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2002

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DIFFERENCES AMONG MYCORRHIZAL FUNGI FOR MINERAL UPTAKE PER ROOT LENGTH OF SWITCHGRASS GROWN IN ACIDIC SOIL

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ABSTRACT

Plants commonly encounter deficient and/or toxic levels of mineral elements when grown in acidic soil, and arbuscular mycorrhizal fungi (AMF) have potential to overcome many of these effects. Switchgrass (*Panicum virgatum* L.) was grown in acidic Lily soil (Typic Hapludult) at pH_{Ca} 4 and 5 (soil: 10 mM CaCl_2 , 1:1) and inoculated with *Glomus* (*G.*) *clarum*, *G. diaphanum*, *G. etunicatum*, *G. intraradices*, *Gigaspora* (*Gi.*) *albida*, *Gi. margarita*, *Gi. rosea*, and *Acaulospora* (*A.*) *morrowiae* to determine differences among mycorrhizal (AM) plants for mineral uptake per root length (RL). Shoots of AM plants grown in pH_{Ca} 4 and 5 soil had extensive mineral nutrient content (per plant) differences, and AM plants grown in pH_{Ca} 4 soil generally had higher and wider ranges of mineral contents than plants grown in pH_{Ca} 5 soil. Mineral uptake per RL varied

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extensively among AM plants. The AM plants generally enhanced uptake of phosphorus (P), nitrogen (N), sulfur (S), potassium (K), calcium (Ca), magnesium (Mg), zinc (Zn), and copper (Cu) and reduced uptake of manganese (Mn), iron (Fe), boron (B), and aluminum (Al). The *G. etunicatum* plants particularly had higher P, N, S, K, Mg, Zn, and Cu uptake compared to the other AM plants. Most AMF isolates used were effective in enhancing mineral uptake and reducing excess amounts of toxic elements in shoots.

INTRODUCTION

Plants commonly encounter deficient and/or toxic levels of mineral elements when grown in acidic ($\text{pH} < \sim 5$) soil.^[1,2] Arbuscular mycorrhizal fungi (AMF) have potential to help overcome many detrimental effects in acidic soil and provide plant tolerance to these conditions.^[2-7] One beneficial effect of AMF for alleviating mineral stresses in acidic soil has been attributed to the ability of AMF hyphae to extend beyond the usual nutrient absorption zone of roots and transport essential nutrients to the host plant that roots per se would not otherwise contact, especially P.^[2] Improved tolerance of plants to acidic soil may also be attributed to restricted acquisition of and/or exposure to toxic elements, especially Al and Mn.^[6,8-20]

Plant species and genotypes within species exhibit large differences for tolerance to acidic soils,^[21-24] and so do AMF species and isolates differ in providing plant tolerance to acidic soil.^[6,9,11,15,16,25-28] Much of this has been attributed to AMF enhancement of essential mineral nutrient acquisition and providing plant protection against toxic elements.^[2] Nevertheless, effectiveness of AMF colonized roots for acquiring mineral elements has received only limited attention. For example, the dominant mycorrhizal contribution to maize (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] grown in two tropical soils, regardless of soil pH, was associated with enhanced P uptake per RL (P_{RL}).^[17] The P_{RL} uptake values were generally 2-3-fold higher for mycorrhizal (AM) compared to nonmycorrhizal (nonAM) plants.^[29] Differences were also noted among AMF species.^[30] For example, *Acaulospora* (*A.*) *laevis* subterraneum clover (*Trifolium subterraneum* L.) had 2.5–3.0-fold higher P_{RL} uptake values compared to *Glomus* sp and *Scutellospora* (*S.*) *calospora* plants.

The objective of this study was to determine differences among eight AMF isolates for mineral uptake per RL of switchgrass (*Panicum virgatum* L.) grown in acidic soil.

