Mycorrhiza (1994) 4:185–191

Mycorrhiza

Original papers

Growth and nutrient uptake of sorghum cultivated with vesicular-arbuscular mycorrhiza isolates at varying pH

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Abstract. This study was conducted to determine the effects of different pH regimes on root colonization with four vesicular-arbuscular mycorrhiza (VAM) isolates, and VAM effects on host plant growth and nutrient uptake. Sorghum [*Sorghum bicolor* (L.) Moench] was grown at pH 4.0, 5.0, 6.0 and 7.0 (±0.1) in hydroponic sand culture with the VAM isolates *Glomus etunicatum* UT316 (isolate E), *G. intraradices* UT143 (isolate I), *G. intraradices* UT126 (isolate B), and an unknown *Glomus* isolate with no INVAM number (isolate A). Colonization of roots with the different VAM isolates varied differentially with pH. As pH increased, root colonization increased with isolates B and E, remained unchanged with isolate I, and was low at pH 4.0 and high at pH 5.0, 6.0, and 7.0 with isolate A. Isolates E and I were more effective than isolates A and B in promoting plant growth irrespective of pH. Root colonization with VAM appeared to be independent of dry matter yields or dry matter yield responsiveness (dry matter produced by VAM compared to nonmycorrhizal plants). Dry matter yield responsiveness values were higher in plants whose roots were colonized with isolates E and I than with isolates A and B. Shoot P concentrations were lower in plants colonized with isolates E and I than with isolates A and B or nonmycorrhizal plants. This was probably due to the dilution effect of the higher dry matter yields. Neither the VAM isolate nor pH had an effect on shoot Ca, Mg, Zn, Cu, and Mn concentrations, while the VAM isolate affected not only P but also S, K, and Fe concentrations. The pH × VAM interaction was significant for shoot K, Mg, and Cu concentrations.

Key words: Dry matter yields – Sand culture – Shoot concentrations of P, K, Ca, Mg, S, Mn, Fe, Cu, and Zn – *Sorghum bicolor*

Introduction

Vesicular-arbuscular (VA) mycorrhiza (VAM) isolates vary in responsiveness, establishment, and colonization with plants depending on growth medium pH (El-Kherbawy et al. 1989; Fabig et al. 1989; Mosse 1972a, b). Spore germination can be affected by pH, though this effect varies among isolates (Bartolome and Schenck 1990; Daniels and Trappe 1980; Green and Graham 1976). VAM hyphal growth can also be affected by pH (Bartolome and Schenck 1990). Differential colonization of VAM at different pH has been noted (El-Kherbawy et al. 1989), but the response was inconsistent, and relationships between pH and root colonization are not well understood (Sparling and Tinker 1978). Root colonization and dry matter yield (DMY) responsiveness [dry matter produced by VAM compared to nonmycorrhizal (non-VAM) plants] appear to be independently related to pH. For example, growth medium pH may alter VAM effects on DMY responsiveness, but not affect root colonization (Hayman and Tavares 1985).

The effect of low pH on VAM fungi may be due to H^+ concentration as well as changes in solubility of nutrients and toxic elements in the growth medium (Siqueira et al. 1984). However, a clear separation of the direct effects of H^+ from those of toxic elements (primarily Al and Mn) has not been reported. This present study was conducted to determine effects of different pH regimes on root colonization with VAM isolates, and VAM effects on host plant growth and nutrient uptake.

