

EFFECT OF URBAN EXPANSION ON ARBUSCULAR MYCORRHIZAL FUNGAL MEDIATION OF LANDSCAPE TREE GROWTH

by Linda B. Stabler, Chris A. Martin, and Jean C. Stutz

Abstract. Field and glasshouse pot studies were conducted to determine effects of urban expansion on arbuscular mycorrhizal fungal (AMF) populations and AMF impact on landscape tree growth. Soil and root segments were collected and evaluated for root colonization by AMF of trees at remnant Sonoran Desert sites and nearby, formerly desert, drip-irrigated residential landscape sites in the Phoenix, Arizona, USA, metropolitan area. Native desert trees had greater colonization by AMF than residential landscape trees, and AMF species composition differed at the two site types. A glasshouse pot experiment using AMF inocula from the desert or residential sites was used to evaluate AMF effects on growth and carbon fluxes of three landscape trees in 12-L (3-gal) polyethylene containers relative to non-AMF controls. Growth and P nutrition of *Acacia smallii* and *Fraxinus uhdei* were increased by AMF colonization. *Acacia* carbon assimilation was increased by AMF root colonization. Soil respiration by *Acacia* and *Fraxinus* tree roots was decreased by AMF root colonization. Growth and carbon fluxes of *Parkinsonia microphylla* were not affected by AMF. We conclude that AMF might significantly increase landscape tree carbon storage potential depending on tree species, AMF population characteristics, soil water availability, and improved P uptake.

Key Words. Urban forest; gas exchange; photosynthesis; mycorrhizae.

Public concerns about urban expansion, environmental degradation, and a lowering of the quality of urban life have helped to spur interest in management of city trees as an ecosystem resource (Rowntree 1998). Urban trees in the United States potentially store between 350 and 750 million metric tons of carbon (Nowak 1993).

Arbuscular mycorrhizal fungi (AMF) are obligatory endophytes that form symbiotic associations with approximately 90% of all higher plants (Kendrick and Berch 1985). Past research has shown that AMF affect host plant growth, P uptake, water status, and resistance to biotic and abiotic stresses (Menge et al. 1978; Sanchez-Diaz and Honrubia 1994; Copeman et al. 1996). AMF might extract an estimated 5% to 20% of labile photosynthates from colonized plant roots (Eissenstat et al. 1993). AMF have been shown to differentially colonize plant roots, causing a variety of effects on plant growth, biomass allocation, and photosynthesis (Abbott and Gazey 1994; Martin and Stutz 1994; Fidelibus et al. 2000).

Evaluation of the nature and function of mycorrhizal associations in managed city landscapes has only recently begun. Presently, it is unknown to what extent urban expansion might impact AMF population characteristics and AMF effects on landscape tree carbon sink potential. Preliminary evaluation of AMF populations along a time-since-development gradient from Phoenix's urban core to the city's edge showed that recently developed areas (less than 5 years) had less species diversity than landscapes developed 20 to 40 years ago (Stutz and Martin 1998).

Cities such as Phoenix are places of elevated atmospheric CO₂ (Stabler and Martin 2000). Because AMF have been shown to stimulate belowground carbon sink strength under conditions of elevated CO₂ (Berntson et al. 1997), the potential might exist for AMF to increase the carbon sink potential of managed urban landscape trees. One objective of this research was to

investigate how land-use change associated with urban expansion affects AMF population and colonization characteristics by comparing patterns of root colonization of native trees at remnant Sonoran Desert sites to those of landscape trees at nearby, recently developed residential sites. Another objective was to determine if there are differences in the ability of AMF populations from remnant desert or residential sites to affect landscape tree growth.

METHODS

Field Study

Population and colonization characteristics of AMF were evaluated at suburban residential and remnant desert sites at the fringe of the greater Phoenix, Arizona, metropolitan area (33°N 112°W) on the northeast edge of the Sonoran Desert in the southwest United States. Climate in the Phoenix area is typically arid; mean annual precipitation in this region is only 180 mm (7.2 in.), with approximately 50% occurring as summer thunderstorms and the remainder associated with winter frontal systems advecting from the Pacific Ocean. Mean monthly temperature minimum and maximum of 5.1°C (41°F) and 41.0°C (106°F) occur in January and July, respectively.

The remnant desert sites ($n = 3$) were located within the South Mountain Preserve, a publicly owned desert park at the southern fringe of the Phoenix metropolitan area. The dominant woody vegetation at the three desert sites was *Parkinsonia microphylla* (foothill palo verde), *Larrea tridentata* (creosote bush), and *Ambrosia deltoidea* (bursage). The ranges of some desert soil chemical properties were pH: 7.6 to 8.0; EC: 0.7 to 1.0 dS/m; extractable P: 7 to 20 ppm; and total N: 13 to 25 ppm. The suburban residential sites ($n = 3$) were drip-irrigated, single-family residential yards immediately adjacent to the preserve. Each of the residential yards was landscaped with a mixture of native and exotic vegetation between 1989 and 1990 on subdivision properties with a mean size of 890 m² (9,575 ft²). The ranges of

some residential soil chemical properties were pH: 7.7 to 8.1; EC: 1.0 to 2.3 dS/m; extractable P: 5 to 38 ppm; and total N: 17 to 82 ppm. Overall, the number of plants per unit surface area at the desert sites was about 1.2 times greater than the residential sites; however, overall canopy coverage of landscape plants at the residential sites was about 3.5 times greater than canopy coverage of native vegetation at the desert sites.

