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Geographic isolates of *Glomus* increase root growth and whole-plant transpiration of *Citrus* seedlings grown with high phosphorus

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Abstract Four *Glomus* species/isolates from arid, semi-arid and mesic areas were evaluated for their effects on growth and water use characteristics of young *Citrus volkameriana* (′Volkamer′ lemon) under well-watered conditions, followed by three soil-drying episodes of increasing severity (soil moisture tensions of –0.02, –0.06, and –0.08 MPa) and recovery conditions. Arbuscular mycorrhizal (AM) plants were also compared to non-AM plants given extra phosphorus (P) fertilizer. AM plants and non-AM plants had similar shoot size (dry weight and canopy area), but all AM fungus treatments stimulated root growth (dry weight and length). Leaf P concentrations were 12–56% higher in AM plants than non-AM plants. Enhanced root growth was positively correlated with leaf P concentration. In general, AM plants had greater whole-plant transpiration than non-AM plants under well-watered conditions, under mild water stress and during recovery from moderate and severe soil drying. This suggests a faster recovery from moisture stress by AM plants. AM plants had lower leaf conductance than non-AM plants when exposed to severe soil drying. Although the greatest differences were between AM and non-AM plants, plants treated with *Glomus* isolates differed in colonization level, leaf P concentration, root length, transpiration flux and leaf conductance.

Keywords Arbuscular mycorrhizae · Conductance · Water stress

Introduction

Citrus roots normally form symbiotic associations with arbuscular mycorrhizal (AM) fungi (Rayner 1935). In mycorrhizal associations, plants supply labile photosynthates to fungi, while fungi aid in the uptake of nutrients, especially P. The potential for AM fungi to increase plant growth under conditions of low soil P has been well documented (Graham et al. 1996). Graham et al. (1987) suggested that the effect of AM fungi on plant water relations is a secondary consequence of enhanced host P nutrition. However, some *Glomus* isolates have been shown to stimulate root growth of citrus independent of plant P nutrition (Eissenstat et al. 1993; Graham and Syvertsen 1984; Peng et al. 1993).

Mycorrhizal fungi can affect plant water relations (Nelsen 1987), but the mechanisms involved are unclear. *Glomus mosseae* enhanced growth, leaf transpiration and conductance of *Garcinia mangostana* L. and also caused a 67–88% improvement in P uptake efficiency (Masri et al. 1998). Yano-Melo et al. (1999) reported that *Glomus clarum* and *Glomus etunicatum* enhanced growth, photosynthesis and transpiration rates of *Musa*, but these effects were probably caused by improved host P nutrition. AM fungi increased root length of *Citrus jambhiri* Lush and increased whole plant transpiration when soil was moist. They hastened stress of container plants during soil drying because soil water was depleted faster by AM plant than non-AM plants (Levy et al. 1983).

AM fungal isolates vary in their ability to colonize roots, stimulate plant uptake of P (Graham et al. 1982), and increase plant growth (Camprubi and Calvet 1996; Graham et al. 1996). Identifying exceptional AM fungal species and/or geographic isolates of a single species from different edaphic conditions that enhance plant performance might be of practical benefit to citriculture. Under field conditions, AM fungal isolates that enhance root growth of seedling transplants could help mitigate desiccation injury (Davies and Albrigo 1994) because larger root systems can explore a greater volume of soil for water.

We hypothesized that growth and water-use characteristics of AM plants would differ from those of non-AM plants that were well supplied with P. Because functional differences may exist among AM fungal isolates of different geographic origins, we also hypothesized that inoculation of citrus seedlings with *Glomus* isolates from

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arid, semi-arid or mesic areas would result in different patterns of plant growth and water use. These hypotheses were tested by evaluating the effects of four *Glomus* isolates from disparate edaphic conditions on growth and whole-plant transpiration of young *Citrus volkameriana* Ten. and Pasq. ('Volkamer' lemon) under well-watered conditions, three soil-drying episodes of increased severity and recovery conditions. The effects of these *Glomus* isolates were tested under conditions of high P. Non-AM control plants were given extra P fertilizer in an attempt to examine AM and non-AM plants of similar size. 'Volkamer' lemon was chosen as host plant because it is a common citrus rootstock used in commercial orchards.