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Published as Paper No. 9987, Journal Series, Nebraska Agricultural Research Division from Project No. 12–166

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Materials and methods

This experiment was conducted in a greenhouse with 16 h light (June–July) and 32±6° C using hydroponic sand. Seeds of NB9040 sorghum [*Sorghum bicolor* (L.) Moench] were surface sterilized with 0.5% sodium hypochlorite for 45 min, washed with distilled water, and germinated in rolled paper towels. Two 5-day-old seedlings were transplanted to each 1.8-l plastic pot filled with 3.5 kg of autoclaved (60 min at 120° C and 0.14 MPa) and washed silica sand (Ottawa Silica Co., Ottawa, Ill.[1]). Pots were watered every 3 h from 6:30 to 21:30 with nutrient solution pumped from four 100-l reservoirs (one per pH treatment) through polyethylene tubing to the sand surface. During early stages of growth, plants were watered with 250 ml of nutrient solution per flush (lasting 1 min), and the volume was increased to 400 ml during later stages of growth.

The nutrient solution composition (modified from Clark 1982) was: 25.68 N (8:1 nitrate:ammonium), 7.24 K, 1.94 Cl, 1.82 S, 1.55 Mg, and 0.20 Na in mM, and 65 Fe (as ferric hydroxyethylethylenediaminetriacetate), 50 B, 18 Mn, 8.0 P, 4.6 Zn, 1.6 Mo, and 1.2 Cu in μM. The solution pH was adjusted to the appropriate value by adding 1 N KOH or HCl as needed.

Treatments were arranged in a split plot design with the different treatments randomized within complete blocks with four replications. Treatments consisted of four different pH regimes [4.0, 5.0, 6.0 and 7.0 (±0.1)] allocated in the main plot, and four VAM isolates plus one non-VAM control allocated in the split plot.

VAM inoculum was placed 5 cm below roots in each pot before seedlings were transplanted. Inocula consisted of four VAM isolates [*Glomus etunicatum* UT316 (isolate E), *G. intraradices* UT143 (isolate I), *G. intraradices* UT126 (isolate B), and an unknown *Glomus* isolate with no INVAM number (isolate A)]. Each pot contained approximately 7500 spores of each VAM isolate mixed in autoclaved (20 min at 120° C and 0.14 MPa) inert clay carrier (15 g per pot). The VAM isolates were obtained from a commercial source (NPI, Salt Lake City, Utah). The non-VAM treatment consisted of the same amount of inert clay carrier containing autoclaved spores of each VAM isolate.

Plants were harvested after 45 days growth with VAM (50-day-old plants). Shoots were severed just above the crown, dried at 50° C for a minimum of 5 days, weighed, ground to pass a 40-mesh (0.5 mm) screen, pressed into 500-mg pellets (33 mm diameter), and analyzed for Ca, Cu, Fe, K, Mg, Mn, P, S, and Zn by energy-dispersive x-ray fluorescence (Knudsen et al. 1981).

Roots of plants were washed from sand, cut into 1-cm segments, mixed thoroughly, and their total fresh weight determined. Approximately 2 g fresh weight of roots was stored in 50% ethanol at 4° C for determination of root colonization, and the remaining sample reweighed for fresh weight. Remaining roots were dried at 50° C and weighed. Total root by weight compensated for fresh weight samples taken for determination of colonization.

Percentages of VAM colonization with roots was determined on 1.0-g fresh weight samples by putting the root tissue in 10% KOH for 3 min in an autoclave (120° C and 0.14 MPa) to clear roots, washing with deionized water, acidifying with 10% HCl for 2 h, and staining with aqueous trypan blue (500 ml glycerol, 250 ml water, 250 ml lactic acid, and 0.5 g trypan blue) in an autoclave for 3 min (120° C and 0.14 MPa) (Koske and Gemma 1989; Phillips and Hayman 1970). Stained roots were rinsed with water and immersed in clear lactoglycerol (500 ml glycerol, 250 ml water, and 250 ml lactic acid). Root colonization was assessed using the gridline intersect method from visual observations determined under a dissecting microscope (Giovannetti and Mosse 1980). The presence or absence of colonization was observed on 250 root segments, and the percentage of root colonization calculated.

DMY responsiveness was calculated as the percentage of dry matter produced by VAM compared to non-VAM plants. Data were analyzed using a General Linear Model from SAS (SAS User's Guide 1985). Least significant difference (LSD) values ($P<0.05$) were used to make comparisons among means. Pearson correlation coefficients listed in the text were significant at $P<0.05$.

