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R.B. Clark · R.W. Zobel · S.K. Zeto

Effects of mycorrhizal fungus isolates on mineral acquisition by *Panicum virgatum* in acidic soil

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Abstract Plant ability to withstand acidic soil mineral deficiencies and toxicities can be enhanced by root-arbuscular mycorrhizal fungus (AMF) symbioses. The AMF benefits to plants may be attributed to enhanced plant acquisition of mineral nutrients essential to plant growth and restricted acquisition of toxic elements. Switchgrass (*Panicum virgatum* L.) was grown in pH_{Ca} (soil:10 mM $CaCl_2$, 1:1) 4 and 5 soil (Typic Hapludult) inoculated with *Glomus clarum*, *G. diaphanum*, *G. etunicatum*, *G. intraradices*, *Gigaspora albida*, *Gi. margarita*, *Gi. rosea*, and *Acaulospora morrowiae* to determine differences among AMF isolates for mineral acquisition. Shoots of mycorrhizal (AM) plants had 6.2-fold P concentration differences when grown in pH_{Ca} 4 soil and 2.9-fold in pH_{Ca} 5 soil. Acquisition trends for the other mineral nutrients essential for plant growth were similar for AM plants grown in pH_{Ca} 4 and 5 soil, and differences among AMF isolates were generally higher for plants grown in pH_{Ca} 4 than in pH_{Ca} 5 soil. Both declines and increases in shoot concentrations of N, S, K, Ca, Mg, Zn, Cu, and Mn relative to nonmycorrhizal (nonAM) plants were noted for many AM plants. Differences among AM plants for N and Mg concentrations were relatively small (<2-fold) and were large (2- to 9-fold) for the other minerals. Shoot concentrations of mineral nutrients did not relate well to dry matter produced or to percentage root colonization. Except for Mn and one AMF isolate, shoot concentrations of Mn, Fe, B, and Al in AM plants were lower than in nonAM plants, and differences among AM plants for these minerals ranged from a low of 1.8-fold for Fe to as high as 6.9-fold for Mn. Some AMF isolates were effective in overcoming acidic soil mineral deficiency and toxicity problems that commonly occur with plants grown in acidic soil.

Key words *Acaulospora* · *Gigaspora* · *Glomus* · Alleviation of toxic minerals · Mineral nutrient concentrations · Low pH soil · Switchgrass

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R.B. Clark (✉) · R.W. Zobel · S.K. Zeto
US Department of Agriculture, Agricultural Research Service, Appalachian Farming Systems Research Center, 1224 Airport Rd., Beaver, WV 25813-9423, USA
e-mail: rclark@afsrc.ars.usda.gov
Fax: +1-304-256-2921

Introduction

Plants grown in acidic soil (<5.0–5.5) commonly encounter relatively severe mineral stresses (Foy 1992; Marschner 1991). The H^+ associated with soil acidity has indirect effects on mineral elements in low pH soils so that deficiencies of P, Ca, Mg, K, and Zn and toxicities of Al and Mn commonly appear. Of the deficiencies/toxicities that plants may encounter when grown in acidic soil, Al toxicity is considered to be the major disorder (Foy 1992). Al is highly soluble at low pH and is toxic to plants at relatively low concentrations. It also interacts with other mineral nutrients essential to plant growth, especially P, Ca, and Mg, so that these essential nutrients often become more limiting. Not only is excess Al damaging to root growth and development (Foy 1992), but Al as well as Fe oxides so prevalent in acidic soils (Manning and Goldberg 1996) adsorb P and make it unavailable to plants. Acidic soil conditions often denote relatively high moisture and cationic elements (Ca, Mg, K) are also commonly leached from root growth zones. Under acidic soil conditions, lime or other pH-raising materials and fertilizers are often added to replenish mineral nutrients and reduce Al and Mn toxicities. Mn is also readily soluble at low soil pH and may become toxic to plants (Foy 1992).

Increasing mineral availability and reducing mineral toxicity for plants grown in acidic soil may be achived

using arbuscular mycorrhizal fungi (AMF) (Bethlenfalvay 1992; Linderman 1992, 1994; Marschner 1991; Sieverding 1991; Sylvia and Williams 1992). Such beneficial effects of AMF have been partially explained by an increase in effective root surface area beyond normal root absorption zones as fungal hyphae extend further into soil than nonmycorrhizal (nonAM) roots. Thus, plants can acquire mineral nutrients that would otherwise be unavailable at root surfaces (Marschner 1991). In addition, mycorrhizal (AM) plants may be more able to resist acquisition and/or have increased protection against some of the toxic elements than nonAM plants (Bethlenfalvay and Franson 1989; Clark and Zeto 1996a, b; Howeler et al. 1987; Maddox and Soileau 1991; Medeiros et al. 1994a; Raju et al. 1988; Saif 1987; Schenck and Siqueira 1987; Sieverding 1991).

Differences among AM plants for growth and mineral nutrient acquisition in acidic soil or under acidic conditions have been reported (Clark and Zeto 1996a, b; Lambais and Cardoso 1993; Medeiros et al. 1994a–c; Saggin and Siqueira 1995; Saggin et al. 1995; Sieverding 1991). Many such studies examine only limited nutrients, particularly P, and not the continuum of nutrients essential to plant growth; few report on the acquisition of toxic elements. The objective of our study was to compare eight AMF isolates from three genera for acquisition of the majority of mineral nutrients essential to plant growth, and of Al, which is commonly toxic. Switchgrass (*Panicum virgatum* L.) was used in the study because of its relatively high dependence on AMF.