MATERIALS AND METHODS

The AMF isolates used in this study are listed in Table 1. Seven of the isolates were obtained from the INVAM Program (International Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi, West Virginia University, Morgantown) and one isolate (*Gi. margarita*) was obtained from D. D. Douds (USDA-ARS, Philadelphia, PA). Considerable description and conditions for isolation of the AMF isolates are provided in Morton et al.^[31]

Acidic Lily soil (fine loamy, siliceous, mesic, Typic Hapludult) collected from south central West Virginia was used to grow plants. Some properties of the soil before steam treatment were 43% sand, 39% silt, 18% clay; 4.7% organic matter (Walkley-Black procedure); 3.89 pH_{Ca} (soil : 10 mM CaCl₂, 1 : 1) and 4.48 pH_W (soil : water, 1 : 1); 0.06 dS m⁻¹ electrical conductivity (soil : water, 1 : 1); 3.09 P (Bray-I extractable), 70.0 S, 69.5 K, 45.8 Ca, 5.06 Mg, 2.30 Na (1 M NH₄-acetate extractable), 302 Al (1 M KCl extractable), 33.1 Mn, 53.8 Fe, 0.716 Zn, 0.125 Cu (5 mM DTPA extractable), 0.93 B (hot water extractable) in mg kg⁻¹ soil; 3.82 cmol_c kg⁻¹ soil cation exchange capacity; and 88% Al saturation. Methods of analyses for the various elements/ properties are described in Page et al.^[32]

Air-dried soil was sieved to pass a 2-mm screen, steam treated at 100°C for 30 min, allowed to cool at ambient temperature overnight, again steam treated at 100°C for 20 min, and allowed to stand seven days before being fertilized with NH₄NO₃ at 143 mg kg⁻¹ soil. One batch of soil was not amended to provide soil near pH_{Ca} 4, while a second batch had pH_{Ca} increased to 5 with 2.5 g CaCO₃ kg⁻¹ soil. The amount of CaCO₃ added was limited so that conditions for amended soil still remained fairly acidic.

Inoculum of each AMF isolate was multiplied in the laboratory using sudangrass [*Sorghum bicolor* (L.) Moench] as the host plant grown in Lily soil : sand (1 : 1) mixtures (pH_{Ca} = 5.5). Inoculum of each AMF isolate consisted of soil : sand mix containing root fragments + hyphae + spores. Similar potential of each AMF isolate was added to soil. Because *Gigaspora* AMF did not readily form spores during inoculum multiplication yet readily colonized roots (R. B. Clark and S. K. Zeto, personal observations), inoculum of each AMF isolate was added to soil at given spore counts. In the plant growth soil mixes, *Acaulospora* and *Glomus* inocula had 10000 spores kg⁻¹ soil and *Gigaspora* inocula had 1000 spores kg⁻¹ soil. In all cases, relatively good root colonization percentages were obtained for plants grown in both pH_{Ca} 4 and 5 soil.^[9] NonAM soil received 125 g of control inoculum kg⁻¹ soil, which consisted of soil mix + root fragments where sudangrass had been grown under similar conditions as for AMF multiplication except with no added AMF. Each inoculum was mixed thoroughly with steam treated soil and soil mixes were put in pots (2.0 kg pot⁻¹) for growth of plants.

Table 1. AMF Number, Scientific Name, INVAM/Descriptor Information, Shoot and Total Dry Matter (DM), and Total Root Length (RL) of Switchgrass Grown in pH_{Ca} 4 and 5 Soil with Eight AMF Isolates