Materials and methods

Uniform (0.15-m mean height), non-mycorrhizal, 2-month-old seedlings of 'Volkamer' lemon were transplanted into 8-l polyethylene containers, painted white on the outside to increase surface albedo. Containers were filled with a 3:1 (v:v) soil mixture of coarse silica sand (particle size <4.25 mm) blended with pasteurized Gilman clay loam (pH 7.3, EC 0.25 dS/m, 11.3 g sodium bicarbonate extractable P/kg soil, 13.2 g organic matter/kg soil). At transplanting, seedling plants were inoculated with one of four AM fungal isolates or were not inoculated as a control.

Single-isolate cultures from roots of *Prosopis* spp. were started at Arizona State University for three of the isolates using multiple spores of a similar morphotype extracted from a successive trap culture (Stutz and Morton 1996). Trap cultures had been started using rhizosphere soil collected from arid and semi-arid areas of southwestern North America (Stutz et al. 2000). These isolates included *Glomus mosseae* (Nicol. & Gerde.) Gerde. & Trappe isolate 51C collected from *Prosopis glandulosa* var. *glandulosa* Woot. (honey mesquite) growing in an arid, Chihuahuan desert scrub in Padre Canyon., Tex., USA (31.4° N, 105.6° W), *G. mosseae* isolate 114C collected from *Prosopis velutina* Woot. (velvet mesquite) growing in a semi-arid, Sinoloan thornscrub near Mazacahui, Sonora, Mexico (29.5°N, 110.1°W), and isolate 25A of an undescribed *Glomus* sp. (morphotype AZ112) collected from velvet mesquite in arid, Sonoran Desert scrub near Wittmann, Ariz. USA (33.4°N, 112.3°W). The fourth isolate, *Glomus intraradices* Schenck & Smith isolate FL208, obtained from the International Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi (West Virginia University, Morgantown, W.Va., USA)„ was originally collected in a citrus orchard in Orlando, Fla. USA (Morton et al. 1993).

AM fungal inocula consisted of infected Sudan grass root pieces, spores and a 1:1 (v:v) soil mixture of silica sand and Gilman clay loam placed subjacent to the citrus seedling transplant roots. Inoculum potential had been previously determined using the most probable number method (Alexander 1982) with Sudan grass as a host plant. Plants were inoculated with approximately 3.3×10^4 propagules of *G. mosseae* 51C or 144C or *G. intraradices* FL208, or with approximately 7.4×10^3 propagules of *Glomus* sp. 25A (because of the limited amount of inoculum). The volume of inoculum added to each pot ranged from 75 to 150 cm^3. Control plants were transplanted without inoculum, but received a drench of mixed inoculum filtrate passed through a 45-µm filter in order to establish a soil microbiota similar to the other AM fungal treatments.

After potting, all plants were fertilized with 11.8 g of isobutylidene diurea slow-release fertilizer (20N-0P-16.6K-2Fe-1.4Mn) plus 5 g of magnesium sulfate. Additionally, plants inoculated with AM fungi received 21.7 g of concentrated superphosphate (0N-19.6P-0 K) while non-AM plants (controls) were given 91.8 g superphosphate (based on unpublished data of Martin and Stutz) in an effort to equalize plant size. Plants were grown for 2.5 months in a glasshouse (26°C day/15°C night, 30% PAR exclusion, 1.0–1.4 MPa VPD) under well-watered conditions. Soil moisture tension was >–0.01 MPa as measured by soil tensiometers (Soil Moisture Equipment Co., Santa Barbara, Calif., USA) positioned halfway down the container profile of each plant. Plants were irrigated equally in excess of container capacity with deionized water every third day.