Materials and methods

The AMF isolates used are listed in Table 1. Seven isolates were obtained from INVAM, West Virginia University, Morgantown, and one isolate (*Gigaspora margarita*) was obtained from D.D. Douds (USDA-ARS, Philadelphia). Additional description and conditions for the isolation of these AMF isolates are provided by Morton et al. (1993).

We used acidic Lily soil (fine loamy, siliceous, mesic, Typic Hapludult) collected near the Appalachian Farming System Research Center, USDA-ARS, Beaver, W.V. Properties of the soil before steam pasteurization were 43% sand, 39% silt, 18% clay; 4.7% organic matter (Walkley-Black procedure); 3.89 pH_{Ca} (soil: 10 mM $CaCl_2$, 1:1) and 4.48 pH_W (soil:water, 1:1); 0.06 dS m^{-1} electrical conductivity (EC; 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 NH_4–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 are described in Page et al. (1982).

Air-dried soil was sieved to pass a 2-mm screen, steam pasteurized at 100 °C for 30 min, allowed to cool at ambient temperature overnight, again steam pasteurized at 100 °C for 20 min, and allowed to stand 7 days before being fertilized with NH_4NO_3 at 143 mg kg^{-1} soil. Sterilization procedures did not enhance soluble Mn as may occur in some acidic soils (R.B. Clark and S.K. Zeto, unpublished data). 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 $CaCO_3$ kg^{-1} soil to maintain fairly severe acidic conditions.

Table 1 Scientific names, INVAM/other descriptor information, and isolation soil pH and P level (mg kg^{-1}) of AMF isolates used in association with switchgrass in acidic soil. The numbers in column 1 are those used to identify AMF isolates in the figures (*NA* = Information not available or not provided)

Isolate number	AMF isolate	INVAM/ other descriptor[a]	Isolation soil pH[a]	Isolation soil P[a]
1	Nonmycorrhizal	NonAM		
2	*Glomus intraradices*	WV894A	4.4	11
3	*Gigaspora rosea*	BR151A	NA	NA
4	*Gigaspora albida*	BR214	6.1	8
5	*Glomus etunicatum*	WV579A	4.6	4
6	*Gigaspora margarita*	DAOM 194757	NA	NA
7	*Acaulospora morrowiae*	WV107	3.7	17
8	*Glomus diaphanum*	WV579B	4.6	4
9	*Glomus clarum*	WV751	NA[b]	NA

[a] Information taken from Morton et al. (1993)
[b] Isolated from native pasture near maple forest in West Virginia (Morton et al. 1993), so soil would likely be acidic

Inoculum of each AMF isolate was multiplied in our laboratory using sudangrass [*Sorghum bicolor* (L.) Moench] as the host plant grown in Lily soil:sand (1:1) mixtures (pH_{Ca} = 5.5) and consisted of soil:sand mix containing root fragments + hyphae + spores. Inoculum was added to soil to provide similar inoculum potentials for each AMF isolate. Preliminary experiments were conducted using methods of Moorman and Reeves (1979) with maize (*Zea mays* L.) to evaluate inoculum potential in the soil used in this experiment. Because *Gigaspora* species did not readily form spores during inocula multiplication (R.B. Clark and S.K. Zeto, personal observations), inoculum of each AMF isolate added to soil was provided as given spore counts. In the plant growth soil mixes, *Acaulospora* and *Glomus* inocula had 10,000 spores kg^{-1} soil and *Gigaspora* inocula had 1,000 spores kg^{-1} soil. Relatively good root colonization percentages were obtained for plants grown in these soil mixes at both pH_{Ca} 4 and 5 (Table 2). Soil mixes for nonAM plants received 125 g of control inoculum per kg soil. Control inoculum consisted of soil mix + root fragments of sudangrass grown under similar conditions except with no AMF. Each inoculum was mixed thoroughly with pasteurized soil and dispensed into pots (2.0 kg pot^{-1}).

Seeds of the switchgrass cultivar 'Cave-in-Rock' were surface sterilized with 70 mM NaOCl (household bleach) for 5 min and rinsed thoroughly before being planted into pots. Pots were irrigated manually with distilled water as needed during the experiment. Leaching from pots did not occur, and plants did not experience water deficit. Care was taken not to splash water or soil onto plant parts during irrigation. Plants were thinned to three per pot 10 days after sowing and grown for 88 days in a glasshouse from mid-April to mid-July. The glasshouse had additional light from high-pressure sodium halide (1000 W) lamps to provide light at 400–500 μmol m^{-2} 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, the temperature did not vary more than 3 °C from 28 °C in the light period and 23 °C in the dark period.

Shoots were severed from roots at harvest ~1 cm above the soil surface and lower stalks were rinsed thoroughly with distilled water and blotted dry. The tissue was dried at 60 °C for a minimum of 3 days and weighed. Roots were thoroughly rinsed free of soil when placed on 2-mm screens, blotted dry, cut into 1–2 cm segments and thoroughly mixed. Representative fresh weight samples were collected for root colonization. The remainder of the root tissue was dried at 60 °C and weighed. Roots collected for determination of AMF colonization were cleared in 1.78 M

KOH and stained with 0.52 mM trypan blue (Phillips and Hayman 1970). Root segments were microscopically examined (×50 magnification) and the percentage of root segments containing vesicles/arbuscules in root cells and/or roots with hyphal infections was determined using the gridline intersect method (Daniels et al. 1981).

