



7-30-2002

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Recommended Citation

Titus, Jonathan H.; Titus, Priscilla J.; Nowak, Robert S.; and Smith, Stanley D. (2002) "Arbuscular mycorrhizae of Mojave Desert plants," *Western North American Naturalist*. Vol. 62 : No. 3 , Article 8. Available at: <https://scholarsarchive.byu.edu/wnan/vol62/iss3/8>

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ARBUSCULAR MYCORRHIZAE OF MOJAVE DESERT PLANTS

Jonathan H. Titus^{1,2,3}, Priscilla J. Titus^{1,3}, Robert S. Nowak², and Stanley D. Smith³

ABSTRACT.—Roots of 15 Mojave Desert plant species were assessed for arbuscular mycorrhizal (AM) colonization in spring and autumn 1999. Another 19 species were assessed in autumn only. Perennial species were AM colonized, whereas annual species contained very low levels of AM hyphae or were nonmycorrhizal. The nonnative tree *Tamarix ramosissima* was also nonmycorrhizal. Levels of hyphae changed over the season in 2 species, arbuscle levels increased in 1 species, and vesicles decreased in 7 species. Mycorrhizal inoculum potential (MIP) was assessed in the soils associated with spring-collected plants. All soils were found to contain MIP. MIP values were not correlated with AM root colonization.

Key words: arbuscular mycorrhizae, Mojave Desert, seasonality, burrows, Nevada Test Site, River Mountains, mycorrhizal inoculum potential.

Arbuscular mycorrhizae (AM) are important components of virtually all terrestrial ecosystems. Over 90% of all higher plants are estimated to be mycorrhizal, and >80% of these form AM relationships (Brundrett 1991). Plant growth is often enhanced by this association, mainly due to an increased ability to take up nutrients, principally phosphorus (Mullen and Schmidt 1993, Smith and Read 1997) and nitrogen (Tobar et al. 1994). This mutualism also enhances plant host drought resistance (Davies et al. 1992), competitive ability (West 1997a, Titus and del Moral 1998), and resistance to fungal pathogens (West 1997b) and insect herbivores (Gange and Bower 1997).

Many studies have found that seasonal factors, which are directly related to the stage of development or physiological state of the host plant, play a major role in AM colonization levels (e.g., Sanders and Fitter 1992a, Mullen and Schmidt 1993, Sanders 1993, Titus and Lepš 2000). For example, AM root colonization is often lowest in early summer because rapid root growth outstrips the spread of AM colonization (Douds and Chaney 1982, Warner and Mosse 1982, Dickman et al. 1984, Ebberts et al. 1987). In addition, temporal factors play a major role in host benefit from AM colonization. For example, AM may benefit plants only during the brief periods when phosphorus

demand is high during fruit production (Fitter 1989, Sanders and Fitter 1992b).

Arbuscular mycorrhizal mutualism is considered to be critical to the survival of most plants in arid environments. Perennial plants in undisturbed arid environments have generally been found to be mycorrhizal (e.g., Trappe 1981, Bloss 1985, Siguenza et al. 1996, Carrillo-Garcia et al. 1999, Stutz et al. 1999). However, the mycorrhizal status of most desert species and the shift in level of colonization over the seasons remain little known. It has been found that mycorrhizal colonization in a semiarid system is higher toward the end of summer than in midwinter (Requena et al. 1996).

This study was conducted to characterize AM colonization of common Mojave Desert plants. First, plants were collected over 2 seasons at the Mojave Global Change Facility (MGCF) located on the Nevada Test Site (NTS). The MGCF is a large-scale experiment being developed to test desert ecosystem responses to 3 global change scenarios: increased summer precipitation, increased nitrogen deposition, and biological soil crust removal. We collected plant roots and soil samples in spring and autumn to examine seasonal changes in AM colonization levels. Second, we examined AM colonization levels of common plants of the River Mountains located southeast of Las Vegas.