After 2.5 months, the plants were subjected to three consecutive soil-drying episodes by withholding water until soil water tensions reached –0.02 MPa, –0.05 MPa, and –0.08 MPa (about 3, 7 and 12 days, respectively), and were then rewatered. Whole-plant transpiration was measured lysimetrically on the last day of well-watered conditions before soil drying, the last day of each soil-drying episode, and the first and second days after rewatering when soil profiles were again moist. Before dawn, containers were placed in white polyethylene bags sealed around the base of the plant trunk with wire ties and weighed. After sunset, containers were reweighed and bags were removed. Whole-plant transpiration water was calculated as the difference between predawn and after sunset weights expressed as a function of final (at harvest) whole-plant canopy leaf area. Containers were never continuously bagged for longer than 18 h.

Mid-day leaf conductance measurements were made using a portable infrared gas analyzer (LI-6200, Li-Cor Inc., Lincoln, Neb., USA) on the same days that whole plant transpiration was measured. Measurements were made in closed system mode on the youngest fully expanded leaves (approximately the fifth leaf from the stem apex after 2.5 months); the same leaves were used for all conductance measurements. Predawn and mid-day leaf water potential measurements were made using a pressure bomb (Soil Moisture Equipment Co.). To limit the effect of these destructive measurements, only four leaf water potential measurements were made: on the last day of well-watered conditions, the last day of the –0.08 MPa drying episode and the subsequent 2 days of recovery after rewatering. Measurements were made on a single leaf per plant starting with the second-youngest fully expanded leaf from the stem apex and proceeding to subsequent older leaves.

All plants were harvested after the recovery period following the last soil-drying episode. Shoots were separated from roots and root systems were carefully extracted from soil by floating in a large water bath. Whole-plant canopy leaf area (m^2/plant) and root length (m/plant) was measured with a digital camera interfaced with a computer (AgVision Digital Imaging System, Pullman, Wash., USA). Shoots and roots were oven dried (70°C for 48 h) and weighed. Phosphorus concentration of leaves was analyzed using ascorbic methods (Watanabe and Olson 1965).

To determine the extent of root colonization by AM fungi, a sample of 1-cm-long root pieces (approximately 1 g fresh weight) was collected from each root system and fixed in formalin-acetic acid-alcohol. Root samples were then cleared and stained using 0.05% trypan blue in acidic glycerol (Koske and Gemma 1989). The magnified intersection method (McGonigle et al. 1990) was used to quantify AM fungal infection. The proportion of root length containing fungus arbuscules, vesicles, and hyphae was determined.

Plants were arrayed in a randomized complete block design of five treatments (four AM treatments and one non-AM control treatment) with 10 single plant replications of each treatment for a total of 50 plants. For all treatment comparisons, an analysis of variance was made using the general linear models procedure (SAS version 6.03, SAS Institute, Cary, N.C., USA). Duncan's multiple range test was used to separate means at $\alpha < 0.05$. Percent root colonization was arc sine transformed before analysis.

Results

Glomus sp. 25A colonized the most root length and produced the most arbuscules and vesicles (Table 1), despite having fewer inoculum propagules than the other *Glomus* isolates. In contrast, *G. mosseae* 51C colonized the least

total root length and produced the fewest arbuscules, vesicles and intraradical hyphae. *G. mosseae* 114C and *G. intraradices* FL208 had intermediate levels of root colonization. Plants inoculated with *Glomus* sp. 25A, *G. mosseae* 114C and *G. intraradices* FL208 had a higher percent root length colonized by hyphae than did *G. mosseae* 51C. All control plants remained non-mycorrhizal.

Plants inoculated with AM fungi had 12–56% higher leaf P concentrations than non-AM plants (Table 2) even though non-AM plants were given extra P fertilizer. Plants inoculated with *Glomus* sp. 25A had the highest leaf P concentrations. Plants inoculated with *G. mosseae* 114C also had higher leaf P concentrations than non-AM plants, but statistically similar leaf P concentrations to those inoculated with *G. mosseae* 51C or *G. intraradices* FL208. Leaf P concentrations of plants inoculated with *G. mosseae* 51C or *G. intraradices* FL208 were statistically similar to those of non-AM plants.