Dried shoot samples were ground to pass a 0.5-mm screen, mixed thoroughly, and 50- to 100-mg samples were weighed into teflon containers. Aliquots of 1.0 ml 15.8 M HNO_3 were added to each container with tissue, and the containers placed in microwave digestion bombs (Parr Instrument Co., Moline, Ill.). Samples were microwaved for 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 and then at ambient temperature. Digested solutions were brought to a final volume of 10 ml with distilled deionized water, 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, Italy), which is a combustion-gas-chromatography procedure (Pella and Colombo 1973).

The experimental design consisted of completely randomized blocks with five replications of each AMF isolate in pH_{Ca} 4 and 5 soils. Data were statistically analyzed using analysis of variance procedures, and differences among treatments were compared using probabilities of significance and least significant difference (LSD) values ($P \leq 0.05$).

Results

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

Information about dry matter (DM) and root colonization differences among AM plants grown in different pH_{Ca} soils is presented (Table 2), even though it is also available in another report (Clark et al. 1999). This is because DM and root colonization information is important to understand shoot mineral nutrient concentrations relative to growth and AMF contact with roots. Differences in DM and root colonization among AMF isolates were large for plants grown in pH_{Ca} 4 and 5 soils (Table 2). For example, the range in DM among AM plants grown in pH_{Ca} 4 (61-fold) was wider than in pH_{Ca} 5 (27-fold) soil. The AM plants with highest DM in both pH_{Ca} 4 and 5 soils were *G. clarum* and *G. diaphanum* plants, and DM for these plants was lower in pH_{Ca} 5 than in pH_{Ca} 4 soil. Similar low DM was noted for *G. intraradices* and *Gi. rosea* as well as nonAM plants grown in pH_{Ca} 4 soil, and for *Gi. rosea* and nonAM plants grown in pH_{Ca} 5 soil. The ranges of root colonization were 9–50% for AM plants grown in pH_{Ca} 4 soil and 18–51% for those grown in pH_{Ca} 5 soil. The AM plants grown in pH_{Ca} 5 soil generally had higher root colonization percentages than plants grown in pH_{Ca} 4 soil.

Shoot P concentrations of AM plants showed 6.2-fold differences when grown in pH_{Ca} 4 soil compared with 2.9-fold differences in pH_{Ca} 5 soil (Fig. 1). Even *G. intraradices* and *Gi. rosea* plants, which had the lowest DM, comparable to that of nonAM plants in pH_{Ca} 4 soil, had >twofold higher P ($P = 0.05$) than nonAM plants. On the other hand, *Gi. rosea* and nonAM plants with comparable and low DM had similar shoot P concentrations in pH_{Ca} 5 soil. Shoot P concentrations in nonAM plants increased ~threefold in pH_{Ca} 5 relative to pH_{Ca} 4 soil, while shoot P concentrations of AM plants in pH_{Ca} 5 soil were similar to or lower than in pH_{Ca} 4 soil. Although *G. clarum* and *G. diaphanum* plants had the highest shoot DM when grown in pH_{Ca} 4 soil, these plants did not have the highest P concentrations. Highest shoot P concentrations were noted in *G. etunicatum* and *Gi. margarita* plants, which had a DM about half that of *G. clarum* and *G. diaphanum* plants. Large differences were found among AM plants grown in pH_{Ca} 4 soil for shoot P concentration and percentage root colonization. For example, *G. etunicatum* plants had the highest P concentration of all AM plants but only 10% root colonization, while *Gi. margarita* plants had the next to highest P concentration and 50% root colonization. P concentrations of plants grown in pH_{Ca} 5 soil were high and similar for *G. intraradices*, *Gi. albida*, *G. etunicatum*, *Gi. margarita*, and *A. morrowiae*, while *G. diaphanum* and *G. clarum* plants had slightly lower P concentrations. The AM plants with the high-

Table 2 Shoot and root dry matter (DM) and root colonization percentages of switchgrass grown in pH_{Ca} 4 and 5 soil with eight AMF isolates

AMF isolate	Shoot DM (mg/plant)		Root DM (mg/plant)		Root colonization (%)	
	pH_{Ca} 4 soil	pH_{Ca} 5 soil	pH_{Ca} 4 soil	pH_{Ca} 5 soil	pH_{Ca} 4 soil	pH_{Ca} 5 soil
NonAM	17	16	8	13	0	0
G. intraradices	12	190	8	67	9	29
Gi. rosea	18	17	10	11	15	18
Gi. albida	99	290	54	38	23	37
G. etunicatum	295	572	141	70	10	22
Gi. margarita	313	525	161	76	50	51
A. morrowiae	348	354	198	180	34	41
G. diaphanum	613	581	429	101	24	28
G. clarum	727	499	515	248	28	35
LSD ($P \leq 0.05$)	143		116		8	