During August 1998, tree roots and soil at each of the desert and residential sites were evaluated for mycorrhizal colonization and AMF species composition. At each of the three desert sites, a single sample of soil and root segments was collected from the undercanopy rhizosphere of three *Parkinsonia microphylla* trees, $n = 9$. At each of the three residential sites, a single sample of soil and root segments was collected from the undercanopy rhizosphere of three landscape trees, $n = 9$. Landscape trees at the three residential sites from which samples were collected included *Acacia smallii* (sweet acacia), *Lysiloma watsonii* (fern-of-the-desert), *Parkinsonia florida* (blue palo verde), and *P. praecox* (palo brea). All samples were collected at a depth of 20 cm (8 in.) below the soil surface. The soil surface at the desert sites was undisturbed, whereas the soil surface at the residential sites was covered with approximately 2.5 cm (1 in.) of 3/8-in., minus decomposing granite mulch.

Root segments were cleared and stained using 0.05% trypan blue following the method of Koske and Gemma (1989), and the percent colonization was estimated by the magnified intersections method (McGonigle et al. 1990). Multigeneration trap cultures were established using the method of Stutz and Morton (1996) to evaluate AMF species composition and richness at representative sites and to produce inoculum for greenhouse experiments. Species composition of AMF at each site was determined by extracting spores from a subsample [100 cm³ (0.11 qt)] of each trap culture (Daniels and Skipper 1982) and examining spore morphotypes using a stereomicroscope and light microscope. Spores of undescribed species were referenced ac-

cording to the International Culture Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi (INVAM) accession code assigned to trap cultures deposited at INVAM in which each unique morphotype was first discovered. Species richness for the desert and residential sites was determined by combining data from the three trees sampled at each of the three site replicates.

Glasshouse Pot Study

Three regionally common landscape tree species were inoculated with one of three AMF population treatments (remnant Sonoran Desert, residential, or non-AMF control) to test for any effects of urban expansion on the ability of AMF to affect landscape tree growth. Single-source, uniform seedlings of *Acacia smallii*, *Fraxinus uhdei* (Shamel ash), and *Parkinsonia microphylla* were either germinated in or potted into 12-L (3 gal) polyethylene containers filled with a soil mixture of washed masonry sand, Gilman clay loam, and #12 silica sand (8:1:1 v/v). Seedlings were used because, especially for *Acacia* and *Parkinsonia*, seed propagation is the method used by regional production nurseries. The soil mixture was formulated to simulate the average particle size distribution and drainage properties of soil collected in the upper 30-cm (12-in.) soil profile of the six field study sites. Before use, the soil mixture was autoclaved twice for 90 min at 100°C (212°F) and had a total porosity of 26.6%, an air-filled porosity of 3.8%, and a water-holding capacity of 22.9%, with 16 ppm extractable P.

Third-generation trap cultures consisting of root segments, culture media, and spores from one desert or one residential site were used as inocula. In the desert inoculum, *Glomus eburneum* comprised approximately 50% of the spores present, and *Acaulospora morrowiae* comprised approximately 35%. Other species present in the desert inoculum, in order of prevalence, were *A. trappei*, *G. occultum*, and *G. intraradices*. In the residential inoculum, *G. spurcum* comprised approximately 40% of the spores present, and *A.*

trappei comprised approximately 40%. Other species present in the residential inoculum, in order of prevalence, were *G. occultum*, *G. intraradices*, and *Glomus* sp. AZ123. A volume of inoculum with approximately 2×10^5 spores [80 cm³ (0.08 qt) for the desert inoculum and 110 cm³ (0.12 qt) for the residential inoculum] was added subjacent to three germinated seedlings per pot for *Acacia* and *Parkinsonia*. One week after germination, *Acacia* and *Parkinsonia* seedlings were thinned to one per pot. *Fraxinus* seedlings were first germinated and grown in a sterile sand substrate to a uniform height of approximately 10 cm (4 in) before potting and inoculation. Inoculum was added subradically during potting into each of the 12-L (3 gal) containers. All non-AMF control trees received a 150-ml (0.16-qt) drench of mixed inoculum filtrate to establish similar soil microbiota as trees treated with AMF inoculum.