Table 1 Percent citrus root length having only arbuscules, vesicles, or internal hyphae and total arbuscular mycorrhizal (AM) fungal colonization. Control plants remained non-mycorrhizal. Values are treatment means, *n*=10. Means followed by the same letter within a column are not significantly different, Duncan's multiple range test, α=0.05

AM fungus	Arbuscules	Vesicles	Hyphae	Total
Glomus sp. 25A	45.5a	11.3a	24.0a	76 a
G. mosseae 51C	4.3c	1.4b	6.0b	11 c
G. mosseae 114C	18.0bc	6.0ab	22.5a	47 b
G. intraradices FL208	21.1b	5.3ab	29.9a	58 b

Shoot dry weight and canopy leaf area of AM plants and non-AM plants were similar (Table 2). In contrast, AM fungi generally stimulated root growth. Specifically, root dry weight and total root length were 1.2–1.3 times higher in plants inoculated with *Glomus* sp. 25A, *G. mosseae* 114C or *G. intraradices* FL208 than non-AM high P plants (Table 2). Root length of plants colonized by *G. mosseae* 51C was only 1.06 times higher than that of non-AM plants.

When well watered, plants colonized with *Glomus* sp. 25A or *G. intraradices* FL208 transpired about 1.3 times more water than non-AM control plants (Table 3). Whole-plant transpiration of all plants was incrementally reduced by about 13%, 50% and 90% in response to the –0.02, –0.05, and –0.08 MPa soil-drying episodes, respectively. All AM plants transpired more water than non-AM plants under –0.02 MPa soil water deficiency conditions. Two days after recovery from –0.02 MPa soil drying, plants colonized with *Glomus* sp. 25A or *G. intraradices* FL208 still transpired more water than non-AM plants. Under –0.05 and –0.08 MPa soil water deficiency conditions, transpiration fluxes of AM and non-AM plants were similar. After 2 days of recovery from –0.05 MPa soil drying, all AM plants transpired more water than non-AM plants. But after 2 days of recovery from –0.08 MPa soil drying, only plants inoculated with *G. mosseae* 114C or *G. intraradices* FL208 transpired more water than non-AM plants.

When well watered, plants inoculated with *G. mosseae* 114C had higher leaf conductance than non-AM plants (Table 4). When exposed to –0.02 MPa soil dry-

Table 2 Dry weight, canopy leaf area, root length and leaf P concentration of *Citrus volkameriana* inoculated or not with one of four *Glomus* isolates. Values are treatment means, *n*=10. Means followed by the same letter within a column are not significantly different, Duncan's multiple range test, α=0.05

AM fungus	Shoot dry wt. (g/plant)	Root dry wt. (g/plant)	Canopy leaf area (m^2/plant)	Root length (m/plant)	Leaf P (mg/g)
Glomus sp. 25A	17.1a	7.5a	0.109a	3.54a	2.55a
G. mosseae 51C	16.1a	7.2a	0.108a	3.06ab	1.83bc
G. mosseae 114C	16.2a	7.8a	0.103a	3.48a	2.13b
G. intraradices FL208	16.6a	7.5a	0.090a	3.53a	2.00bc
Control	16.2a	6.2b	0.089a	2.90b	1.63c

Table 3 Whole-plant transpiration of *C. volkameriana* 2.5 months after root inoculation with AM fungi and growth under well-watered conditions followed by exposure (*S*) to three consecutive soil-drying cycles of increased water deficit (–0.02, –0.05, –0.08 MPa) and 2 days of recovery (*R1* and *R2*) after rewatering. Values are treatment means, *n*=10. Means followed by the same letter within a column are not significantly different, Duncan's multiple range test, α=0.05