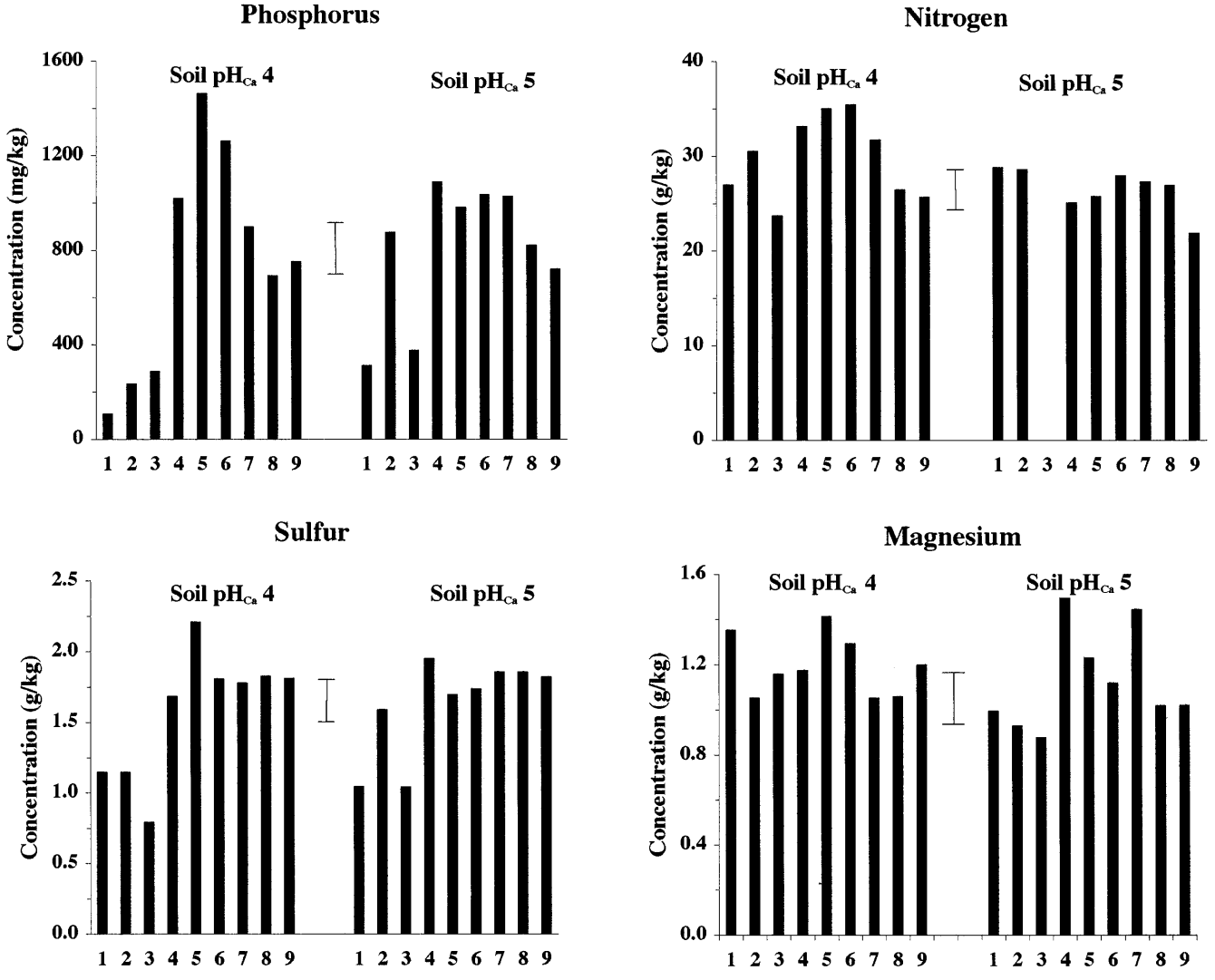

Fig. 1 Shoot concentrations of phosphorus, nitrogen, sulfur, and magnesium of switchgrass colonized by various AMF isolates and grown in pH_{Ca} 4 and 5 soils. The bars are LSD values ($P=0.05$). See Table 1 for AMF isolates corresponding to numbers

est and similar P concentrations had root colonization percentages of 22 and 51%.

The differences in shoot N and Mg concentration among AM as well as nonAM plants grown in pH_{Ca} 4 and 5 soil were relatively small: <1.5-fold for N and <1.7-fold for Mg (Fig. 1). Nevertheless, some AM plants showed significant differences in both N and Mg. N concentrations in some AM plants grown in pH_{Ca} 4 soil were slightly higher than for plants grown in pH_{Ca} 5 soil, while Mg concentrations in AM plants were similar in pH_{Ca} 4 and 5 soil. In pH_{Ca} 5 soil, *Gi. albida* and *A. morrowiae* plants had highest Mg concentrations relative to the other AM plants. For S, shoot concentration differences among AM plants were 2.8-fold for plants grown in pH_{Ca} 4 and 1.9-fold in pH_{Ca} 5 soil (Fig. 1). *G. etunicatum* plants grown in pH_{Ca} 4 soil had highest S, while several AM plants had similar, relatively high S concentrations when grown in pH_{Ca} 5 soil. Lowest S was noted in *Gi. rosea* plants either in pH_{Ca} 4 or 5 soil.

Shoot Ca concentrations were relatively low with small differences (2.3-fold) between AM plants grown in pH_{Ca} 4 soil; nonAM plants had Ca concentrations similar to those noted for AM plants (Fig. 2). Except for *Gi. rosea* plants, which had relatively high shoot Ca concentrations, AM plants grown in pH_{Ca} 5 soil had <1.3-fold differences in shoot Ca. Shoot Ca concentrations were considerably higher in plants grown in pH_{Ca} 5 than 4 soil because of $CaCO_3$ added to increase soil pH. Shoot K concentrations differed by 6.3-fold among AM plants grown in pH_{Ca} 4 soil and by 3.2-fold for those grown in pH_{Ca} 5 soil (Fig. 2). Lowest K concen-