All trees were then grown for 5 months in an environmentally controlled glasshouse (55% light exclusion). The daily range of air temperature at canopy height and VPD was 18°C to 31°C (64°F to 88°F) and 1 to 3 MPa, respectively. At the start of the study, each tree was fertilized with 12 g (0.42 oz) of 20N-0P-16.6K-2Fe-1.4Mn (slow release, N source as isobutylidene diurea). Trees were not allowed to experience any moisture stress by watering each in excess of container capacity every 5 days using an automated drip-irrigation system for the duration of the study. Trees were arranged in a randomized complete block design with five replicates for each treatment, for a total of 15 experimental units per tree species.

Total shoot length and trunk caliper [5 cm (2 in.) above the substrate surface] was measured on 1 and 153 days after potting (DAP). On 150 DAP, midday leaf gas exchange and soil respiration were measured using a LI-6200 portable photosynthesis system (LI-COR, Lincoln, NE). Gas exchange measurements were made on 10-cm (4-in.) herbaceous shoot segments of *Parkinsonia* and the most recently expanded leaves of *Acacia* and

Fraxinus using a 0.25-L (0.23-qt.) chamber attached to the LI-6200 operating in closed system mode. For soil respiration measurements, polyvinyl chloride cylindrical collars [7-cm (2.8-in.) height, 10-cm (4-in.) inside diameter] were inserted into the potting soil to a depth of 2 cm (0.8 in.) more than 24 hr before measurements were made. A soil respiration chamber (LI-COR 6000-09) attached to the LI-6200 was fitted onto the collar such that the chamber air supply manifold was 1 to 2 cm (0.4 to 0.8 in.) above the potting soil surface. A foam gasket was placed between the collar and the chamber to prevent air leaks. Soil respiration per pot was derived from the average of two consecutive CO₂ flux measurements. Specific root respiration was calculated as soil respiration divided by root dry weight (RDW).

On 153 DAP, the study was terminated. Samples of root material from all plants were stained as described above and evaluated for AMF colonization. Shoots and roots were separated and dried in a drying oven at 60°C (140°F) for 72 hr and dry weights recorded. Pulverized leaf tissue samples were analyzed for P concentration by the ascorbic method (Wantabe and Olson 1965).

For both field and glass-house pot studies, all statistical comparisons were made by ANOVA using the SAS[®] GLM procedure (PC SAS, version 6.03, Cary, NC) and Statview[®]5 (SAS Institute, Cary, NC) software. The level of significance was set at $\alpha = 0.05$, and pairwise treatment comparisons were made using the Tukey-Kramer method. Percent AMF colonization data were arcsine transformed

to approximate a normal distribution for analysis of treatment effects. Actual percentage means are reported.

RESULTS

Field Study

Roots of native trees at the remnant Sonoran Desert sites were colonized by AMF to a greater extent than were landscape tree roots at the nearby residential sites because of greater root colonization with hyphae (Figure 1). Roots of residential trees were also colonized by septate, nonmycorrhizal fungi, which were not found on roots of desert trees.

Two species of *Acaulospora* and nine species of *Glomus* were detected in trap cultures from residential and desert sampling sites (Table 1). None of the AMF species occurred at all the sampling sites, but *A. trapei* was detected at all of the residential sites and two of the three desert sites. The

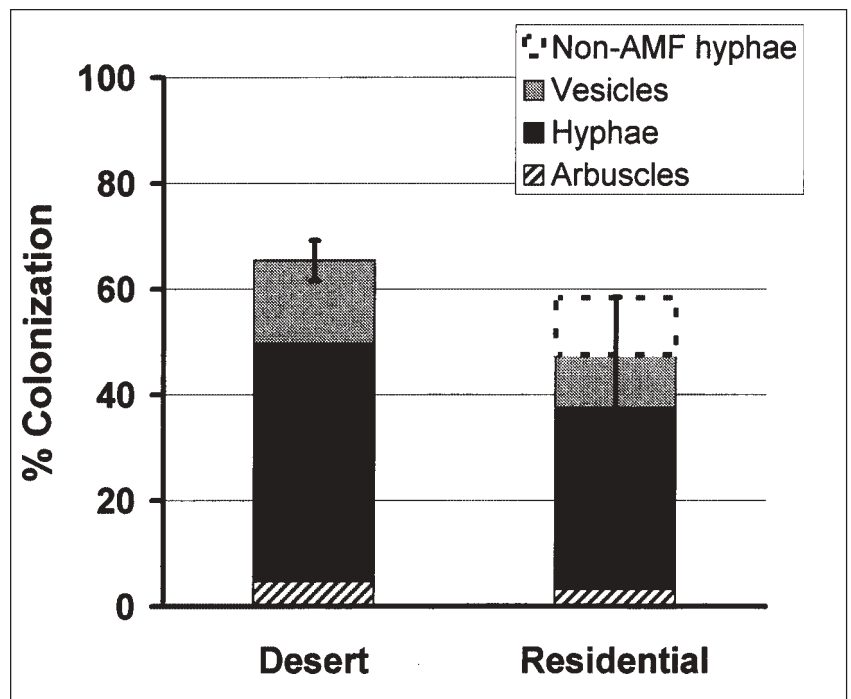


Figure 1. Levels of arbuscular mycorrhizal fungal (AMF) colonization of native trees at remnant Sonoran Desert and landscape trees at residential sites in the Phoenix metropolitan area. Error bars are 2 SE of total colonization by AMF, $n = 9$.