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METHODS

The MGCF site is located in the northern Mojave Desert in Nye County, Nevada, USA (36°49'N, 115°55'W), 90 km northwest of Las Vegas at an elevation of 960–975 m. The NTS, a U.S. Department of Energy facility, experiences minimal disturbance. Unlike much of the Mojave Desert, the NTS has not been grazed by cattle or utilized by off-road vehicles for at least 50 years. The area has a largely intact biological soil crust that covers ~20% of the soil surface (J. Titus unpublished data). The River Mountains site is located 15 km southeast of Las Vegas (36°03'N, 114°55'W) at an elevation of 700–800 m. Due to the rugged rocky substrate, much of the area is largely undisturbed even though biological soil crusts are not common.

Vegetation at both sites is a *Larrea tridentata*–*Ambrosia dumosa* plant community (Ostler et al. 1999, taxonomy based on Hickman 1993). Common shrubs include the evergreen *Larrea tridentata*; the deciduous *Ambrosia dumosa*, *Lycium pallidum*, *L. andersonii*, *Krascheninikovia lanata*, *Acamptopappus shockleyi*; and the evergreen gymnosperm *Ephedra nevadensis*. A common subshrub is *Polygala subspinosa*. Common perennial forbs include *Sphaeralcea ambigua* and *Baileya multiradiata*. Abundant native grasses are *Pleuraphis rigida* (C₄), *Achnatherum hymenoides* (C₃), and the short-lived *Erionueron pulchellum* (C₄). The non-native annual grass *Bromus madritensis* ssp. *rubens* is common in shrub understories. Vegetation at the NTS is further described in Beatley (1967, 1976) and Jordan et al. (1999).

The Mojave Desert experiences sporadic, low annual precipitation, with annual rainfall of <200 mm. Winter rains are widespread and may last several days. Summer storms generally occur in July and August and are usually local, intense, and unpredictable. Relative humidity is low (<20% is common), resulting in very high potential evaporation. Moisture is the primary limitation to plant growth in the Mojave Desert (Turner and Randall 1989, Smith et al. 1997). Temperatures are extreme, with a mean minimum winter temperature of –10°C and maximum summer temperature >47°C. A large diurnal temperature fluctuation occurs throughout the year (Bowers 1987). Soils are aridisols and are characterized by spatial heterogeneity in nutrients, infiltration,

and texture (Romney et al. 1973, 1980). Nitrate, ammonium, and phosphorus levels vary from 50, 4, and 20 ppm, respectively, in areas beneath larger shrubs to 3, 1, and 9 ppm in areas between shrubs (J. Titus unpublished data). Soils are basic with a mean pH of 8.2. Mounds and burrows created by the activities of small mammals, particularly kangaroo rats (*Dipodomys* spp.) and desert tortoises (*Gopherus agassizii*), are common and frequently located at the base of shrubs.