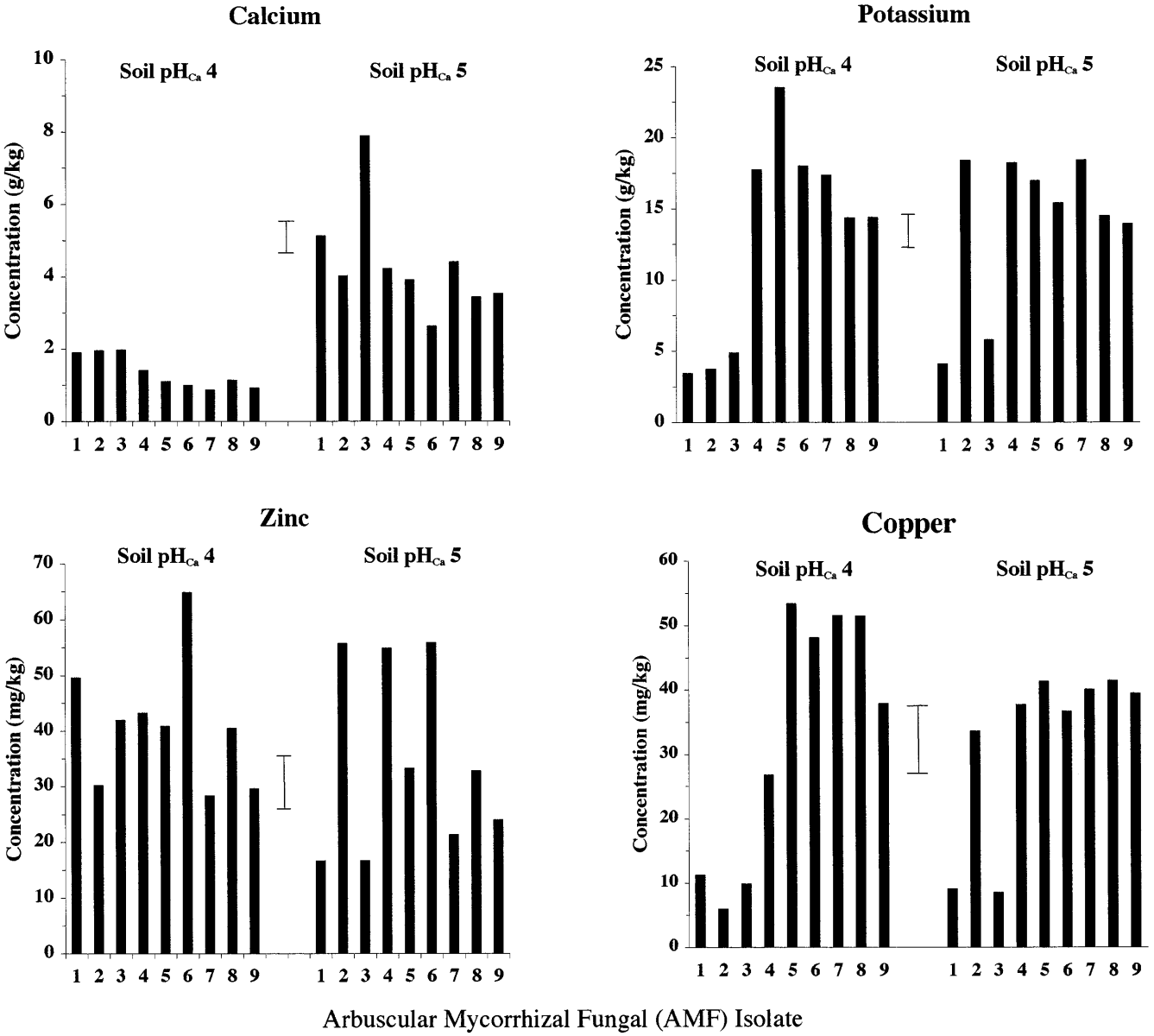

Fig. 2 Shoot concentrations of calcium, potassium, zinc, and copper of switchgrass colonized by various AMF isolates and grown in pH_{Ca} 4 and 5 soils. The bars are LSD values ($P=0.05$). See Table 1 for AMF isolates corresponding to numbers

trations were noted for *Gi. rosea* and *G. intraradices* plants grown in pH_{Ca} 4 soil and *Gi. rosea* plants grown in pH_{Ca} 5 soil; these were comparable to nonAM plants. Of the AM plants with enhanced K, *G. etunicatum* had the highest concentration. *G. diaphanum* and *G. clarum* had the highest DM but only ~0.6-fold K concentrations relative to *G. etunicatum* plants grown in pH_{Ca} 4 soil. Except *Gi. rosea* plants, which had lowest K, AM plants had very similar K concentrations when grown in pH_{Ca} 5 soil.

NonAM plants had shoot Zn concentrations as high as AM plants, except *Gi. margarita* plants, when grown in pH_{Ca} 4 soil (Fig. 2). Except for *Gi. margarita* plants, which had high Zn, AM plants grown in pH_{Ca} 4 soil showed small Zn differences (1.5-fold). In pH_{Ca} 5 soil, *Gi. margarita*, *Gi albida*, and *G. intraradices* plants had Zn concentrations twice those of the other AM plants. NonAM plants grown in pH_{Ca} 4 soil had ~threefold higher Zn than when grown in pH_{Ca} 5 soil. The lowest shoot Cu concentrations were noted for *G. intraradices* and *Gi. rosea* plants grown in pH_{Ca} 4 and in *Gi. rosea* plants grown in pH_{Ca} 5 soil (Fig. 2). Cu concentration differences among AM plants grown in pH_{Ca} 4 and 5 soil were 9.0- and 4.9-fold, respectively. Several AM plants had similar and relatively high Cu concentrations when grown in pH_{Ca} 4 or 5 soil, and AM plants generally had slightly higher Cu concentrations in pH_{Ca} 4 than in pH_{Ca} 5 soil.