AM fungus	Whole-plant transpiration (l H_2O per m^2 canopy leaf area/day)								
	Well watered	–0.02 MPa			–0.05 MPa			–0.08 MPa	
		S	R1	R2	S	R1	R2	S	R1	R2
Glomus sp. 25A	1.73a	1.39a	1.60a	0.90a	0.52a	0.90ab	1.12a	0.08ab	0.85a	0.78ab
G. mosseae 51C	1.50ab	1.41a	1.54a	0.83ab	0.96a	1.12a	1.14a	0.13a	0.69bc	0.80ab
G. mosseae 114C	1.61ab	1.38a	1.46ab	0.82ab	0.64a	0.94ab	1.11a	0.10ab	0.80ab	0.85a
G. intraradices FL208	1.74a	1.51a	1.63a	0.88a	0.55a	0.81b	1.13a	0.07b	0.83a	0.91a
Control	1.31b	1.17b	1.28b	0.73b	0.90a	0.87ab	0.95b	0.08ab	0.63c	0.69b

Table 4 Leaf conductance of *C. volkameriana* 2.5 months after root inoculation with AM fungi and growth under well-watered conditions followed by exposure (*S*) to three consecutive soil-drying cycles of increased water deficit (–0.02, –0.05, –0.08 MPa) and 2 days of recovery (*R1* and *R2*) after rewatering. Values are treatment means, *n*=10. Means followed by the same letter within a column are not significantly different, Duncan's multiple range test, $\alpha = 0.05$

AM fungus	Leaf conductance (mmol/m²/s)									
	Well watered	–0.02 MPa			–0.05 MPa			–0.08 MPa		
		S	R1	R2	S	R1	R2	S	R1	R2
Glomus sp. 25A	83.6ab	77.5c	110.5a	181.6b	40.2b	71.2b	167.1bc	23.1b	105.5a	99.6b
G. mosseae 51C	67.8c	104.1b	140.6a	198.7ab	78.9a	129.1a	150.4bc	22.1b	63.6c	86.1c
G. mosseae 114C	93.7a	144.9a	165.0ab	221.0a	94.3a	133.8a	206.1a	21.3b	85.2b	104.3ab
G. intraradices FL208	82.2ab	135.2a	161.5a	201.7ab	43.5b	65.1b	140.4c	19.1b	99.2a	115.3a
Control	79.3bc	106.9b	135.3b	182.6b	84.7a	127.1a	174.4b	27.5a	101.2a	108.9ab

Table 5 Pre-dawn and afternoon leaf water potentials of *C. volkameriana* under well-watered conditions (*W* mean soil water tension ≥ –0.01 MPa) 2.5 months after root inoculation with AM fungi and subsequent exposure to severe water deficit (*S* soil water tension –0.08 MPa) and 2 days of recovery (*R1* and *R2*) after rewatering. Values are treatment means, *n*=10. Means followed by the same letter within a column are not significantly different, Duncan's multiple range test, $\alpha = 0.05$

AM fungus	Leaf water potential (MPa)							
	W		S		R1		R2	
	Pre-dawn	Afternoon	Pre-dawn	Afternoon	Pre-dawn	Afternoon	Pre-dawn	Afternoon
Glomus sp. 25A	–0.69b	–1.05a	–3.10bc	–3.66b	–0.74ab	–1.29b	–0.29a	–1.35b
Glomus mosseae 51C	–0.43a	–0.88a	–2.34a	–2.39a	–0.30a	–1.02a	–0.32a	–1.31b
Glomus mosseae 114C	–0.64ab	–0.91a	–2.88bc	–3.42b	–0.81ab	–1.45a	–0.41a	–1.28b
Glomus intraradices FL208	–0.54ab	–0.96a	–3.18c	–3.61b	–0.97b	–1.33b	–0.34a	–1.40b
Control	–0.61ab	–1.00a	–2.48ab	–3.21b	–0.68ab	–1.10a	–0.35a	–0.78a