Plant Collection

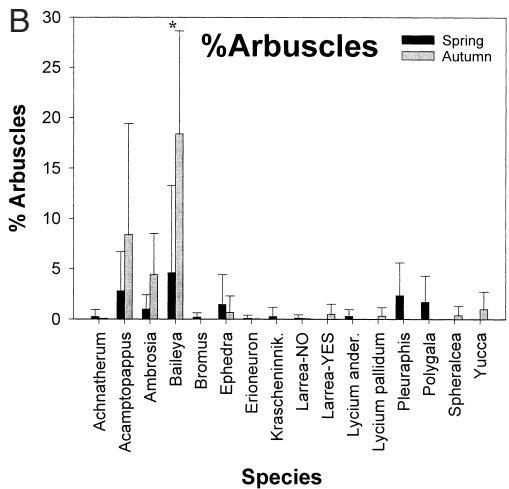
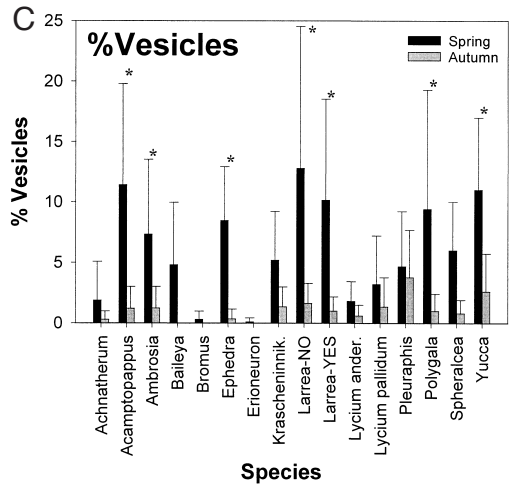
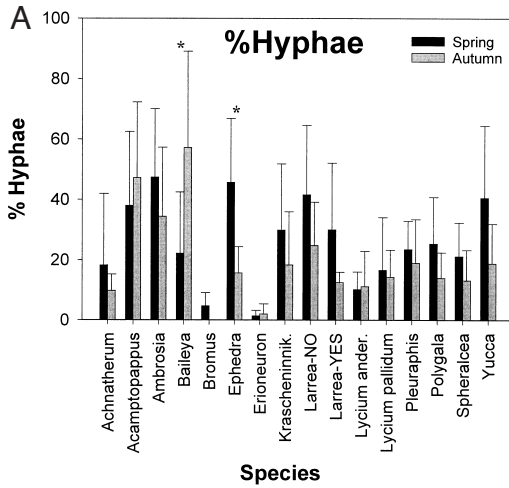
We collected roots from common LDER species in spring (May–June) and autumn (September–November) 1999 for assessment of AM colonization ($n = 10$ for each species in each sampling period). Spring is usually the period of growth and reproduction for most species collected in this study, but 1999 was a dry spring with an annual precipitation of 94 mm (S. Zitzer unpublished data). Thus, plant activity was strongly reduced. Autumn, generally a dry season in the Mojave, was dry in 1999. Roots were collected from *Larrea tridentata* plants both with and without small mammal burrows. Roots of plants common in the River Mountains were collected in autumn 1999 ($n = 5$) and stored in a freezer.

Staining

Roots were separated, washed, cleared, and stained with trypan blue (Brundrett et al. 1994). Using a dissecting microscope, we estimated percent AM colonization of fine roots (<1 mm in diameter). A grid of 1-cm squares was placed below a petri plate that contained the root sample. One hundred locations in which a root crossed a line on the grid were scored for hyphae, arbuscles, and vesicles. We examined many samples under higher power to ascertain that the structures were indeed AM. The number of mycorrhizal “hits” is used as an estimate of percent root colonized by the 3 AM structures (Brundrett et al. 1994).

Mycorrhizal Inoculum Potential

Mycorrhizal inoculum potential (MIP) is an index of the quantity of inoculum in the soil as measured by the percent AM fungal colonization of corn roots (Moorman and Reeves 1979, Titus et al. 1998). MIP was assessed only for the species collected at the NTS. Ten soil



Figs. 1A–C. Mean percent arbuscular mycorrhizal hyphae, vesicles, and arbuscules in spring and fall in 15 species at the Nevada Test Site in the Mojave Desert ($n = 8, 9, \text{ or } 10$). Vertical bars represent 1 standard deviation. NO and YES refer to *Larrea tridentata* without burrows and with burrows, respectively. A column marked with * is significantly different across seasons by Scheffé’s test. See Table 1 for ANOVA F and P values. See Table 2 for differences between species by Tukey’s post-hoc test at $P \leq 0.05$.