AMF No.	AMF Isolate	INVAM/Descriptor [†]	Plant DM		Total RL m Plant ⁻¹
			Shoot	Total	
pH _{Ca} 4 soil					
1	Nonmycorrhizal (nonAM)	—	16	24	1.5
2	<i>Glomus</i> (G.) <i>intraradices</i>	WV894A	12	20	1.4
3	<i>Gigaspora</i> (Gi.) <i>rosea</i>	BR151A	18	28	1.9
4	<i>Gigaspora</i> (Gi.) <i>albida</i>	BR214	99	133	7.5
5	<i>Glomus</i> (G.) <i>etunicatum</i>	WV579A	295	436	22.9
6	<i>Gigaspora</i> (Gi.) <i>margarita</i>	DAOM 194757	313	474	24.1
7	<i>Acaulospora</i> (A.) <i>morrowiae</i>	WV107	348	546	23.8
8	<i>Glomus</i> (G.) <i>diaphanum</i>	WV579B	613	1042	46.3
9	<i>Glomus</i> (G.) <i>clarum</i>	WV751	727	1242	50.2
pH _{Ca} 5 soil					
1	Nonmycorrhizal (nonAM)	—	16	29	2.3
2	<i>Glomus</i> (G.) <i>intraradices</i>	WV894A	190	257	16.7
3	<i>Gigaspora</i> (Gi.) <i>rosea</i>	BR151A	17	28	2.2
4	<i>Gigaspora</i> (Gi.) <i>albida</i>	BR214	290	528	17.3
5	<i>Glomus</i> (G.) <i>etunicatum</i>	WV579A	572	642	45.1
6	<i>Gigaspora</i> (Gi.) <i>margarita</i>	DAOM 194757	525	601	35.8
7	<i>Acaulospora</i> (A.) <i>morrowiae</i>	WV107	354	535	24.4
8	<i>Glomus</i> (G.) <i>diaphanum</i>	WV579B	581	682	54.0
9	<i>Glomus</i> (G.) <i>clarum</i>	WV751	499	701	45.8
	LSD (<i>P</i> ≤ 0.05)		143	259	14.6

[†] Information taken from Morton et al. (1993), except for *Gi. margarita* whose information came from D. D. Douds (USDA-ARS, Philadelphia, PA).

Seeds of the switchgrass cultivar “Cave-in-Rock” were surface sterilized with 70 mM NaOCl for 5 min and rinsed thoroughly before being sown in pots. Pots were irrigated manually with distilled water as needed during the experiment to alleviate leaching from pots, and plants did not undergo water deficit. Care was taken not to splash water or soil onto plant parts during irrigation. Plants were thinned to three pot⁻¹ 10 days after sowing. Plants were grown for 88 days (mid-April to mid-July) in a glasshouse. Additional artificial light from high-pressure sodium halide (1000 W) lamps was provided at 400–500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density at plant height during cloudy days and to provide adequate light to maintain 16 h light periods. Throughout the experiment, temperature ranges did not vary more than 3°C from temperature settings of 28°C for the light period and 23°C for the dark period.

Shoots were severed from roots ~1 cm above the soil surface at harvest, lower stalks were rinsed thoroughly with distilled water and blotted dry, and tissue dried at 60°C for a minimum of three d and weighed. Roots were thoroughly rinsed free of soil when placed on 2 mm screens, blotted dry, cut into 1–2 cm segments, thoroughly mixed, and a representative fresh weight sample collected for root length (RL) determination. Remaining roots were dried at 60°C similar to shoots and weighed. Total RL was determined using a Comair RL scanner (Commonwealth Aircraft Corp Ltd, Melbourne, Australia¹). After total RL measurements were completed, root segments were dried, weighed, and dry matter (DM) included in the total plant dry weight.

Dried shoot samples were ground to pass a 0.5 mm screen, thoroughly mixed, and 50 to 100 mg samples were weighed into Teflon containers. To each container with tissue, 1.0 mL 15.8 M HNO₃ was added, and the Teflon containers placed in microwave digestion bombs (Parr Instrument Co., Moline, IL¹). Samples were microwaved 4 min at 70% followed by 2 min at full power of 635 W. Samples were allowed to cool in the microwave for 5 min before being removed for additional cooling at ambient temperature. Digested solutions were brought to a final volume of 10.0 mL with distilled deionized water. Solutions were filtered and stored in plastic containers at 10°C until analyzed for mineral elements by inductively coupled plasma spectroscopy. Nitrogen in shoot tissue was determined using a Carlo Erba elemental analyzer (Model EA1108, Carlo Erba, Milan, Italy¹), which is a combustion-gas-chromatography procedure.^[33] Shoot mineral contents (mg or μg in shoots plant⁻¹) were calculated by multiplying tissue weight by mineral concentration. Mineral uptake was calculated as content of each mineral element per total RL.