ing, plants inoculated with *Glomus* sp. 25A had the lowest leaf conductance. During –0.05 MPa soil drying, plants inoculated with *Glomus* sp. 25A or *G. intraradices* FL208 had the lowest leaf conductance, but when exposed to –0.08 MPa soil drying, AM plants had lower leaf conductance than non-AM plants. Two days after recovery from –0.05 MPa soil drying, plants inoculated with *G. mosseae* 114C or *G. intraradices* FL208 had the highest and lowest leaf conductances, respectively. Two days after recovery from –0.08 MPa soil drying, plants inoculated with *G. mosseae* 51C had the lowest leaf conductance. Differences in transpiration and leaf conductance in response to AM fungal treatments during –0.08 MPa soil drying and subsequent recovery were generally lower than during –0.02 or –0.05 MPa soil drying and rewatering (Tables 3, 4).

Leaf water potentials of AM plants and non-AM plants were similar under well-watered conditions before soil drying (Table 5). During –0.08 MPa soil drying, leaf water potentials of plants inoculated with *G. mosseae* 51C were least negative. Usually plants inoculated with *G. mosseae* 51C also had the least negative leaf water potential on the first day of recovery from –0.08 MPa soil drying. By the afternoon of the second day of recovery from –0.08 MPa soil drying, leaf water potential of all AM plants was similar though more negative than that of non-AM plants.

Discussion

In this study, we achieved our goal of growing AM plants and non-AM plants of similar shoot size by applying additional P fertilizer to non-AM plants. However, even with the different allotments of P fertilizer, all AM fungal treatments stimulated root growth compared with non-AM plants. In addition, leaf P was lowest in non-AM plants. These results are in accord with findings of Levy et al. (1983), who reported that *G. intraradices* increased root length of rough lemon (*Citrus jambhiri* Lush) seedlings. In addition, we found strong positive correlations between leaf P levels and root dry weight and length (r = 0.71 and 0.83, respectively). Thus, the different patterns of citrus root growth may have been related to the ability of *Glomus* isolates to enhance P nutrition, even when leaf P for all plants was above the level sufficient for normal growth of citrus (>1 mg/g tissue P; Davies and Albrigo 1994). We did not measure root P concentration or tissue concentrations of other elements. It is possible that AM also enhanced P nutrition in roots or the tissue concentrations of other elements.

Patterns of whole-plant transpiration under well-watered conditions in association with patterns of root growth and colonization by AM fungi suggest that the higher water use by AM citrus seedlings similar in shoot size to non-AM seedlings was caused by mycorrhiza stimulation of root growth. Our findings agree with those

of Levy et al. (1983), who reported higher transpiration by mycorrhizal rough lemon seedlings when soil was moist and lower transpiration of mycorrhizal citrus in containers under conditions of limited soil water availability; AM plants depleted available soil water sooner than non-AM plants. Although a positive correlation between citrus root hydraulic conductivity and root system size has been shown for *Citrus* (Graham and Syvertsen 1984), another possible mechanism for AM-mediated increases in host plant transpiration is the direct transport of water to roots through external hyphae. However, the maximal rate of water movement to roots through hyphae is thought to be relatively low (Graham and Syvertsen 1984). Therefore, the enhancement of plant transpiration and leaf conductance by *Glomus* isolates under well-watered conditions may best be seen as an indirect result of increased root size. Graham et al. (1987) asserted that the effect of AM fungi on citrus water uptake was primarily a result of improved plant nutrition, especially P.

Mycorrhizal plants had higher whole plant transpiration fluxes than non-AM plants under the –0.02 MPa soil-drying episodes, but not during the –0.05 or –0.08 MPa soil-drying episodes. Although AM fungus treatments did not significantly affect plant water loss during –0.05 MPa soil drying, there was a trend toward lower whole-plant transpiration by plants inoculated with *G. mosseae* 114C, *Glomus* sp. 25A, or *G. intraradices* FL208 than non-AM plants. During recovery (especially after 2 days) from –0.05 and –0.08 MPa soil-drying episodes after rewatering, transpiration was generally higher in AM plants than in non-AM plants. This suggests that AM plants recovered faster from moisture stress than non-AM plants. In particular, plants colonized by *G. intraradices* FL208 or *G. mosseae* 114 were better able to extract soil water after rewatering than non-AM plants. Although we did not measure the extent to which AM fungal isolates produced external hyphae, it is possible that plant water uptake after rewatering was enhanced directly by external hyphae acting as external root conduits.