Results

Percentage root colonization by VAM isolates varied with pH (Fig. 1). Isolate A had highest root colonization at pH 5.0, 6.0, and 7.0, but root colonization with this isolate was lower at pH 4.0. The root colonization of the VAM isolates did not differ at pH 4.0. Root colonization with isolates E and B increased as pH increased, and percentage of root colonization with isolate I was not affected by pH. Isolates B and I had lower root colonization than the other VAM isolates.

Mean shoot DMYs of sorghum plants colonized with various VAM isolates were significantly reduced at pH 7.0 (2.76 mg per plant) compared to the other pH regimes (3.40 at pH 4.0, 3.36 at pH 5.0, and 3.26 pH 6.0 in mg per plant). Similar results were noted for whole plant DMYs (3.92 at pH 7.0 compared to 4.77 at pH 4.0, 4.74 at pH 5.0, and 4.60 at pH 6.0 in mg per plant). Even though root DMYs of plants colonized with the various VAM isolates showed trends similar to shoot and whole plant DMYs, the pH × VAM interaction was significant and thus mean root DMY comparisons were inappropriate. Plants colonized with isolates E and I had higher shoot and whole plant DMYs over the pH regimes studied than plants colonized with isolates A and B or with non-VAM plants; DMYs of plants colonized with isolate E were sligthly higher than those of isolate I (Fig. 2). Differences in DMYs

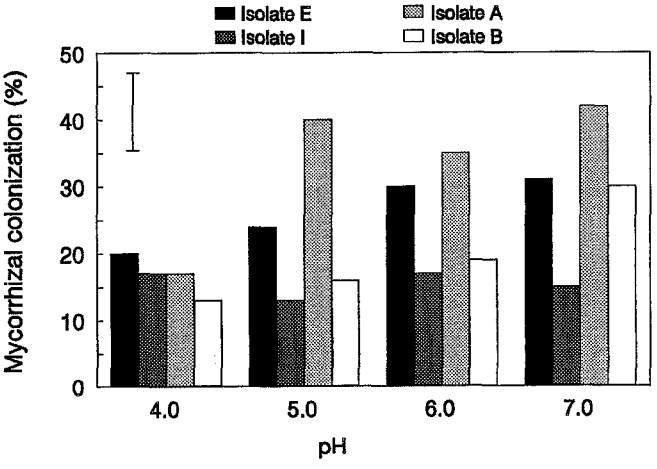

Fig. 1. Mycorrhizal colonization of the roots of sorghum plants grown in sand at pH 4.0, 5.0, 6.0, or 7.0. The *bar* indicates least significant difference (LSD) at $P<0.05$