The experimental design consisted of completely randomized blocks with five replications of each AMF isolate in both pH_{Ca} 4 and 5 soil. Data were

¹Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement.

statistically analyzed using analysis of variance procedures, and differences among treatments and means were compared using probabilities of significance and least significant difference (LSD) values ($P \leq 0.05$).

RESULTS

Probability differences were significant ($P \leq 0.01$) between soil pH_{Ca} 4 and 5 and among AMF isolates for contents of each mineral element for plants grown in both pH_{Ca} 4 and 5 soil (data not shown).

Mineral Contents

Plants colonized with the various AMF isolates had large differences in shoot mineral contents (mg or $\mu\text{g plant}^{-1}$) for each element (Table 2). Even though mineral contents generally followed DM (Table 1), many of the mineral differences could not be explained exclusively by DM differences among plants. Mineral contents were generally higher in plants grown in pH_{Ca} 4 than in pH_{Ca} 5 soil. The *G. etunicatum* plants with lower DM compared to some other AM plants greatly benefited acquisition of many elements, especially P, when plants were grown in pH_{Ca} 4 soil. For plants grown in both pH_{Ca} 4 and 5 soil, *G. diaphanum* plants were effective in reducing Mn, and *A. morrowiae* plants had considerably lower Zn than many of the other AM plants.

Phosphorus Uptake

Phosphorus uptake values per RL (P_{RL}) (mineral uptake values per RL are represented by the mineral symbol and the subscript RL in each case) were considerably higher for AM plants that enhanced DM and RL (Fig. 1, Table 1) compared to AM plants that did not enhance DM or RL. The AMF isolates that did not increase DM or RL above that of the nonAM plants were *Gi. rosea* and *G. intraradices* plants grown in pH_{Ca} 4 soil and *Gi. rosea* plants grown in pH_{Ca} 5 soil. That is, ~ 2 -fold differences in P_{RL} were noted among AM plants that had enhanced DM in both pH_{Ca} 4 and 5 soil. Differences between the highest P_{RL} values for AM plants compared to nonAM plants was 18-fold for plants grown in pH_{Ca} 4 soil and 9-fold for plants grown in pH_{Ca} 5 soil. Overall, AM plants grown in pH_{Ca} 4 soil had slightly higher P_{RL} values than plants grown in pH_{Ca} 5 soil. The AM plants with highest P_{RL} values were *G. etunicatum* and *Gi. margarita* plants grown in pH_{Ca} 4 soil and *Gi. margarita* plants grown in pH_{Ca} 5 soil. Highest P_{RL} values were not related to highest shoot P content or greatest amount of RL or DM.

Table 2. Shoot Contents (per Plant) of P, N, S, K, Ca, Mg, Zn, Cu, Mn, Fe, B, and Al of Mycorrhizal Switchgrass Grown in pH_{Ca} 4 and 5 Soil with Eight AMF Isolates