Stomatal behavior of citrus leaves is not thought to be closely coupled to water potential (Syvertsen and Lloyd 1994), but might respond to non-hydraulic signals such as abscisic acid (ABA). Drying soil stimulates ABA production in roots and AM fungi may increase xylem ABA concentrations during drought stress (Ebel et al. 1997). Our data are consistent with the findings of Levy and Krikun (1980), who postulated that AM fungi affect stomatal aperture independent of root hydraulic conductivity. They found that mycorrhizal and non-mycorrhizal *Citrus jambhiri* plants had similar leaf water potentials but different rates of leaf conductance following water stress. Moreover, Druge and Schonbeck (1992) concluded that increased transpiration and growth of mycorrhizal flax (*Linum usitatissimum* L.) was related to enhanced root cytokinin levels. Green et al. (1998) found that the influence of *G. intraradices* on transpiration of *Rosa* remained even after leaves were detached from their roots. Thus, the effects of *Glomus* isolates on plant water status we observed may also be related to mycorrhiza modulation of root hormone synthesis or non-hydraulic root-to-shoot chemical signaling.

Although the greatest differences in this study were between AM and non-AM plants, plants treated with different *Glomus* isolates did differ in colonization level, leaf P concentration, root length, transpiration flux and leaf conductance. These differences in functional diversity between isolates did not appear to be linked to the original habitat (arid, semi-arid or mesic) of the isolate. For example, plants inoculated with *G. mosseae* 114C, an isolate from a semi-arid Sinoloan thornscrub community, transpired more water than non-AM plants 2 days after recovery from severe soil drying. A similar response was observed in plants inoculated with *G. intraradices* FL208, an isolate from a Florida citrus orchard. In contrast, Stahl and Smith (1984) found differences in the water relations of *Agropyron smithii* in response to soil drying when grass plants where inoculated with *G. microcarpum* isolates from xeric and more mesic habitats in Wyoming. Functional variation was also observed between the two *Glomus* isolates from xeric habitats used in this study. *G. mosseae* 51C (isolated from a Chihuahuan desert scrub community) was a poor colonizer of ′Volkamer′ lemon seedlings and was least effective in stimulating root extension. In contrast, *Glomus* sp. 25A (isolated from a Sonoran desert scrub community) was the best colonizer of lemon seedlings; plants inoculated with this isolate had the highest leaf P concentrations. Functional variation was also observed between the two *G. mosseae* isolates used in this study. *G. mosseae* 51C was less infective (colonized a lower percent root length of citrus) and less effective in terms of stimulating root growth than *G. mosseae* 114C. Differences in functional diversity between *G. mosseae* isolates from different habitats have been reported previously (Bethlenfalvay et al. 1989; Stahl and Christensen 1991).

In summary, four AM fungus isolates of the genus *Glomus* from areas with different edaphic and climatic conditions stimulated root growth and P uptake of ‘Volkamer’ lemon seedlings under conditions of high P. These effects are most convincing in light of our attempt to produce mycorrhizal and non-mycorrhizal plants of similar size by giving additional P fertilizer to non-AM plants. Under well-watered conditions, AM plants generally transpired more water than non-AM plants. In addition, AM plants were generally able to use more water than non-AM plants once rewatered after soil drying. Mycorrhiza effects reported in this study may have been a secondary consequence of AM-enhanced host P nutrition because root growth was highly correlated with leaf P concentration. Functional variation between *Glomus* isolates from different habitats (arid, semi-arid or mesic) was observed, but these differences did not appear to be linked to the original habitat of the isolate. Ultimately, *Glomus* isolates that increase root growth and whole-plant transpiration might improve the field performance of young citrus rootstock and mitigate

against desiccation after soil drying by amplifying the potential for root exploration of soil for water.

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