AMF species richness at each sampling site ranged from five to seven species at the residential sites and four to five species at the desert sites. Eight of the 11 detected AMF species occurred at both residential and desert sites. Two AMF species, *G. microaggregatum* and *Glomus* sp. AZ123, occurred only at residential sites, and one species, *A. morrowiae*, was only detected at one of the desert sites.

Glasshouse Pot Study

Roots of all trees inoculated with the non-AMF control drench remained nonmycorrhizal. Both remnant Sonoran Desert and residential AMF populations colonized roots of trees differently (Figure 2). Roots of *Acacia* and *Fraxinus* inoculated with either the desert or residential AMF population treatments were strongly mycorrhizal, while roots of *Parkinsonia* were not (Figure 2). Notably, four of five replicates of *Parkinsonia* inoculated

Table 1. Arbuscular mycorrhizal fungal (AMF) species detected in trap cultures from three suburban residential and three Sonoran Desert sites in the Phoenix metropolitan area.

AMF species	Residential	Desert
<i>A. morrowiae</i>		X
<i>A. trapei</i>	X	X
<i>G. eburneum</i>	X	X
<i>G. fasciculatum</i>		X
<i>G. intraradices</i>	X	X
<i>G. microaggregatum</i>	X	
<i>G. mosseae</i>	X	X
<i>G. occultum</i>	X	X
<i>G. spurcum</i>	X	
<i>Glomus</i> sp. AZ112	X	X
<i>Glomus</i> sp. AZ123	X	

with the residential AMF treatment remained uncolonized, and no arbuscules were seen on in the fifth. The residential AMF treatment elicited a 60% increase in P uptake by *Acacia* compared with the nonmycorrhizal control treatment (Table 2). Both desert and residential AMF treatments caused roughly a 100% increase in P uptake by *Fraxinus* compared with the nonmycorrhizal control treatment. Neither AMF from the residential or desert sites altered P uptake by *Parkinsonia*.

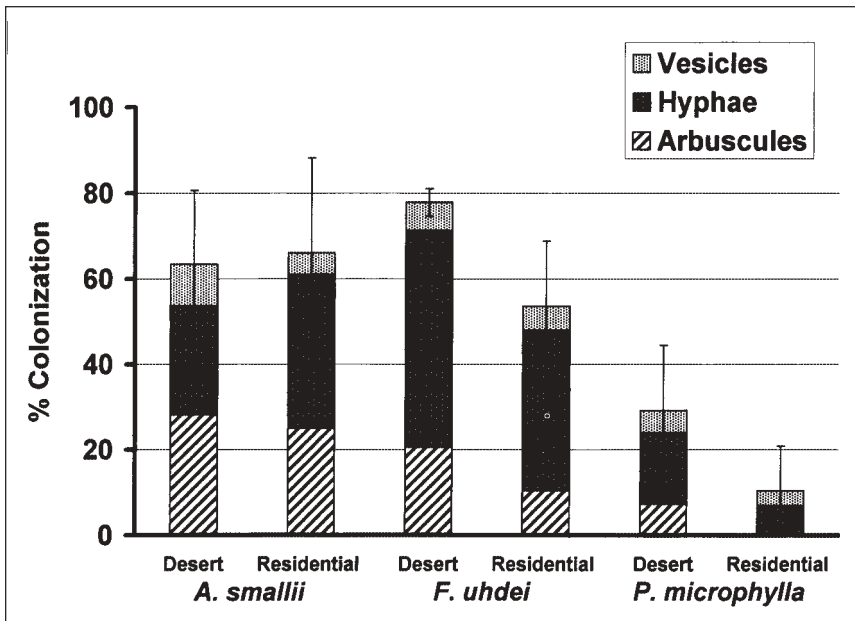


Figure 2. Percentage of root colonization of *Acacia smallii*, *Fraxinus uhdei*, and *Parkinsonia microphylla* in response to arbuscular mycorrhizal fungal (AMF) inoculum derived from under canopy rhizosphere of trees at remnant Sonoran Desert or nearby residential sites in the Phoenix metropolitan area. Error bars are 2 SE of total colonization by AMF, n = 5.

In general, AMF differentially affected growth of the three landscape trees (Table 2). For *Acacia*, AMF from the desert sites increased tree total shoot length (SL), trunk caliper (CL), total dry weight (TDW), shoot dry weight (SDW), root dry weight (RDW), and shoot to root ratio (SR) compared with

Table 2. Effect of arbuscular mycorrhizal fungal (AMF) inoculum derived from under canopy rhizosphere of trees at remnant Sonoran Desert or nearby residential sites in the Phoenix metropolitan area on total shoot length, trunk caliper, total dry weight (TDW), shoot dry weight (SDW), root dry weight (RDW), shoot to root ratio (SR), and leaf phosphorus concentration (P) of three Southwest landscape trees.