AMF Isolate	P μg	N mg	S μg	K mg	Ca μg	Mg μg	Zn μg	Cu μg	Mn μg	Fe μg	B μg	Al μg
pH _{Ca} 4 soil												
NonAMF	2	0.4	19	0.06	30	19	0.8	0.2	19	8	0.51	15.7
<i>G. intraradices</i>	3	0.4	14	0.05	23	13	0.4	0.1	17	3	0.24	5.1
<i>Gi. rosea</i>	5	0.5	14	0.09	34	21	0.8	0.2	20	3	0.35	6.9
<i>Gi. albida</i>	98	3.8	162	1.71	145	118	4.5	3.1	58	16	1.27	30.6
<i>G. etunicatum</i>	409	8.8	626	6.72	314	417	11.5	12.3	207	57	2.14	39.3
<i>Gi. margarita</i>	347	9.6	529	5.36	291	378	20.8	15.2	204	53	1.63	48.6
<i>A. morrowiae</i>	293	10.1	601	5.68	295	348	10.3	15.0	226	52	—	51.7
<i>G. diaphanum</i>	418	15.4	1108	8.70	700	646	25.1	31.1	128	139	4.42	75.6
<i>G. clarum</i>	535	15.7	1293	10.22	666	865	21.0	27.0	452	97	11.25	86.1
pH _{Ca} 5 soil												
NonAMF	5	0.4	16	0.06	79	16	0.3	0.1	2	2	0.34	4.1
<i>G. intraradices</i>	164	6.2	302	3.44	776	179	10.4	7.3	22	24	1.48	21.2
<i>Gi. rosea</i>	6	—	17	0.09	130	14	0.3	0.1	3	4	0.24	4.7
<i>Gi. albida</i>	310	8.0	563	5.17	1209	442	16.1	10.9	39	55	2.04	39.8
<i>G. etunicatum</i>	556	15.3	963	9.66	2235	705	18.9	22.4	114	76	2.90	50.4
<i>Gi. margarita</i>	539	16.7	912	7.96	1393	579	30.1	19.5	163	92	2.65	51.0
<i>A. morrowiae</i>	352	8.7	643	6.35	1554	513	7.5	13.7	150	78	2.23	34.5
<i>G. diaphanum</i>	462	14.6	1052	8.19	1952	592	19.0	24.3	74	96	4.67	63.9
<i>G. clarum</i>	351	10.3	881	6.82	1736	502	11.7	19.3	122	71	2.46	59.7
LSD ($P \leq 0.05$)	114	4.3	226	1.91	390	182	7.8	7.1	82	37	1.13	25.4

Figure 1. Phosphorus and nitrogen uptake per root length (RL) of switchgrass grown in pH_{Ca} 4 and 5 soil with eight AMF isolates. See Table 1 for numbers identifying AMF isolates. The $\bar{\text{I}}$ in graphs represents LSD values ($P \leq 0.05$).

Nitrogen and Sulfur Uptake

The N_{RL} values varied extensively among AM plants, and AM plants grown in pH_{Ca} 4 soil generally had higher N_{RL} values than AM plants grown in pH_{Ca} 5 soil (Fig. 1). Differences between N_{RL} values for nonAM and AM plants

with the highest value were only ~ 2.0 – 2.5 -fold for plants grown in both $\text{pH}_{\text{Ca}} 4$ and 5 soil. However, a couple of AM plants had considerably higher N_{RL} values in $\text{pH}_{\text{Ca}} 4$ than in $\text{pH}_{\text{Ca}} 5$ soil. Even though wide differences were noted among AM plants for S_{RL} values for most AM plants, plants grown in $\text{pH}_{\text{Ca}} 4$ and 5 soil had relatively similar values (Fig. 2).

Figure 2. Sulfur and potassium uptake per root length (RL) of switchgrass grown in $\text{pH}_{\text{Ca}} 4$ and 5 soil with eight AMF isolates. See Table 1 for numbers identifying AMF isolates. The $\bar{\text{I}}$ in graphs represents LSD values ($P \leq 0.05$).