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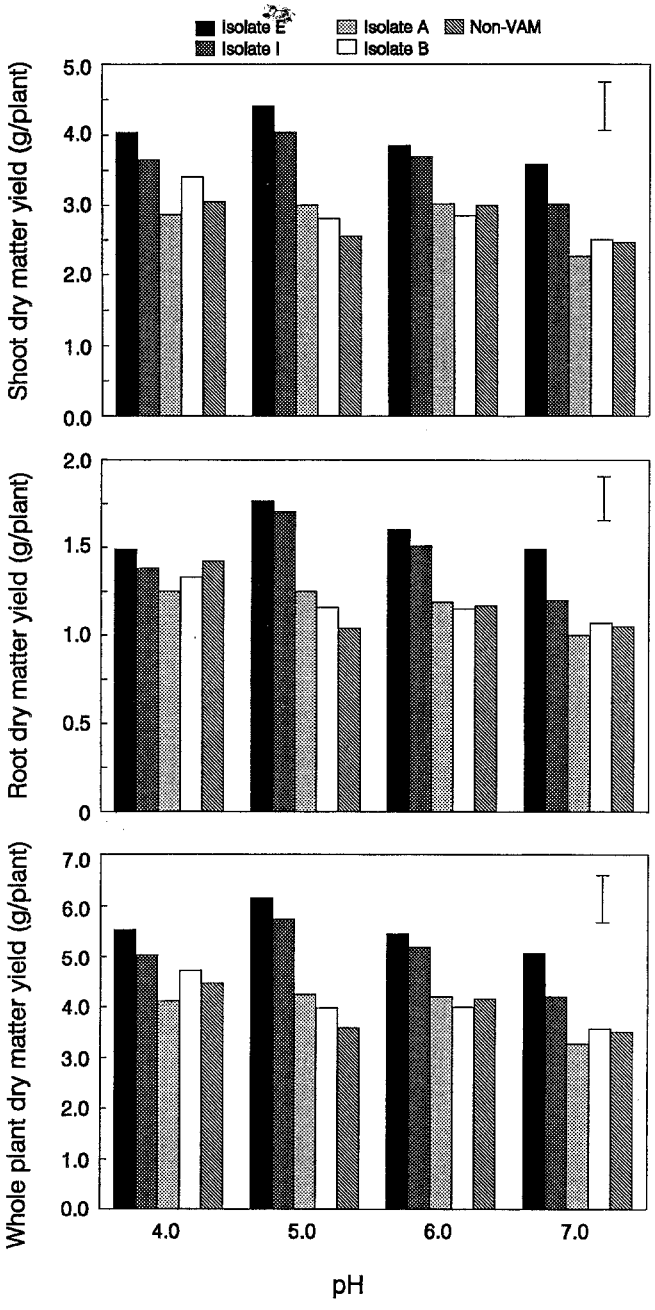

Fig. 2. Shoot, root, and whole plant dry matter yields of vesicular-arbuscular mycorrhiza (VAM) and non-VAM sorghum grown in sand at pH 4.0, 5.0, 6.0, or 7.0. The *bars* indicate LSD at $P<0.05$