Tree/AMF inoculum	Shoot length (cm)	Trunk caliper (mm)	TDW (g)	SDW (g)	RDW (g)	SR	P (mg/g)
<i>Acacia smallii</i>							
Sonoran Desert	95.9 a ^z	55 a	23.2 a	12.5 a	10.7 a	1.2 b	25 ab
Residential	88.9 a	48 a	12.6 ab	8.0 ab	4.6 ab	1.7 a	32 a
Non-AMF control	35.8 b	22 b	2.3 b	1.0 b	1.4 b	0.7 b	22 b
<i>Fraxinus uhdei</i>							
Sonoran Desert	65.2 a	72 a	40.2 a	21.4 a	18.8 a	1.1 a	29 a
Residential	53.1 a	63 ab	29.9 ab	17.4 a	12.5 a	1.4 a	27 a
Non-AMF control	59.1 a	53 b	19.8 b	9.6 b	10.2 a	0.9 a	14 b
<i>Parkinsonia micophylla</i>							
Sonoran Desert	54.5 a	53 a	3.6 a	2.6 a	1.0 a	2.6 a	25 a
Residential	55.4 a	56 a	6.6 a	4.7 a	1.9 a	2.5 a	29 a
Non-AMF control	35.1 a	49 a	2.0 a	1.1 a	0.9 a	1.2 b	22 a

^zValues are treatment means, $n = 5$, except $n = 3$ for leaf P. Values followed by the same letter within a column by species are not significantly different, $\alpha < 0.05$ Tukey-Kramer mean separation.

those of non-AMF controls. AMF from the residential sites increased these same *Acacia* growth variables except for TDW, SDW, and RDW, which were similar to those of the non-AMF controls. Growth of *Fraxinus* appeared to be less affected by the AMF communities than was *Acacia*. In comparison with the non-AMF control trees, we found that CL, TDW, and SDW were increased for *Fraxinus* trees inoculated with AMF from desert sites, while only SDW was increased for *Fraxinus* trees inoculated with AMF from the residential sites. Growth of *Parkinsonia* was the least affected by AMF. Compared with non-AMF control trees, we found that only SR was increased, by about 2.1 times, for *Parkinsonia* trees inoculated with AMF from the desert sites.

Remnant Sonoran Desert and residential AMF populations increased carbon assimilation (A) by *Acacia* leaves by about 80% compared with the non-AMF control treatment (Table 3). In addition, both AMF populations decreased specific soil respiration (Rsp) of *Acacia* roots by about 70% compared with the control treatment.

The desert AMF population reduced Rsp of *Fraxinus* roots by about 40% compared with the residential AMF population or the non-AMF control treatment. Neither desert nor residential AMF populations affected A of *Fraxinus*, or A and Rsp of *Parkinsonia*.

DISCUSSION

Previous research has shown that soil disturbance substantially lowers AMF diversity (Giovannetti and Gianinazzi-Pearson 1994). The process of urbanization, and in particular the change from a relatively natural, undisturbed desert habitat into suburban communities of medium-density single-family homes with intensively managed landscapes typically begins with disturbance of the rhizosphere profile. Therefore, we may assume that the initial disturbances associated with the transition of our residential sites from their original undisturbed desert habitat into a residential land use had an adverse effect on the residing native AMF population structure (Roldan et al. 1997). Our data showed that about 10 years after

Table 3. Effect of arbuscular mycorrhizal fungal (AMF) inoculum derived from under canopy rhizosphere of trees at remnant Sonoran Desert or nearby residential sites in the Phoenix metropolitan area on carbon assimilation (A) and specific root respiration (Rsp) of three southwest U.S. landscape trees.

Tree/AMF inoculum	A ($\mu\text{mol}/\text{m}^2/\text{s}$)	Rsp ($\mu\text{mol}/\text{m}^2/\text{s}/\text{g}$)
<i>Acacia smallii</i>		
Sonoran Desert	16.2 a ^z	0.36 b
Residential	17.7 a	0.46 b
Non-AMF control	9.5 b	1.60 a
<i>Fraxinus uhdei</i>		
Sonoran Desert	6.8 a	0.07 b
Residential	6.9 a	0.11 ab
Non-AMF control	8.2 a	0.13 a
<i>Parkinsonia microphylla</i>		
Sonoran Desert	10.4 a	1.24 a
Residential	11.8 a	0.86 a
Non-AMF control	9.4 a	1.05 a

^zValues are treatment means, $n = 5$. Values followed by the same letter within a column by species are not significantly different, $\alpha < 0.05$ Tukey-Kramer mean separation.

disturbance and landscape installation, the association of AMF species found in soil at the residential sites was different from that of nearby remnant desert habitats and this difference was accompanied by less root colonization with hyphae.