Plants grown in pH_{Ca} 4 soil had higher shoot Mn concentrations than plants in pH_{Ca} 5 soil (Fig. 3). The

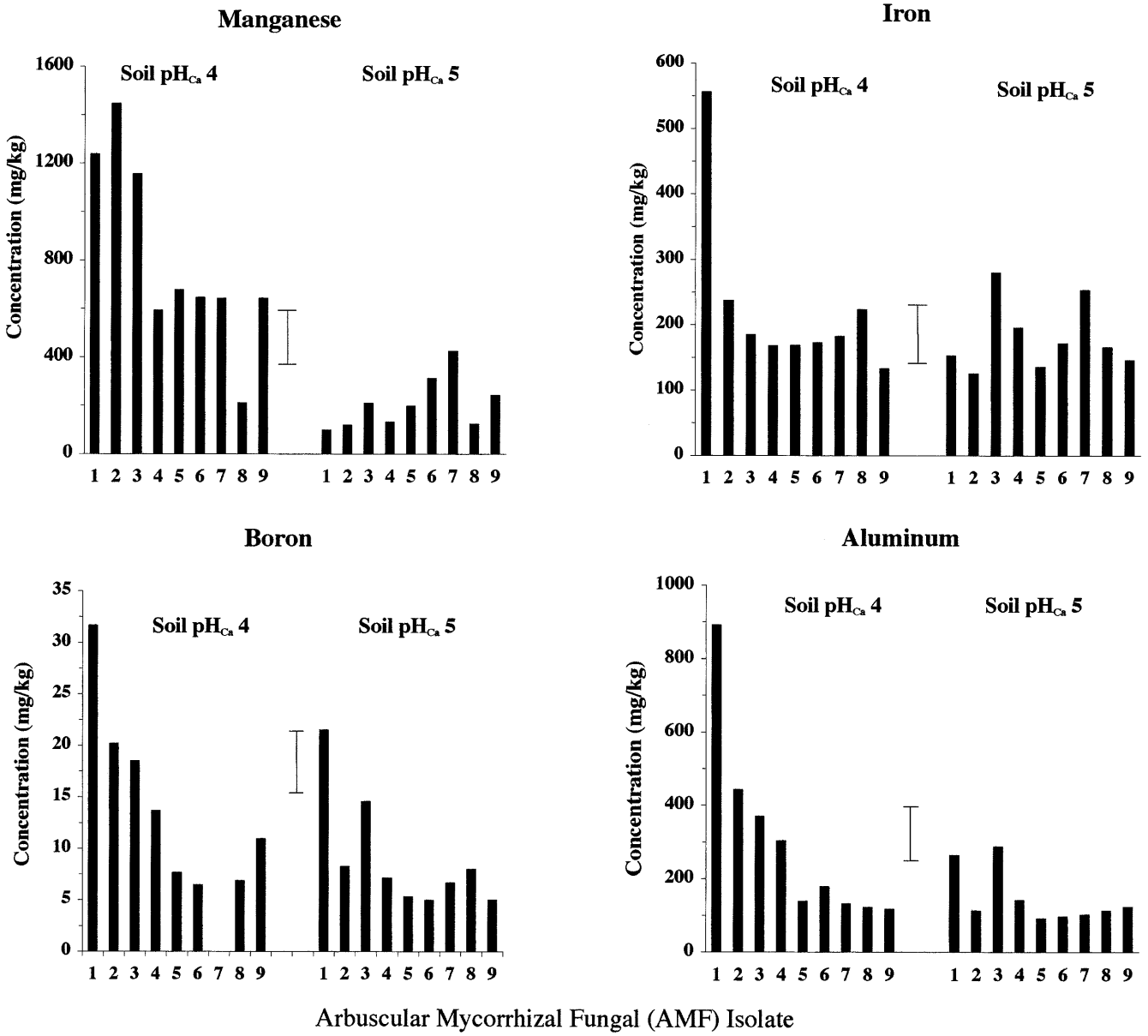

Fig. 3 Shoot concentrations of manganese, iron, boron, and aluminum of switchgrass colonized by various AMF isolates and grown in pH_{Ca} 4 and 5 soils. The bars are LSD values ($P=0.05$). See Table 1 for AMF isolates corresponding to numbers

AM plants grown in pH_{Ca} 4 soil differed by 6.9-fold in Mn concentration, compared with 3.4-fold differences in pH_{Ca} 5 soil. *G. intraradices* and *Gi. rosea* plants grown in pH_{Ca} 4 soil had the highest shoot Mn concentrations. Differences in Mn concentrations of AM plants were relatively small and generally slightly higher than those of nonAM plants in pH_{Ca} 5 soil. *G. diaphanum* plants grown in both pH_{Ca} 4 and 5 soils had the lowest Mn concentrations of all AM plants. In pH_{Ca} 4 soil, shoot Fe concentration of AM plants was ~threefold lower than in nonAM plants (Fig. 3). For AM plants grown in pH_{Ca} 4 and 5 soils, Fe concentrations were similar, and differences among AM plants were only about twofold.