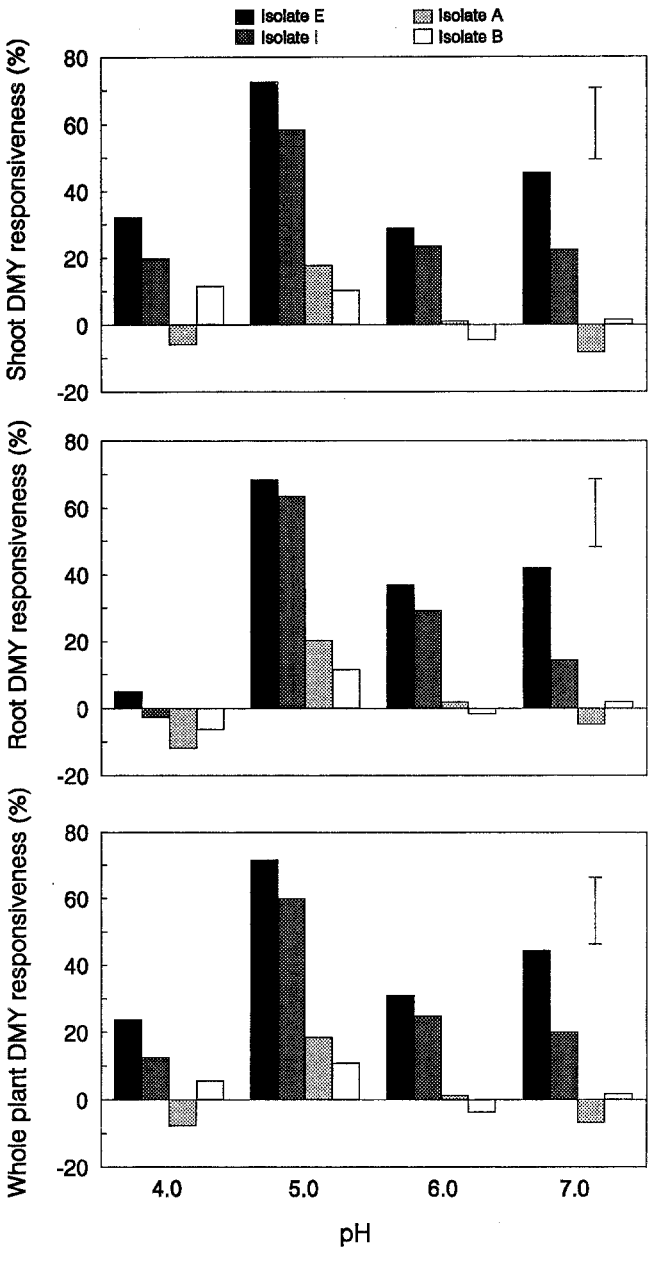

Fig. 3. Shoot, root, and whole plant dry matter yield (*DMY*) responsiveness (percentage of dry matter produced by VAM compared to non-VAM plants) of sorghum grown in sand at pH 4.0, 5.0, 6.0, or 7.0. The *bars* indicate LSD at $P<0.05$

between plants colonized with isolates E and I or isolates A and B were especially large at pH 5.0. Whole plant DMYs of plants colonized with isolates E and I were 41 and 28% higher, respectively, than non-VAM plants. Plants colonized with isolate E had more constant DMYs over the pH regimes studied than the other VAM isolates. From pH 4.0 to pH 7.0, whole plant DMYs were reduced 8, 16, 21, 24, and 21% in plants colonized with isolates E, I, A, and B, and non-VAM plants, respectively, compared to the highest DMYs obtained at any pH regime. Shoot and root DMYs of plants colonized with isolates A and B were similar to those of non-VAM plants over the pH regimes studied.

Values of DMY responsiveness for shoots, roots, and whole plants were highest in plants colonized with isolate E, followed by plants colonized with isolate I, and lowest in plants colonized with isolates A and B (Fig. 3). None of the DMY responsiveness values were below zero for plants grown at pH 5.0, but several of the values were near or below zero for plants grown at pH 4.0, 6.0, and 7.0, especially for plants colonized with isolates A and B.

Shoot P concentrations differed with pH only in plants colonized with isolates A and B or in non-VAM plants at pH 6.0 and 7.0 (Table 1), while pH had no effect on the concentrations of the other nutrients for all VAM isolates or for non-VAM plants (Tables 1–5). In contrast, colonization by VAM isolates had significant effects on the concentrations of P and also on S, K, and Fe. Plants colonized with isolates E and I generally had higher S concentrations than plants colonized with isolates A and B or non-VAM plants (Table 1). Plants colonized with isolate B and non-VAM plants had higher K concentrations than plants colonized with isolates E and I (Table 2). Plants colonized with isolate A had higher shoot Fe concentrations than plants colonized with isolates E and B or non-VAM plants (Table 5). The pH × VAM interactions were significant for shoot K (Table 2), Mg (Table 3), and Cu (Table 4) concentrations.

Shoot mineral contents were higher in plants colonized with isolates E and I than in plants colonized with isolates A and B or in non-VAM plants (Tables 1–5). Since mean shoot DMYs were lower at pH 7.0 and similar but somewhat higher at the other pH regimes, shoot mineral contents of all elements, except Ca and Mn, tended to be lower at pH 7.0 than at pH 4.0, 5.0, and 6.0.

Discussion

Decreases in shoot DMYs at pH 7.0 cannot be explained by pH effects on mineral concentrations because mineral concentrations were not reduced at this higher pH. The decreased plant growth at pH 7.0 may have caused increases in the concentrations of nutrients (concerning effect). Reduction in DMYs as nutrient medium pH increased has previously been reported in VAM studies with sorghum and wheat (*Triticum aestivum* L.) (Fabig et al. 1989) and sweetgum (*Liquidambar styraciflua* L.) (Yawney et al. 1982).