Re-establishment of AMF populations at the residential sites after initial disturbance and landscape installation may be dependent on three factors: the mode of AMF dispersal, the time elapsed since disturbance (Jasper et al. 1991), and the biophysical environment at these intensively managed residential landscapes. At present, we know of no studies examining modes of AMF dispersal into urban areas, though we speculate that such modes might include wind dispersal, the local and regional transport of mycorrhizal nursery stock to landscape transplant sites, and/or movement of AMF spores and assemblages by humans. Also, cultural practices such as watering and fertilization, the root characteristics of the host plant and host-fungus compatibility, and edaphic conditions such as pH, nutrient levels,

moisture, salinity, and temperature can have a substantial effect on AMF population characteristics (Brundrett 1991).

Although AMF are generally thought to have little host specificity, there may be a certain degree of plant/endophyte compatibility, and some plants may even resist AMF colonization (Brundrett 1991). In the present study, we found that growth, carbon assimilation and root respiration properties, and P nutrition of three regionally common landscape trees in response to AMF population from residential or desert sites were different. AMF colonization elicited increased growth and P uptake for both *Acacia smallii* and *Fraxinus uhdei*, but the data suggest that the responses of the two trees to AMF colonization may have been via different mechanisms. Mycorrhizal effects on growth of *Acacia* and *Fraxinus* trees may have been the result of changes in photosynthate production and/or partitioning (Syvertsen and Graham 1990). Though Peng et al. (1993) reported that soil respiratory fluxes from AMF plants were 37% higher than from non-AMF plants, we found that AMF colonization actually resulted in a lowering of carbon respired from roots of *Acacia* and *Fraxinus* when normalized to root size.

For *Acacia*, shoot and root growth enhancement was accompanied by increased A and lower Rsp, which gives clear evidence of an increase in photosynthate production coincident with a lower carbon cost to benefit ratio (Rsp/A) of the AMF association. These effects were more pronounced for *Acacia* trees inoculated with AMF from the desert site than the residential site. Recently, Fidelibus et al. (2000) showed that AMF populations from undisturbed Sonoran Desert soils were a more effective promoter of citrus plant growth than AMF populations from desert cultivated soils because of a lower carbon cost to benefit ratio.

Unlike *Acacia*, AMF enhancement of *Fraxinus* tree size was due only to increases in shoot growth. Root dry weights of mycorrhizal and non-

mycorrhizal *Fraxinus* were similar. Like *Acacia*, these effects were more evident for *Fraxinus* trees inoculated with AMF from the desert sites than residential sites. Though enhancement of *Fraxinus* shoot growth by AMF was not accompanied by an increase in A, it was accompanied by a near 50% reduction in Rsp for trees inoculated with AMF from the desert site. These data suggest that the likely cause of AMF enhancement of *Fraxinus* shoot growth was a lower carbon cost to benefit ratio accompanied by an increase in P nutrition even in the absence of increased photosynthate production.

AMF had no statistically significant impact on growth and P uptake of *Parkinsonia microphylla*, most likely because of variation in growth characteristics of seedlings. Though AMF colonization of *Parkinsonia* roots under well-watered experimental conditions was poor, *Parkinsonia* roots at the unirrigated desert sites were highly colonized by AMF. These differences in colonization suggest that *Parkinsonia* might show some host specificity and resist colonization when soil moisture is readily available, as would be the normative case in irrigated Phoenix residential landscapes.

CONCLUSION

Our data suggest that urbanization can alter the composition of AMF populations and that modification of the soil environment, particularly the practice of landscape irrigation, might reduce AMF colonization of some tree roots. Our data also suggest that AMF can increase tree carbon storage potential in the Phoenix metropolitan area, although this capacity in managed residential landscapes might be somewhat less than in nearby undisturbed soils because of a higher carbon cost to benefit ratio. Ultimately, the ability of AMF to increase landscape tree growth is likely a function of tree species and factors such as water availability and enhanced P uptake.