Potassium, Calcium, and Magnesium Uptake

The AM plants that had enhanced RL and DM had considerably higher K_{RL} values compared to nonAM and AM plants that did not enhance RL or DM in both pH_{Ca} 4 and 5 soil (Fig. 2). Differences in K_{RL} values among the AM plants that enhanced growth in both pH_{Ca} 4 and 5 soil were relatively narrow (< 2 -fold). The Ca Ca_{RL} values were generally lower for AM plants grown in pH_{Ca} 4 than in pH_{Ca} 5 soil (Fig. 3). Differences among AM plants for Ca_{RL}

Figure 3. Calcium and magnesium uptake per root length (RL) of switchgrass grown in pH_{Ca} 4 and 5 soil with eight AMF isolates. See Table 1 for numbers identifying AMF isolates. The $\bar{\pm}$ in graphs represents LSD values ($P \leq 0.05$).

values were relatively narrow for plants grown in $\text{pH}_{\text{Ca}} 4$ soil and fairly broad for plants grown in $\text{pH}_{\text{Ca}} 5$ soil, and Ca_{RL} values were relatively narrow for the various AM plants. Differences among AM plants for Mg_{RL} values when grown in $\text{pH}_{\text{Ca}} 4$ soil were relatively narrow compared to AM plants grown in $\text{pH}_{\text{Ca}} 5$ soil (Fig. 3).

Figure 4. Zinc and copper uptake per root length (RL) of switchgrass grown in $\text{pH}_{\text{Ca}} 4$ and 5 soil with eight AMF isolates. See Table 1 for numbers identifying AMF isolates. The $\bar{x}$ in graphs represents LSD values ($P \leq 0.05$).

Micronutrient Uptake

Considerable differences were noted for the Zn_{RL} and Cu_{RL} values of AM plants grown in both pH_{Ca} 4 and 5 soil (Fig. 4). The Mn_{RL} , Fe_{RL} , and B_{RL} values were consistently higher for AM plants grown in pH_{Ca} 4 than in pH_{Ca} 5 soil, and differences among AM plants grown in pH_{Ca} 4 soil were larger compared to plants grown in pH_{Ca} 5 soil (Figs. 5 and 6). These Mn_{RL} , Fe_{RL} , and B_{RL} values

Figure 5. Manganese and iron uptake per root length (RL) of switchgrass grown in pH_{Ca} 4 and 5 soil with eight AMF isolates. See Table 1 for numbers identifying AMF isolates. The $\pm$ in graphs represents LSD values ($P \leq 0.05$).

Figure 6. Boron and aluminum uptake per root length (RL) of switchgrass grown in pH_{Ca} 4 and 5 soil with eight AMF isolates. See Table 1 for numbers identifying AMF isolates. The $\pm$ in graphs represents LSD values ($P \leq 0.05$).

were usually highest for nonAM or AM plants that did not enhance DM and RL. That is, many AM plants had restricted uptake of Mn, Fe, and B. The *Gi. rosea* plants had highest Fe_{RL} values when plants were grown in pH_{Ca} 4 soil. Except for Cu_{RL}, nonAM plants had the highest or nearly highest values of the other micronutrients.

Aluminum Uptake

The Al_{RL} values were markedly higher for *Gi. rosea* plants (did not enhance DM or RL) than for the other AM plants (enhanced DM and RL) grown in pH_{Ca} 4 soil (Fig. 6). Most AM plants restricted uptake of Al. The AM plants grown in pH_{Ca} 5 soil had considerably lower Al_{RL} values than AM plants grown in pH_{Ca} 4 soil.