Table 1. Shoot P and S concentrations and contents of sorghum grown with various VAM isolates at pH 4.0, 5.0, 6.0, and 7.0. For the identification of the VAM isolates, see Materials and methods. LSD, Least significant difference

pH	Phosphorus VAM isolate					Sulfur VAM isolate				
	E	I	A	B	Non-VAM	E	I	A	B	Non-VAM
Concentration (mg g^{-1})										
4.0	0.78	0.83	0.89	0.83	0.88	1.23	1.25	1.30	1.29	1.32
5.0	0.75	0.80	0.99	1.03	1.14	1.27	1.27	1.35	1.36	1.43
6.0	0.68	0.75	0.88	0.95	0.97	1.24	1.27	1.30	1.34	1.35
7.0	0.73	0.89	1.00	0.85	1.11	1.26	1.32	1.32	1.31	1.33
LSD (0.05)			0.18					0.12		
Content (mg per plant)										
4.0	3.15	3.03	2.54	2.81	2.68	4.95	4.51	3.74	4.41	4.01
5.0	3.29	3.20	2.94	2.87	2.90	5.58	5.12	4.03	3.81	3.64
6.0	2.64	2.74	2.66	2.72	2.89	4.77	4.70	3.88	3.80	4.03
7.0	2.61	2.66	2.26	2.12	2.69	4.49	3.96	2.99	3.27	3.26
LSD (0.05)			0.69					0.92		

Table 2. Shoot K and Ca concentrations and contents of sorghum grown with various VAM isolates at pH 4.0, 5.0, 6.0, and 7.0

pH	Potassium VAM isolate					Calcium VAM isolate				
	E	I	A	B	Non-VAM	E	I	A	B	Non-VAM
Concentration (mg g^{-1})										
4.0	31.5	35.1	33.3	33.0	33.8	3.09	3.29	2.94	3.23	2.89
5.0	29.2	32.1	33.7	33.9	34.8	2.88	3.03	3.07	3.14	2.72
6.0	29.5	29.6	31.9	36.5	37.7	2.98	2.77	3.05	3.23	3.27
7.0	33.5	34.4	31.9	28.9	32.8	3.31	2.87	3.11	2.94	2.83
LSD (0.05)			6.2					0.78		
Content (mg per plant)										
4.0	128	129	94	113	103	12.5	12.1	8.5	11.0	8.8
5.0	130	131	100	96	88	12.8	12.3	9.2	8.9	6.9
6.0	114	107	97	104	112	11.6	10.1	9.3	9.2	9.8
7.0	120	104	73	72	82	11.7	8.7	6.9	7.2	6.8
LSD (0.05)			32					3.2		

Table 3. Shoot Mg concentrations and contents of sorghum grown with various VAM isolates at pH 4.0, 5.0, 6.0, and 7.0

pH	Magnesium VAM isolate				
	E	I	A	B	Non-VAM
Concentration (mg g^{-1})					
4.0	1.21	1.20	1.07	1.45	1.12
5.0	1.41	1.38	1.28	1.00	1.10
6.0	1.31	1.18	1.43	1.30	1.32
7.0	1.12	1.33	1.16	1.45	1.24
LSD (0.05)			0.28		
Content (mg per plant)					
4.0	4.90	4.41	3.13	4.86	3.41
5.0	6.16	5.59	3.80	2.78	2.77
6.0	5.07	4.33	4.26	3.74	3.93
7.0	3.98	3.99	2.64	3.59	2.98
LSD (0.05)			1.14		

Interspecific variations of DMY responsiveness at different pH regimes have been reported (Fabig et al. 1989). In our study, isolates E and I were most effective in increasing plant growth at the different pH regimes used. DMY responsiveness of VAM isolates was highest at pH 5.0 (Fig. 3), especially for isolates E and I, indicating that this pH was favourable for the VAM isolates used in this study to increase plant growth. Plants whose roots were colonized with isolates A and B had low DMY responsiveness values, and some values were even negative. As such, DMYs were not increased by these VAM isolates over the pH regimes studied.