LITERATURE CITED

- Abbott, L.K., and C. Gazey. 1994. An ecological view of the formation of VA mycorrhizas. *Plant Soil* 159:69–78.
- Berntson, G.M., P.M. Wayne, and F.A. Bazzaz. 1997. Below-ground architectural and mycorrhizal responses to elevated CO₂ in *Betula alleghaniensis* populations. *Function. Ecol.* 11:684–695.
- Brundrett, M. 1991. Mycorrhizas in natural ecosystems. *Adv. Ecol. Res.* 21:171–313.
- Copeman, R.H., C.A. Martin, and J.C. Stutz. 1996. Tomato growth in response to salinity and arbuscular mycorrhizal fungi from saline and nonsaline soils. *HortScience* 31:341–344.
- Daniels, B.A., and H. D. Skipper. 1982. Methods for the recovery and quantitative estimation of propagules from soil vesicular arbuscular mycorrhizal fungi, pp 29–35. In Schenk, N.C. (Ed.). *Methods and Principles of Mycorrhizal Research*. American Phytopathological Society, St. Paul, MN.
- Eissenstat, D.M., J.H. Graham, J.P. Syvertsen, and D.L. Drouillard. 1993. Carbon economy of sour orange in relation to mycorrhizal colonization and phosphorus status. *Ann. Bot.* 71:1–10.
- Fidelibus, M.W., C.A. Martin, G.C. Wright, and J.C. Stutz. 2000. Effect of arbuscular mycorrhizal (AM) fungal communities on growth of 'Volkamer' lemon in continually moist or periodically dry soil. *Sci. Hortic.* 84:127–140.
- Giovannetti, M., and S. Gianinazzi-Pearson, 1994. Biodiversity in arbuscular mycorrhizal fungi. *Mycol. Res.* 98:705–715.
- Jasper, D.A., L.K. Abbott, and A.D. Robson. 1991. The effect of soil disturbance on vesicular arbuscular mycorrhizae in soils from different vegetation types. *New Phytol.* 118:471–476.
- Kendrick, B., and S. Berch. 1985. Mycorrhizae: Applications in agriculture and forestry, pp 109–152. In Robinson, C.W., and J.A. Howell (Eds.). *Comprehensive Biotechnology and Bioengineering: The Principles, Applications, and Relations of Biotechnology and Industry, Agriculture, and Medicine*, Vol. 4. Paragon Press, London, England.
- Koske, R.E., and J.N. Gemma. 1989. A modified procedure for staining roots to detect VA mycorrhizas. *Mycol. Res.* 92:486–489.

- Martin, C.A., and J.C. Stutz. 1994. Growth of argentine mesquite inoculated with VAM fungi. *J. Arboric.* 20:134–138.
- McGonigle, T.P., M.H. Miller, D.C. Evans, G.L. Fairchild, and J.A. Swan. 1990. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytol.* 115:495–501.
- Menge, J.A., C.K. Labanauskas, E. Johnson, and K.G. Platt. 1978. Partial substitution of mycorrhizal fungi for phosphorus fertilization in greenhouse culture of citrus. *Soil Sci. Am. Proc.* 42:926–930.
- Nowak, D.J. 1993. Atmospheric carbon reduction by urban trees. *J. Environ. Manage.* 37:207–217.
- Peng, S., D. Eissenstat, J.H. Graham, K. Williams, and N.C. Hodge. 1993. Growth depression in mycorrhizal citrus at high phosphorus supply. *Plant Physiol.* 101:1063–1071.
- Roldan, A., C. Garcia, and J. Albaladejo. 1997. AM fungal abundance and activity in a chronosequence of abandoned fields in a semiarid Mediterranean site. *Arid Soil Res. Rehab.* 11:211–220.
- Rowntree, R. 1998. Urban forest ecology: conceptual points of departure. *J. Arboric.* 24:62–71.
- Sanchez-Diaz, M., and M. Honrubia. 1994. Water relations and alleviation of drought stress in mycorrhizal plants, pp 167–178. In Giannazzi, S., and H. Scheupp (Eds.). *Impact of arbuscular mycorrhizas on sustainable agriculture and natural ecosystems.* Birkhauser Verlag, Basel, Switzerland.
- Stabler, L.B., and C.A. Martin. 2000. Temporal and spatial patterns of air temperature and CO₂ concentration in metropolitan Phoenix. *Third Symp. Urban Environ.* 3:201–202.
- Stutz, J.C., and C.A. Martin. 1998. Arbuscular mycorrhizal fungal diversity associated with ash trees in urban landscapes in Arizona. *Phytopathology* 88:86.
- Stutz, J.C., and J.B. Morton. 1996. Successive pot cultures reveal high species richness of arbuscular endomycorrhizal fungi in arid ecosystems. *Can. J. Bot.* 74:1883–1889.
- Syvertsen, J.P., and J.H. Graham. 1990. Influence of vesicular arbuscular mycorrhizae and leaf age on net gas exchange of citrus leaves. *Plant Physiol.* 94:1424–1428.
- Wantabe, F.S., and S.R. Olson. 1965. Test of ascorbic method for determining phosphorus in water and sodium bicarbonate extracts from soil. *Soil Sci. Soc. Proc.* 29:677–678.

Acknowledgments. This research was funded in part by the International Society of Arboriculture Research Trust John Z. Duling Grant Program and by the National Science Foundation grant no. DEB-9714833

**Urban Horticultural Ecology Research Group
Department of Plant Biology
Arizona State University
Tempe, AZ , U.S. 85287-1601*