Shoot B concentrations were lower in AM than in nonAM plants in both pH_{Ca} 4 and 5 soils, and were generally slightly higher in pH_{Ca} 4 than in pH_{Ca} 5 soil (Fig. 3). Differences among AM plants for shoot B concentration were similar in pH_{Ca} 4 and 5 soils (3.1- and 2.9-fold, respectively). In both pH_{Ca} 4 and 5 soil, AM plants with enhanced DM generally had lower B than AM plants with no enhanced DM. *Gi. rosea* plants had higher shoot B than the other AM plants when grown in pH_{Ca} 5 soil. Shoot Al concentration was twofold higher in nonAM plants than in AM plants grown in pH_{Ca} 4 soil (Fig. 3). NonAM plants grown in pH_{Ca} 4 soil had 3.3-fold higher Al than in pH_{Ca} 5 soil. *Gi. rosea*, *Gi. albida*, and *G. intraradices* plants grown in pH_{Ca} 4 soil and *Gi. rosea* plants in pH_{Ca} 5 soil had higher Al concentrations than the other AM plants. AM

plants with enhanced DM had lower shoot Al concentrations than AM plants with no enhanced DM, in both pH_{Ca} 4 and 5 soils. AM plants with enhanced DM in both pH_{Ca} 4 and 5 soils had similar shoot Al concentrations.

Shoot mineral concentrations in AM plants did not relate well with percentage root colonization.

Discussion

The ability of AM plants to promote growth in mineral-deficient soils has been related to increased acquisition of mineral nutrients essential to plant growth, especially P (Bolan 1991; Hetrick 1989; Marschner and Dell 1994) and Zn and Cu (George et al. 1994; Li et al. 1991b; Marschner and Dell 1994; Sharma et al. 1994). Studies have reported increased acquisition of P (Graw 1979; Nurlaeny 1995; Raju et al. 1988; Saif 1987; Silva et al. 1994; Siqueira et al. 1990; Yawney et al. 1982) and other macronutrients such as S, Ca, Mg, and K (Clark and Zeto 1996b; Lambais and Cardoso 1993; Medeiros et al. 1994a–c; Nurlaeny 1995; Raju et al. 1988; Saif 1987; Siqueira et al. 1990) when plants were grown in acidic soil. P may not be the only or even the main mineral nutrient limiting plant growth in some acidic soils. An example of this was noted for maize colonized with three *Glomus* isolates and grown in two acidic soils (Clark and Zeto 1996b). Shoots showed no enhanced P acquisition, and P in shoot tissue was not deficient. However, Ca, Mg, and K were below critical limits in nonAM plants. Thus, these nutrients, which are commonly deficient in acidic soils, may have limited growth in the acidic soils. Ca, Mg, and K were greatly enhanced by the AMF when plants were grown in the acidic soils.

Soil P has been known to limit growth of many plants grown in Lily soil (R. B. Clark and S. K. Zeto, personal observations), and added P is normally needed for plants grown in this soil. The AMF isolates used in our study enhanced P acquisition relative to nonAM plants, even when no enhancement in DM was noted. Large differences among AM plants in P concentration were also noted, indicating that some AMF isolates were more effective than others in enhancing P acquisition. The large differences in P concentration in the AM plants were not related to DM production or percentage root colonization. Examples of this were: *G. intraradices* and *Gi. rosea* plants which had twofold higher P concentrations than nonAM plants, even though DM was similar to nonAM plants grown in pH_{Ca} 4 soil; *G. clarum* and *G. diaphanum* plants grown in pH_{Ca} 4 soil had highest DM, but P concentrations in these plants were only about half those of other AM plants with lower DM; and *Gi. margarita* and *G. etunicatum* plants grown in soil at both pH_{Ca} 4 and 5, where these AM plants had comparable DM and shoot P concentrations, but percentage root colonization of *Gi. margarita* plants was considerably higher than for *G. etunicatum* plants. Similar results were noted for sorghum [*Sorghum bicolor* (L.) Moench] and maize grown under acidic conditions or in acidic soil (Clark and Zeto 1996a, b; Medeiros et al. 1994a–c). Whether P concentrations in AM plants were sufficient to produce optimum DM or could potentially inactivate toxic Al (and Mn) is unknown, but shoot P for several grasses has been reported to be >1000 mg kg^{-1} and yet to be deficient (Smith 1986).

Shoot Ca and Mg concentrations for AM plants grown in pH_{Ca} 4 soil were near those considered to be deficient for many grasses (2.0–2.5 g kg^{-1} for Ca and 1.3–1.5 g kg^{-1} for Mg) (Smith 1986). Shoot K concentrations for nonAM and *Gi. rosea* and *G. intraradices* plants were below levels considered to be deficient (1.5–2.0 g kg^{-1}), but other AM plants had shoot K concentrations near or above this level. Shoot concentrations of both Zn and Cu in AM plants grown in pH_{Ca} 4 and 5 soils were above those considered to be deficient in grasses (10–20 mg kg^{-1} for Zn and mg 5–8 mg kg^{-1} for Cu). Most of the AM plants had greater mineral acquisition than nonAM and AM plants that grew poorly in this acidic Lily soil.

Many AMF isolates have been reported to enhance plant acquisition of mineral nutrients essential to plant growth and to alleviate nutrient deficiencies encountered by plants when grown in soil with deficient nutrient levels, particularly in acidic soil (Clark 1997; Marschner and Dell 1994). The differences among AMF isolates for P as well as other mineral nutrients may be attributed to (1) differences among AMF for hyphal spread and density away from roots (Bürkert and Robson 1994; Jakobsen et al 1992a, b; Li et al. 1991a, c), (2) ability of AMF to increase nutrient availability, especially P, in soil through enhanced phosphatase/ phytase activity (Dinkelaker and Marschner 1992; Khalil et al. 1994; Tarafdar and Claassen 1988; Tarafdar and Jungk 1987; Tarafdar and Marschner 1994; Thiagarajan and Ahmad 1994) and/or excretion of solubilizing materials such as ethylene (Ishii et al. 1996), flavonoides (Ishii et al. 1997), volatile substances (Gemma and Koske 1988; Koske 1982), and growth regulating compounds (Barea and Azcón-Aguilar 1982; Danneberg et al. 1992; Thiagarajan and Ahmad 1994), and (3) ability of AMF to change rhizosphere soil pH (Gianinazzi-Pearson and Azcón-Aguilar 1991; Li et al. 1991c; Smith and Smith 1990).