DISCUSSION

A major effect that many of the AMF isolates used in this study had on this switchgrass cultivar grown in acidic soil was to increase RL (Table 1). Plants with greater amounts of RL should have had greater ability to obtain mineral nutrients from existing volumes of soil compared to plants with lower amounts of RL, because more surface area would be available for acquiring minerals. However, the effect of AMF hyphae per se at increasing root surface area available to access mineral nutrients is unknown, since hyphal length/mass in soil was not determined. It is most likely that AMF hyphae were important in increasing surface area for mineral acquisition. One important effect many acidic soils have on roots is to inhibit elongation because of toxic elements like Al and Mn.^[1] Excess Al may also inhibit hyphal elongation.^[34] As such, the Al and possibly Mn contained in the acidic soil used in this study might have had major effects on both host root and AMF hyphal elongation. It was evident that this acidic soil inhibited RL of the switchgrass grown without AMF (Table 1). This batch of Lily soil had high Al (88% of macronutrient cationic exchange) and low P (3.1 mg kg^{-1} soil), and should have imposed relatively severe Al toxicity and/or P deficiency on plants. Where this soil was used in other studies, Lily soil imposed fairly severe Al toxicity on plants.^[9,35] Most of the AMF isolates used in this study effectively alleviated some growth inhibiting stresses that this soil imposed on the switchgrass cultivar grown, and enhanced both RL and DM (Table 1). Two AMF isolates were ineffective in pH_{Ca} 4 soil (*G. intraradices* and *Gi. rosea*) and one in pH_{Ca} 5 soil (*Gi. rosea*). Two AMF isolates that were especially effective in both pH_{Ca} 4 or 5 soil were *G. clarum* and *G. diaphanum*, with *G. etunicatum* also being highly effective in pH_{Ca} 5 soil. An interesting response of AMF on increasing RL was that most isolates were more effective in pH_{Ca} 4 than in pH_{Ca} 5 soil, so these AMF isolates likely had relatively good tolerance to soil acidity. This might be expected since most isolates were isolated from acidic soils.^[31]

With increased RL, AM plants should have been able to acquire higher concentrations and/or contents of mineral nutrients essential to plant growth.

Higher shoot mineral concentrations^[12] and contents (Table 2) were noted for many of the AM plants, and enhanced shoot DM could not account for all of the mineral content increases noted. The marked differences among AM plants for RL might indicate that AMF could have considerably different effects on plant acquisition of mineral nutrients. This led us to consider mineral uptake relative to RL by the AM plants to evaluate differences for this trait to help explain some of the differences noted.

Information about host plant P (and other mineral nutrient) uptake associated with RL is limited. Since P is the most frequently reported mineral nutrient enhanced in AM plants,^[36–38] considerable amounts of information are available about uptake and transport of P in AM plants.^[39–41] In addition, information about such factors as growth media P supply, plant P demand, mycorrhizal influence on growth and plant P acquisition and use, and P uptake associated with hyphae is also extensive.^[39,40]

The P_{RL} values reported for AM and nonAM plants of a few studies have been compared, and AM plants generally had 2.0–2.5-fold higher P uptake than nonAM plants.^[29] Similar differences were noted for AM and nonAM maize and soybean grown in two soils with pH 4.7, 5.6, and 6.4.^[17] Large differences between AM and nonAM plants for P_{RL} values might be expected, but information comparing AMF isolate differences for mineral uptake is scarce. One such study reported *S. calospora*, *Glomus* sp., and *A. laevis* subterraneum clover (pH 5.3) to have 1.9–2.5-fold differences, with *S. calospora* plants being highest and *Glomus* sp. plants being lowest.^[42]

Calculations from data in the literature also indicated that AMF isolates had mineral uptake differences associated with RL. For example, P_{RL} values for *S. calospora* subterraneum clover grown with varied levels of P were consistently lower than *Glomus* sp. plants, but mineral uptake was even higher when *Glomus* sp. and *S. calospora* inocula were combined.^[43] However, P_{RL} differences between *Glomus* sp. and *G. caledonium* cucumber (*Cucumis sativus* L.) were not significantly different.^[44] *Glomus* sp. (*G. etunicatum*-like) and *Gi. margarita* cowpea (*Vigna unguiculata* L.), pigeonpea [*Cajanus cajan* (L.) Millsp.], and groundnut (*Arachis hypogaea* L.) grown in fertile topsoil and infertile subsoil at pH 6.0 had wide differences for P_{RL} values.^[45] *Glomus* sp. plants consistently had higher P_{RL} values than *Gi. margarita* plants grown in both a topsoil (72 mg P kg⁻¹ soil) and a subsoil (< 0.1 mg P kg⁻¹ soil). Similar differences in P_{RL} values were noted for AM cowpea and groundnut grown in a topsoil, but not for AM pigeonpea. In other studies, *G. etunicatum*, *G. intraradices*, and *G. diaphanum* maize grown in two acidic soils (pH_{Ca} 4.2 and 4.6) had no differences in P_{RL} values.^[10]