**Corresponding author: Chris A. Martin*

Résumé. Des études sur le terrain et en serre ont été menées afin de déterminer les effets de l'expansion urbaine sur les populations de mycorhizes arbusculaires ainsi que l'impact de ces dernières sur la croissance des arbres ornementaux. Des échantillons de sol et de segments de racines d'arbres, en provenance des derniers résidus de sites du désert de Sonoran et de ses environs (anciennement un désert et aujourd'hui des parterres paysagers avec système d'irrigation, dans la zone métropolitaine de Phoenix, Arizona), ont été recueillis et évalués en fonction de la colonisation des racines par ces mycorhizes. Ces mycorhizes colonisaient de façon plus abondante les arbres indigènes du désert que les arbres ornementaux en milieu résidentiel; la composition en mycorhizes était également différente dans les deux types de sites. Une expérience en serre employant une inoculation de mycorhizes arbusculaires provenant du désert ou encore de sites résidentiels a été menée afin d'évaluer les effets de ces mycorhizes sur la croissance et le flux de carbone sur trois espèces d'arbres ornementaux en contenant de polyéthylène de 12 litres, et ce par rapport à des arbres non mycorhizés. La croissance et la nutrition en phosphore de *Acacia smallii* et de *Fraxinus uhdei* ont été accrues par la colonisation en mycorhizes arbusculaires. L'assimilation en carbone a été accrue chez l'*Acacia* grâce à la colonisation des racines par ces mycorhizes. La respiration dans le sol des racines de l'*Acacia* et du *Fraxinus* était moindre en raison de la colonisation des racines par ces mycorhizes. La croissance et les flux de carbone du *Parkinsonia microphylla* n'était pas affecté par les mycorhizes arbusculaires. Nous en concluons que les mycorhizes arbusculaires peuvent accroître significativement le potentiel d'emmagasinage du carbone chez les arbres ornementaux, et ce dépendant de l'espèce d'arbre, des caractéristiques des populations de mycorhizes arbusculaires, de la disponibilité en eau dans le sol et l'amélioration des capacités de captage du phosphore.

Zusammenfassung. Um die Effekte der Ausdehnung von arbuskulären Mycorrhiza (AMF)-Populationen zu bestimmen und den Einfluß von AMF auf das Wachstum von Bäumen zu bestimmen, wurden Studien an getopften Pflanzen im Freiland und Gewächshaus durchgeführt. Es wurden an verschiedenen Wüstenstandorten und an ehemals wüsten- jetzt bewässerten Siedlungsbereichen in Phoenix, Arizona; Boden- und Wurzelsegmente gesammelt und nach ihrer Kolonisation mit AMF bewertet. Die natürliche Wüstenflora zeigte eine bessere Kolonisation durch AMF als die Bäume der besiedelten Räume und die AMF

Artenzusammensetzung variierte an diesen beiden Standorten. Ein Gewächshausexperiment, welches AMF Inokulate aus der Wüste oder der bewässerten Fläche nutzte, wurde genutzt, um die AMF-Effekte auf Wachstum und Kohlenstofffluß von drei Baumarten in 12-Liter Containern mit den Kontrollen ohne AMF zu vergleichen. Wachstum und P-Versorgung von *Acacia smallii* und *Fraxinus uhdei* wurden durch AMF verstärkt. Die Kohlenstoffatmung von *Acacia* wurde durch die AMF Kolonisation verbessert. Die Bodenatmung von *Acacia* und *Fraxinus* Wurzeln wurde durch die AMF Kolonisation vermindert. Wachstum und Kohlenstofffluß von *Parkinsonia microphylla* wurde nicht durch AMF beeinflusst. Wir schließen daraus, das AMF möglicherweise die Kohlenstoffeinlagerung in Abhängigkeit von der Baumart, AMF Populationscharakteristiken und verbesserter P-Einlagerung bei Zierbäumen verbessern könnte.

Resumen. Se llevaron a cabo estudios de campo y de invernadero para determinar los efectos de la expansión urbana sobre las poblaciones micorrícicas en los árboles (AMF) y el impacto de AMF sobre el crecimiento de los árboles en el paisaje. Se colectaron muestras de suelo y raíces y se evaluaron para conocer la colonización por AMF en árboles de sitios del Desierto de Sonora y áreas residenciales cercanas regadas por goteo en el área metropolitana de Phoenix, Arizona. Los árboles nativos del desierto tuvieron mayor colonización por AMF que aquellos de áreas residenciales, y la composición de especies de AMF fue diferente en las dos áreas. Se usó un experimento de invernadero con inóculos de AMF de áreas desérticas con el fin de evaluar los efectos de AMF sobre el crecimiento y los flujos de carbono de tres especies de árboles en contenedores de polietileno de 12 litros, con relación a controles sin AMF. El crecimiento y la nutrición de P de *Acacia smallii* y *Fraxinus uhdei* se incrementaron por la colonización con AMF. La asimilación de carbono de *Acacia* aumentó con la colonización de las raíces con AMF. La respiración del suelo para las raíces de los árboles de *Acacia* y *Fraxinus* disminuyó con la colonización con AMF. El crecimiento y los flujos de carbono de *Parkinsonia microphylla* no fueron afectados por AMF. Concluimos que AMF puede incrementar significativamente el almacenaje potencial de carbono en los árboles, y el mejoramiento en la disposición de P, dependiendo de la especie, las características de las poblaciones de AMF y la disponibilidad de agua en el suelo.