samples per species were collected in the spring at the same time that plants were harvested. For each soil sample, 600 g of soil was amended with 20% sterile perlite to increase porosity, split in half, and each half placed into 10 × 10-cm freely draining plastic pots. Bioassays were conducted with nonfungicide-treated *Zea mays* seeds. All pots were watered daily with tap water. Fertilizer was applied in 50-mL aliquots per pot of 10% Hoagland’s solution minus phosphorus at planting and at weekly intervals throughout the experiment. The control consisted of 10 pots of sterile soil placed randomly among the treatment pots and planted with corn to determine if contamination by glasshouse AM propagules occurred. Previous work showed that AM propagules, if present, rapidly colonize corn in the glasshouse (Titus et al. 1998). Pots were random-

ized and maintained for 42 days at the University of Nevada–Las Vegas glasshouse facility at 23°–28°C, and rotated every 15 days. Plants were harvested and roots washed and frozen at –5°C until October 1999, at which time roots were assayed for AM colonization as above. For each sample, we averaged the percent colonization of the 2 corn plants to achieve MIP.

Data Analysis

AM colonization levels for species collected in spring and autumn at the NTS were arcsine transformed and compared by 2-way ANOVA at $\alpha = 0.05$. Due to poor sample quality, the sample size for a few of the species was $n = 8$ or $n = 9$. Post-hoc tests were conducted by Tukey’s honestly significant difference test. Spring versus autumn AM colonization levels for each species were compared by Scheffé’s test at $\alpha = 0.05$ (Zar 1984). Scheffé’s test was used instead of 48 t tests to avoid type II error. Species collected at the River Mountains were not compared statistically due to small sample size. The nonparametric Spearman’s rank correlation test (Zar 1984) was conducted between MIP and percent hyphae to

TABLE 1. Two-way ANOVA F and P values for arbuscular mycorrhizae structures from 14 species at the Nevada Test Site in the Mojave Desert in spring and autumn 1999 ($n = 8, 9, \text{ or } 10, P \leq 0.05$ for significance, data arc-sine transformed). See Figures 1A–C for results and Table 2 for results of Tukey's post-hoc tests for species.

AM structure	Variable	F	P
Hyphae (%)	Species	6.840	0.000
	Season	7.474	0.007
	Interaction	2.606	0.002
Arbuscles (%)	Species	12.223	0.000
	Season	7.513	0.007
	Interaction	5.047	0.000
Vesicles (%)	Species	2.720	0.001
	Season	60.631	0.000
	Interaction	2.059	0.015

assess whether these 2 AM components were correlated.

RESULTS

NTS species differed in their levels of AM colonization in all 3 AM structures in both spring and autumn (Figs. 1A–C, Tables 1, 2). Roots of shrubs and perennial herbs generally contained more hyphae and vesicles than the short-lived herbaceous species such as *Bromus* and *Erioneuron* (Figs. 1A, 1C). A similar pattern occurred with the River Mountain species (Table 3), with the annuals having little or no AM colonization. Only a single perennial, the invasive riparian species *Tamarix*, was nonmycorrhizal. Due to the very dry spring and summer, few native annual species were available. *Larrea* without mammal burrows had higher values for AM structures, except for fall arbuscles, than did *Larrea* with mammal burrows; however, differences were not significant. Although *Grayia spinosa* was collected at the NTS, it is included in Table 3 because it was collected only in autumn ($n = 5$). The nonnative annual grass *Bromus madri-tensis* ssp. *rubens* was not present in autumn.

For all species combined hyphae and vesicles decreased from spring to fall and arbuscles increased (Table 1). Only 2 species showed a significant seasonal change in hyphae, and 1 species in arbuscles, but a decrease in vesicles occurred in 7 of the species (Figs. 1A–C). *Baileya* and *Ephedra* showed a seasonal shift in 2 AM structures: increased hyphae and arbuscles for *Baileya* and decreased hyphae and vesicles for *Ephedra*.

Mycorrhizal inoculum potential was significantly different across species ($F = 8.063, P =$

0.000), but post-hoc tests found the only significant difference was with the high MIP of *Yucca schidigera* soil (Fig. 2). Large standard deviations prevented other differences from occurring. MIP and percent hyphae were not correlated by Spearman's rank correlation ($P = 0.076$). Control corn plants were nonmycorrhizal.