Other factors associated with the differences between AMF for mineral acquisition in plants might include the ability to tolerate high soil P levels, to transfer nutrients from soil to root, to enhance translocation of nutrients from roots to shoots, or involvement of soil microorganisms other than AMF. For example, plant acquisition of Zn and Cu depended on soil P level, and these nutrients diminished in plant tissue when P was increased in soil (Lambert et al. 1979; Lambert and Weidensaul 1991). Transport of Zn and Cu from hyphae to roots and from roots to shoots of maize was enhanced in AM relative to nonAM plants (Kothari et

al. 1991a, b; Li et al. 1991b). Zinc acquisition was also enhanced when AM plants were grown with other microorganisms added to soil to enhance Zn solubility (Azaizeh et al. 1995).

The acidic Lily soil used in our study is known to impose toxic Al effects on many plants (Clark et al. 1997) and the 88% Al saturation in this batch of soil would be a major constraint to plant growth. The concentration of Al (302 mg kg^{-1}) relative to other cations was high, and P, which can inactivate Al, was relatively low (3.1 mg kg^{-1}). Mn and Fe were relatively high (33 and 54 mg kg^{-1}, respectively) and might potentially induce toxicities. The relatively large increase in DM for many of the AM plants relative to those with *Gi. rosea* and *G. intraradices* and nonAM plants grown in pH_{Ca} 4 soil indicates that AMF could alleviate the acidic soil toxicity imposed by Lily soil.

The switchgrass cultivar used is considered to be moderately tolerant to soil acidity (Bona and Belesky 1992). Thus growth differences greater than those noted in our study might have been expected for nonAM plants grown in pH_{Ca} 5 compared with pH_{Ca} 4 Lily soil. Switchgrass did not appear to be tolerant of this acidic soil without AMF-root symbiosis, and certain AMF isolatesm, such as *G. clarum* and *G. diaphanum* were more effective in providing tolerance than others (e.g. *G. intraradices* and *Gi. rosea*). Similar to Al, shoot concentrations of Mn, Fe, and B were considerably lower in most AM than in nonAM plants. High concentrations of these elements may be toxic for plants. Shoot concentrations considered to be high or in excess are >500–1000 mg kg^{-1} for Mn, >200–300 mg kg^{-1} for Al and Fe, and >15–25 mg kg^{-1} for B (Smith 1986). The concentrations of each of these minerals were excessive in *G. intraradices*, *Gi. rosea* colarized plants and nonAM plants grown in pH_{Ca} 4 soil.

AMF alleviation of toxicity symptoms and/or reduced acquisition of toxic elements has been reported for Al (Borie and Rubio 1999; Clark and Zeto 1996b; Medeiros et al. 1994a; Wang et al. 1985) and Mn (Arines et al. 1989; Azaizeh et al. 1995; Bethlenfalvay and Franson 1989; Kothari et al. 1990, 1991b; Kucey and Janzen 1987; Medeiros et al. 1994b). AMF have also been implicated in enhancing plant tolerance to mineral toxicities (Keltjens 1997). Differences between AMF in alleviating Mn and Al toxicities have also been reported (Arines et al. 1989; Clark and Zeto 1996a; Habte and Soedarjo 1995, 1996; Koslowsky and Boerner 1989; Medeiros et al. 1994a, b). The mechanism of enhancement of plant tolerance to toxic elements is not fully understood, but AMF-root symbioses and/or root excretion of organic acids have been associated with protection of plants against toxic elements (Keltjens 1997). Reduced Mn acquisition by AM plants grown in calcareous soil was related to diminished numbers of Mn-reducing bacteria in the rhizosphere (Kothari et al. 1990, 1991b; Posta et al. 1994) and to microorganism populations and release of low-molecular-weight root exudates (Posta et al. 1994). In addition, reduced acquisition of toxic elements or alleviation of toxicities has been related to high P acquisition by AM plants (Persad-Chinnery and Chinnery 1996). The high dependence of switchgrass on AMF-root associations reported by Brejda et al. 1993, 1998 and Hetrick et al. 1987 also supports the hypothesis that AMF are involved in plant tolerance of mineral stresses, especially acidic soil mineral stresses. Information on Fe and B acquisition by AM plants is limited, but AM maize grown in two acidic soils showed enhanced Fe only in association with *G. etunicatum* and not *G. diaphanum* or *G. intraradices*. *G. intraradices* plants had higher B than *G. diaphanum* or *G. etunicatum* plants grown in the same soils (Clark and Zeto 1996b).

The benefits of AMF in our study for plants grown in Lily acidic soil may have occured because the AMF used were isolated from acidic soils (Morton et al. 1993). Some AMF are more adapted to acidic than to higher pH soils (Clark 1997; Siqueira and Moreira 1997), and some AMF have greater tolerance of Al-saturated soil for sporulation and hyphal growth than others (Bartolome-Esteban and Schenck 1994). Switchgrass appeared to acquire tolerance to the acidic conditions in the soil used by association with AMF.

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