Zn_{RL} values were higher for *S. calospora* subterraneum clover than for either *Glomus* sp. or *A. laevis* plants, while *A. laevis* plants had slightly higher Zn_{RL} values than *Glomus* sp. plants.^[46] *Glomus* sp. cowpea and groundnut

consistently had higher N, K, Ca, Mg, Zn, Cu, and Fe uptake per RL than did *Gi. margarita* plants grown in fertile topsoil and infertile subsoil.^[45] Only Mn_{RL} values were higher in *Gi. margarita* than in *Glomus* sp. plants grown in these soil layers. Similar results were noted for *Gi. margarita* and *Glomus* sp. pigeonpea grown in the subsoil, but only Zn_{RL}, Cu_{RL}, Fe_{RL}, and Mn_{RL} values were higher in *Glomus* sp. than in *Gi. margarita* plants grown in the topsoil. The N_{RL}, K_{RL}, Ca_{RL}, and Mg_{RL} values were similar for *Gi. margarita* and *Glomus* sp. pigeonpea grown in the topsoil. *G. intraradices*, *G. etunicatum*, and *G. diaphanum* maize grown in acidic soil had similar N_{RL}, S_{RL}, K_{RL}, Ca_{RL}, Mg_{RL}, Zn_{RL}, Cu_{RL}, Mn_{RL}, Fe_{RL}, and B_{RL} values, but *G. intraradices* plants consistently had higher mineral uptake values per RL than *G. etunicatum* and *G. diaphanum* plants.^[10]

Results of the study reported here indicated that the AMF isolates used had dramatic effects on plant responses for uptake of mineral nutrients by the switchgrass grown in low pH Lily soil. Mineral nutrient uptake per RL was dramatically different among AM plants, and those AMF isolates that enhanced DM and RL consistently had higher mineral uptake per RL than AM plants that did not have enhanced DM or RL. Mineral uptake per RL of nonAM plants was similar to that of AM plants that did not enhance DM or RL. Some how, AMF were providing benefits to plants beyond that which could be accounted for by increased RL. These benefits could have possibly come from increased AMF hyphal lengths and/or stimulated activity of mineral nutrient uptake and transport. Differences among hyphae of various AMF have been reported for P uptake.^[42,44,47]

Most of the AMF isolates used in this study were effective in enhancing uptake of mineral nutrients essential to plant growth and restricting elements that may become toxic. As might be expected, the mineral nutrient to be enhanced most extensively in AM plants was P concentration^[10] and content (Table 2), but uptake of many of the other essential mineral nutrients, especially N, S, K, and Mg, were also greatly enhanced (Figs. 1–3). Even though many AMF were effective in enhancing uptake of mineral nutrients, *G. etunicatum* was especially effective in so doing. Although this acidic Lily soil has potential to impose severe Al, and possibly Mn, toxicities on plants, these toxicities were alleviated by inoculation of switchgrass with many of the AMF isolates used. The *G. diaphanum* was especially effective in reducing Mn uptake, *A. morrowiae* reduced Zn, and several AMF isolates were effective in restricting Al uptake. The AMF isolates that were not particularly effective in pH_{Ca} 4 soil were *G. rosea* and *G. intraradices*, and *Gi. rosea* in pH_{Ca} 5 soil. Appropriate AMF have considerable ability to improve tolerance of many plants to acidic soil with pH_{Ca} as low as 4 by enhancing acquisition of mineral nutrients essential to growth and restricting toxic elements like Al and Mn.

ACKNOWLEDGMENTS

The technical assistance of Ms. S. K. Zeto was greatly appreciated. A special thanks is extended to Dr. R. W. Zobel who provided valuable discussion and many contributions in preparation of this manuscript.

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