DISCUSSION

All native perennial species of the Nevada Test Site and River Mountains were found to be mycorrhizal. Short-lived species, particularly nonnative weeds, contained few hyphae, as has been found elsewhere (e.g., Berch et al. 1988, Boerner 1992a, Peat and Fitter 1993, Titus et al. 1998). However, a range of native annuals could not be tested because drought conditions did not allow germination and establishment. An invasive, nonnative tree (*Tamarix*) was found to be nonmycorrhizal. *Tamarix* is an aggressive invader of southwestern U.S. riparian zones (Smith et al. 1998), and nonmycorrhizal status is common in both invasive (Pendleton and Smith 1983, Boerner 1992b, Titus et al. 1998) and wetland species (Peat and Fitter 1993).

Studies of AM colonization for the species tested here are infrequent in the literature. Bethlenfalvay and Dakessian (1984) found that AM colonization levels in *Achnatherum hymenoides* from Reno, Nevada, were 86% in ungrazed plots and 40% in grazed plots, both values much higher than in this study. Cui and Nobel (1992) assessed *Ferocactus cylindraceus* (*F. acanthodes* in their study) and found it to have AM colonization levels very similar to this study (Table 3). The nonnative annual *Salsola kali* has been reported to be nonmycorrhizal (Khan 1974, Miller 1979, Reeves et al. 1979). Although AM colonization of *Salsola* occurred in our study, levels were very low and consisted of hyphae only. It is probable that plant-mycorrhizae mutualism is not functional in this species (Allen et al. 1989).

The presence of an animal burrow near a shrub may have a significant influence on soil nutrients and a wide array of other soil parameters (reviewed in Whitford and Kay 1999). Although animal burrows did not influence AM colonization or MIP values in our study, during more mesic years burrows may cause differences to emerge because of greater

TABLE 2. Growth form characteristics of 14 species collected in the Mojave Desert at the Nevada Test Site in spring and autumn 1999. "Burrows" refer to small mammal burrows at the base of shrubs. Within each column, species with different letters are significantly different in percent AM hyphae, arbuscles, and vesicles by Tukey's post-hoc test results at $P < 0.05$ ($n = 8, 9,$ or 10). See Figures 1A–C for results and Table 1 for 2-way ANOVA F and P values. *Bromus madritensis* is not included here because the species was not present in autumn.

Species	Growth form	Hyphae	Arbuscles	Vesicles
		----- % -----		
<i>Achnatherum hymenoides</i>	perennial C ₃ grass	abc	a	ab
<i>Acanthopappus shockleyi</i>	deciduous shrub	d	b	c
<i>Ambrosia dumosa</i>	drought deciduous shrub	d	ab	abc
<i>Baileya multiradiata</i>	short-lived perennial herb	cd	c	abc
<i>Ephedra nevadensis</i>	evergreen gymnosperm shrub	cd	ab	abc
<i>Erioneuron pulchellum</i>	short-lived perennial C ₄ grass	a	a	a
<i>Krascheninnikovia lanata</i>	deciduous shrub	bcd	a	abc
<i>Larrea tridentata</i> (no burrows)	evergreen shrub	cd	a	c
<i>Larrea tridentata</i> (with burrows)	evergreen shrub	abcd	a	bc
<i>Lycium andersonii</i>	drought deciduous shrub	ab	a	ab
<i>Lycium pallidum</i>	drought deciduous shrub	abc	a	abc
<i>Pleuraphis rigida</i>	perennial C ₄ grass	abcd	ab	abc
<i>Polygala subspinosa</i>	deciduous subshrub	abcd	ab	bc
<i>Sphaeracephala ambigua</i>	perennial herb	abc	a	abc
<i>Yucca schidigera</i>	treelike rosette	bcd	a	bc

TABLE 3. Percent arbuscular mycorrhizal colonization and growth form of plants collected in autumn 1999 in the River Mountains, 15 km southeast of Las Vegas, Nevada, in the Mojave Desert at an elevation of 700–800 m (mean \pm standard deviation, $n = 5$).