The results of our study support the concept that root colonization and DMY responsiveness are independent of each other. Even though root colonization for three of the VAM isolates was higher at pH 7.0 than at pH 4.0, VAM isolates had higher DMY responsiveness values at pH 5.0. In a study using nine VAM

Table 4. Shoot Zn and Cu concentrations and contents of sorghum grown with various VAM isolates at pH 4.0, 5.0, 6.0, and 7.0

pH	Zinc VAM isolate					Copper VAM isolate				
	E	I	A	B	Non-VAM	E	I	A	B	Non-VAM
Concentration (mg g^{-1})										
4.0	50.7	55.1	60.1	54.4	55.8	9.2	9.7	10.2	9.5	10.4
5.0	48.5	49.1	54.8	50.0	53.9	8.0	7.6	9.6	9.9	8.8
6.0	49.1	48.4	57.2	57.4	50.4	7.1	6.4	10.0	10.0	9.8
7.0	54.3	49.7	46.3	49.4	48.8	10.0	9.2	8.8	8.0	7.4
LSD (0.05)			14.4					2.3		
Content (mg per plant)										
4.0	205	205	173	185	171	37.2	35.0	29.4	32.2	31.6
5.0	211	200	165	141	136	35.4	30.5	28.6	28.3	22.4
6.0	190	178	175	173	151	27.6	23.2	30.2	28.7	29.6
7.0	194	150	103	121	118	35.6	27.8	20.2	19.6	18.1
LSD (0.05)			57					9.2		

Table 5. Shoot Fe and Mn concentrations and contents of sorghum grown with various VAM isolates at pH 4.0, 5.0, 6.0, and 7.0

pH	Iron VAM isolate					Manganese VAM isolate				
	E	I	A	B	Non-VAM	E	I	A	B	Non-VAM
Concentration (mg g^{-1})										
4.0	101	91	114	102	96	46.9	48.4	52.1	51.8	47.0
5.0	80	81	87	78	80	53.0	51.8	54.5	60.9	59.3
6.0	87	77	97	86	95	52.3	53.5	55.7	61.4	58.8
7.0	90	75	92	78	76	67.8	61.0	67.6	62.8	61.6
LSD (0.05)			26					15.3		
Content (mg per plant)										
4.0	409	332	336	344	293	191	178	149	177	142
5.0	350	325	263	219	202	235	210	162	173	149
6.0	337	279	294	244	283	203	194	167	174	177
7.0	319	227	208	190	343	240	184	150	154	147
LSD (0.05)			99					51		

species, most VAM colonized well from pH 4.0 to 7.0 even when they did not increase plant growth (Hayman and Tavares 1985). Results from these studies also indicated independent relationships between colonization, DMY responsiveness, and pH. Overall, isolate A had the highest root colonization, but did not enhance shoot or root DMYs. Other results indicated that growth increases were not necessarily proportional to root colonization (Davis et al. 1983). The findings from our study in which growth medium pH 7.0 increased or maintained high root colonization are in agreement with other results (El-Kherbawy et al. 1989) in which VAM colonization of roots was independent of pH. Reduced shoot DMYs (often interpreted as reduced photosynthetic area) at pH 7.0 apparently did not limit carbohydrate supply for fungi development. Our data indicate that pH alone had strong effects on root colonization. These results contrast with those from other studies in which pH per se had no effect on VAM colonization or DMY responsiveness (Siqueira et al. 1984).

