response and P Availability

Soil pH at harvest was between 5.8 and 6.9 for all treatments (Table 6). Soil-available P increased with soluble-P input as did total soil P. The total P input over a 9 week period for the 0.0, 0.2, 0.4, and 1.0 m*M* P solutions was 0, 50, 100, and 250 mg P, respectively. This corresponded to 0, 0.2, 0.45 and 1.1 kg KH_2PO_4 m^{-3} soil. The negative exponential equation describing the response of plant dry weight to soluble P (29) was used to calculate an estimate of P available in the system initially (7 to 13 mg P) and the solution P concentration, which would result in 99% of maximum growth (1.5 m*M* P for sorghum or 1.9 m*M* P for soybean). The $NaHCO_3$-extractable P was 6 mg P pot^{-1} initially and accounted for 50% of the P in the VAM plants; the other 50% could be attributed to uptake from the pool of bound P. Plant growth responses to solution P concentration or soil-available P (measured at the end of the experiment) were different (Table 1). Plant dry weight changed with solution P according to a negative exponential function (29), while the change with soil P was linear ($y = 2.5x - 9.0$, $r^2 = 0.97$; at 0.01 level). Soil available P at harvest was also strongly correlated with leaf and root P (r = 0.94; at 0.01 level), total leaf area (r = 0.97; at 0.01 level), and shoot P content (r = 0.95; at 0.01 level).

Table 5. Colonization of soybean and sorghum roots and fungal biomass of VAM fungi.

Treatment	VAM-fungal colonization of root length	Total intraradical VAM-fungal biomass	Percent VAM-fungal biomass
	%	mg $plant^{-1}$	%
Soybean			
Glomus sp. nov.	37a*	54a	2.1a
G. epigaeum	56c	112b	4.8b
G. fasciculatum	49b	188c	6.0c
G. mosseae	62d	371d	8.2d
Sorghum			
G. fasciculatum	50z	142z	2.9z
G. mosseae	25y	94y	1.8y

* Values with common letters within a column are not significantly different at the 0.05 level (Duncan's Multiple Range Test.

Table 6. Characteristics of Josephine silty clay loam at Week 9 after supporting the growth of soybean or sorghum plants inoculated with VAM fungi or fertilized with P solutions.

Treatment	Soybean			Sorghum		
	Soil pH	Available P	Total P	Soil pH	Available P	Total P
		$\mu g\ g^{-1}$			$\mu g\ g^{-1}$	
P concentration (m*M*)						
0.0	6.1	5.0	305	6.4	4.8	300
0.2	6.2	9.5	318	6.5	8.8	323
0.4	5.9	11.3	331	6.9	11.5	363
1.0	6.0	15.7	360	6.8	15.0	470
VAM fungi						
Glomus sp. nov.	6.0ab*	5.8c	303a	–	–	–
G. epigaeum	6.1b	5.5b	310a	–	–	–
G. fasciculatum	5.9ab	4.7a	300a	6.8a	4.8a	305a
G. mosseae	5.8a	5.0b	308a	6.7a	4.5a	310a

* Values with common letters within a column are not significantly different at the 0.05 level.

DISCUSSION

The comparison of soybean and sorghum plants colonized by VAM fungi with plants grown asymbiotically at different P regimes revealed that many

plant responses to the endophyte corresponded to a specific level of fertilizer-P availability. Dry weight, nodal development, total and average leaflet area, root P-content, and root and shoot N-content of both VAM-hosts were similar to non-VAM plants that received between 0.12 and 0.22 m*M* P under the conditions of this experiment. Such a correspondence in the development of a VAM plant and a non-VAM plant may provide suitable controls in certain applications. However, such plants may be similar in form but dissimilar in function (9, 26).

The present data show morphological and nutritional dissimilarities between VAM plants and plants that received a VAM-equivalent P treatment, which suggest underlying functional differences. Variations in specific leaf area, shoot P-content, micronutrient concentrations, and shoot/root ratios are linked to uptake, assimilation, and allocation processes.

The shoot/root ratio is an important parameter in plant source-sink relationships, as it is a function of carbohydrate and mineral nutrient input and utilization (33). Shoot/root ratios tend to increase with decreasing nutrient stress. This was also observed in VAM plants, where the extraradical mycelium, an extension of the hosts's root system, is known to alleviate P stress (11, 15). Shoot/root ratios in VAM-colonized soybean generally corresponded to that of plants receiving from 0.18 to 0.32 m*M* P, while in sorghum the ratios were higher than that of plants treated with 1.0 m*M* P (Table 1). This finding indicated that in the latter association, fungal colonization was highly conducive to enhanced shoot growth. The high investment of sorghum in root mass and its lower P requirement relative to soybean suggests VAM colonization can be more beneficial to cereals than to legumes in low fertility soils, such as the one used in this study.

The low specific leaf area of VAM soybean plants (Table 2) may be related to the equally low concentrations of P in VAM leaves of both host species (Table 3). It remains to be seen how photosynthetic efficiency and source capacity (33, 35) in VAM plants are affected by these leaf characteristics.

The effect of VAM colonization on micronutrient concentrations in host-plant tissues was striking (Table 4). Complex interactions between P nutrition and micronutrient uptake have been observed (19, 22). The large differences between the enhancement of root and shoot concentrations of these micronutrients in VAM plants may have been due to retention in the fungal storage organs. Little is known about the mechanism of selective exclusion of elements (16). Adaptive advantages in the avoidance of heavy metal toxicity are likely, and have been demonstrated in disturbed ecosystems (17).

The validity of the extent of intraradical VAM-fungal colonization as a measure of host-plant growth response has been questioned (15). In the present study, the relationship between the extent of colonization and growth response was host-specific. Thus, *G. mosseae* was most effective both in enhancing growth and in colonizing soybeans, while *G. fasciculatum* was intermediate in its effect. In sorghum, however, the relationship was reversed. The relative development of host and endophyte in this soil was different from the pattern observed previously in a sand/perlite medium (5), where rapid fungal proliferation resulted in parasitic growth in VAM plants.

The results show that a certain degree of VAM and non-VAM plant equivalence may be achieved by varying the P regimes of non-VAM plants. However, this equivalence may be restricted to morphological characteristics. Further study is needed to understand the physiological differences of VAM and non-VAM plants.

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