Species	Growth form	Hyphae	Arbuscles	Vesicles
<i>Acacia greggi</i>	drought deciduous tree	24 \pm 16	0.02 \pm 0.04	2.4 \pm 2.6
<i>Amaranthus fimbriatus</i>	perennial herb	1.6 \pm 3.6	0	0
<i>Opuntia basilaris</i>	cactus	13 \pm 9	0.7 \pm 1	0.3 \pm 0.8
<i>Boerhavia intermedia</i> var. <i>erecta</i>	perennial herb	1.2 \pm 2.6	0	0
<i>Chamaesyce setiloba</i>	prostrate annual	4.0 \pm 5.6	0	0
<i>Hymenoclea salsola</i>	subshrub or shrub	30 \pm 24	0.8 \pm 1.8	0.8 \pm 1.8
<i>Opuntia acanthocarpa</i>	cactus	18 \pm 6	0	2.0 \pm 2.4
<i>Dalea mollis</i>	mat-forming annual	0	0	0
<i>Eriogonum deflexum</i>	erect annual	0	0	0
<i>Eriogonum inflatum</i>	perennial herb	7.0 \pm 10	1.0 \pm 2.4	0.03 \pm 0.05
<i>Grayia spinosa</i> ¹	deciduous shrub	24 \pm 23	0	3.0 \pm 1.4
<i>Mammillaria tetrancistra</i>	cactus	13 \pm 7	0	0
<i>Pectis papposa</i>	erect annual	14 \pm 8	0.4 \pm 0.9	0.8 \pm 1.1
<i>Opuntia ramosissima</i>	cholla cactus	10 \pm 10	2.0 \pm 4.5	2.4 \pm 3.3
<i>Physalis crassifolia</i>	subshrub	7.2 \pm 2.6	0.4 \pm 0.9	1.2 \pm 1.8
<i>Ferocactus cylindraceous</i>	cactus	6.0 \pm 5.1	0	0
<i>Salsola kali</i>	nonnative annual	1.2 \pm 2.7	0	0
<i>Sphaeracephala ambigua</i>	perennial herb	10 \pm 8	0.5 \pm 1.0	0.5 \pm 1.0
<i>Tamarix ramosissima</i>	non-native tree	0	0	0
<i>Tridens muticus</i>	tufted perennial grass	1.6 \pm 3.6	0	0.4 \pm 0.9

¹Collected at the Nevada Test Site in autumn 1999, $n = 5$.

resource demand by vegetation and greater resource availability in burrow soil.

The decrease in hyphae and vesicles over the seasons is not surprising because plant phosphorus demand and soil moisture levels change over the season, and rates of root growth and turnover vary. For example, Cui and Nobel (1992) found AM colonization to increase in 3 Mojave Desert species from

March to May, perhaps representing fungal colonization of the season's new roots. Arbuscles are sites for the exchange of materials between the plant and fungus and are the best indicators of the quantity of material flow and therefore the intensity of the mutualism. Significant overall increase in arbuscles may be attributable to the marked increase that occurred in just 3 of the species (a significant