Low internal plant P concentrations have often been associated with colonization of host plant roots (Graham et al. 1981; Ratnayake et al. 1978). No significant correlation between shoot P concentration and VAM colonization with roots was found in our study. At low pH, Al and Mn are normally more available from the growth medium, especially from soils (Foy et al. 1978; Lucas and Knezek 1972; Marschner 1986), and may reach concentrations toxic for plant growth and VAM development. High Mn and Al have been reported to reduce VAM colonization of roots (Wang et al. 1985), and probably also affect DMY responsiveness values. The growth medium used in our study received no added Al, and Mn was supplied only at levels required for plant growth. The availability of elements most likely did not increase to toxic levels in the medium with decreasing pH since washed silica sand was used. These results suggest that H^+ per se can affect VAM colonization of roots and DMY responsiveness. Germination of VAM spores was found to be dependent on growth medium pH (Green and Graham 1976). *G. etunicatum* failed to germinate at pH 4.2, and other *Glomus* species were sensitive to acidity (Bartolome and Schenck 1990). A negative effect of high H^+ on spore germination which reduced the chance of root colonization cannot be ruled out in our study.

Shoot P concentrations were generally higher in non-VAM plants than in VAM plants, except for plants colonized with isolate A. The dilution effect of high DMYs could explain differences noted in plants colonized with isolates E and I. However, plants colonized with isolate B had similar shoot DMYs, but reduced P concentrations, compared to non-VAM plants. Plants with relatively low tissue concentrations of P are sometimes considered to have higher P-use efficiency (DMY produced per unit P in tissue) values since the definition of P-use efficiency in this case is the reciprocal of P concentration. Sorghum plants colonized with isolates E and I had higher P-use efficiency values than plants colonized with isolates A and B and non-VAM plants. VAM plants have been reported to have higher P-use efficiency than non-VAM plants (Koide 1991), although VAM-colonized sorghum plants had lower P-use efficiency values than non-VAM plants in other studies because of higher P concentrations in VAM compared to non-VAM plants (Raju et al. 1990b).

Plants colonized with isolates E and I had the highest shoot DMYs and also had the lowest P concentrations. The negative correlation between shoot DMYs and P concentration in our study ($r = -0.58$) indicated that decreases in shoot P concentrations in plants colonized with isolates E and I could be partially attributed to a dilution effect of higher DMYs. Such a dilution effect has also been reported for *Panicum virgatum* (Koslowsky and Boerner 1989).

Time of harvesting may have contributed to differences in P concentrations observed in shoots of VAM and non-VAM plants. Snellgrove et al. (1986) reported that P. concentrations were higher in VAM than in P-fertilized non-VAM plants during early growth stages (about 30 days from plant emergence), but declined faster in VAM plants and were thus lower in VAM than in non-VAM plants at later stages of growth. Such responses probably occurred in our study, and the time of harvesting may have affected comparisons of P concentrations between VAM and non-VAM plants. By the time of harvest (45 days growth with VAM inocula), differential declines in P concentrations in VAM and non-VAM plants may have affected comparisons among VAM isolates.

Relatively high and significant correlations noted between shoot DMYs and contents of K ($r=0.83$), Ca ($r=0.80$), Mg ($r=0.80$), S ($r=0.96$), Mn ($r=0.69$), Fe ($r=0.69$), and Zn ($r=0.76$) indicated that high DMY production was most likely the main factor enhancing contents of these nutrients in plants having highest DMYs (isolates E and I). Correlations between shoot DMYs and mineral concentrations were usually negative, relatively low, and not significant, except for S ($r=-0.43$). Similar results have been noted for K (Dissing-Nielsen 1989; Raju et al. 1988) and Mn (Raju et al. 1990b), although reduced Ca and Mg concentrations in response to root colonization with VAM have been reported (Menge et al. 1982; Timmer and Leyden 1978). Variable VAM effects on Fe concentration have been noted, both increasing (Kucey and Janzen 1987; Rai 1988; Raju et al. 1990a) and decreasing (Pancovsky 1986; Raju et al. 1990b). Positive effects of VAM on Cu uptake have been reported (Killham 1985; Kucey and Janzen 1987).

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