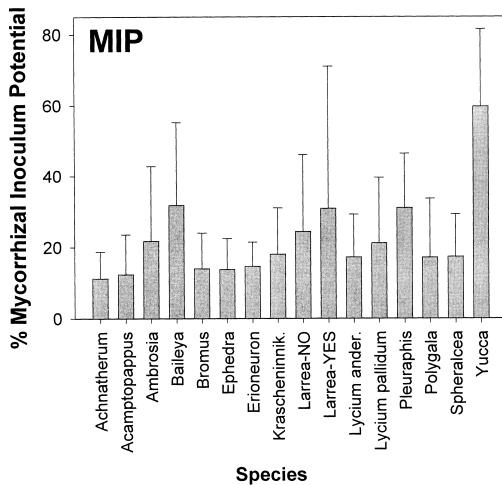


Fig. 2. Mean percent mycorrhizal inoculum potential (MIP) for soil collected from the base of 15 species at the Nevada Test Site in the Mojave Desert ($n = 10$). Vertical bars represent 1 standard deviation. NO and YES refer to *Larrea tridentata* without burrows and with burrows, respectively. Based on Tukey's post-hoc test at $P \leq 0.05$, *Yucca* MIP is significantly greater than that of all the other species; the other MIP values do not differ from each other. See Table 1 for ANOVA F and P values.

increase in *Baileya*). The fact that most of the species showed small increases or decreases in arbuscular levels suggests that for these species the intensity of the mutualism changed little from spring to autumn. This may be due to the fact that 1999 was a drought year and the rate of exchange of materials varied little from spring to autumn. *Baileya* was actively flowering at both collection times, and a heavy phosphorus demand might account for the increase in both arbuscles and hyphae. Because of reduced activity by most plant species in the fall, the other increases in arbuscles that occurred were unexpected. Vesicles indicate carbon storage, and their reduction may indicate a reduced reliance by the plant on the fungus, and hence a reduction in carbon translocation to the fungus. This would be an expected occurrence in autumn, even in a drought year.

Because most perennial arid zone plants in undisturbed environments are mycorrhizal, positive MIP values at the NTS would be expected. Although few studies have been done on arid zone MIPs, they appear to vary seasonally, spatially, and in relation to environmental variables (Al-Agely and Reeves 1995,

Requena et al. 1996), as in more mesic environments (Johnson, Zak et al. 1991, Brundrett et al. 1996). Similar MIP values were found in a related study at the NTS for several of the species (*Ambrosia*, *Pleuraphis*, *Lycium pallidum*, and *Larrea*; Titus et al. in preparation).

AM root colonization and MIP from adjacent soil were not correlated. Many studies have found AM parameters not to be correlated (e.g., Ebberts et al. 1987, Scheltma et al. 1987, Johnson, Pflieger et al. 1991). This may reflect patchiness in the distribution of AM propagules around a plant (Smith and Read 1997); and host species, surrounding vegetation, soil, and climatic and temporal factors are likely to influence AM root colonization levels (Johnson et al. 1992, Sanders and Fitter 1992c, Blaszkowski 1994, Titus and del Moral 1998). Thus, because of the large number of variables that influence AM parameters, a lack of correlation is not surprising.

This study increases our understanding of AM colonization levels of some Mojave Desert plants and illustrates that hyphal and vesicle levels decrease in these species from spring to autumn in a drought year, while arbuscles increase in a few species. This study also demonstrates that MIP levels present in soil adjacent to these species are similar, except for soil surrounding *Yucca*, which has higher MIP levels. Mycorrhizae are critical to the procurement of essential nutrients for desert plants for at least part of their life cycle. Because of this, mycorrhizae play a vital role in competitive outcomes and successional pathways in harsh arid environments where plant community development is very slow.

ACKNOWLEDGMENTS

Thanks to C. Grant for collecting specimens in the field, D. Bryla for mycorrhizal advice, E. Willard for statistical advice, C. Wells for help in the lab, and E. Knight, S. Zitzer, and T. Charlet for logistical support. F. Landau graciously provided support at all levels of this project. D. Housman greatly improved the manuscript. We also thank R. Furlow, the NTS National Environmental Research Park, and employees of Bechtel Nevada for their support. This research was supported in part by NSF (EPS-9871942), with additional support to RSN from the Nevada Agricultural Experiment Station.

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Received 30 January 2001

Accepted 19 June 2001