

Mycorrhizae in a southern California desert: ecological implications

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Perennial plants of 19 families were surveyed for colonization by vesicular–arbuscular mycorrhizal (VAM) fungi at four sites in the Anza–Borrego Desert State Park, California, an area characterized as arid to extremely arid. Soils at all sites were very low in phosphorus and nitrogen and had a coarse sandy texture. The sites were distinct in the floristic composition of their vegetation. All plants (38 species) were colonized by VAM fungi (six species). The distribution of the VAM mycoflora was not random. Site preference by VAM-fungal species was ascribed to an interaction of factors pertaining to the host plants and to edaphic and climatic conditions.

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Les auteurs relevèrent la colonisation de plantes vivaces, appartenant à 19 familles, par des champignons à micorrhize vésiculaire–arbusculaire (VAM), et ce dans quatre sites au State Park du désert d'Anza-Borrego, Californie, région caractérisée par un climat aride à extrêmement aride. Les sols de chaque site avaient une teneur très basse de phosphore et d'azote et leur texture était sableuse et très grossière. La composition floristique différait d'un site à l'autre. Toutes les plantes (38 espèces) étaient colonisées par les champignons à VAM (six espèces). La distribution de la mycoflore à VAM ne se faisait pas au hasard. Le choix des sites par les espèces s'effectuait d'après l'interaction de facteurs reliés aux plantes hôtes et aux conditions édaphiques et climatiques.

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Introduction

The primary stresses imposed on vegetation by arid environments are the lack of water and mineral nutrients (Fisher and Turner 1978). The availability of relatively immobile mineral nutrients, such as P, is lowered when soil water potentials decrease (Olsen *et al.* 1961). This has been shown to result in P-deficient plants as a result of drought stress, even when the P supply is adequate for greater growth (Nelsen and Safir 1982). The hyphae of vesicular–arbuscular mycorrhizal (VAM) fungi serve as extensions of the root systems and are both physiologically and geometrically more effective organs of absorption than the roots themselves (Trappe 1981). Thus, VAM-fungal associations appear to be necessary for growth and survival of plants in deserts (Miller 1979; Reeves *et al.* 1979). This role is apparently not restricted to P nutrition but affects water utilization as well (Safir and Nelsen 1981).

The potential of VAM fungi to desensitize their host plants to temporary water shortage and to improve water utilization when water supply is inadequate (Sieverding 1981) is of prime importance to agricultural practice under arid and semiarid conditions. As VAM fungi have been shown to adapt to edaphic factors (Lambert *et al.* 1980), drought-resistant species or genotypes may also exist. The purpose of this study was to collect VAM fungi from desert communities of diverse floristic and edaphic compositions for subsequent identification and characterization, and to report on the identity and habitat of host plants and their VAM-fungal endophytes.

Materials and methods

Study area

Perennial plants were surveyed for colonization by VAM fungi at four sites in the Anza–Borrego Desert State Park, San Diego County, California. Site selection was based on the floristic composition of the vegetation, the elevation, and the general soil characteristics. Sites were designated after the dominant plant genus. The *Acacia* and *Opuntia* sites were adjacent and located near Mountain Palm Springs, occupying a sandy outwash plain and a playa at elevations of 210 and

215 m, respectively. The *Agave–Yucca* site was at Box Canyon on a sandy slope at an elevation of 820 m. The *Chilopsis* site was an outwash at Yaqui Flat at an elevation of 450 m.

The area can be characterized as arid to extremely arid (Noy-Meir 1973). Rainfall varies with altitude and averages 130 mm annually at Borrego Springs, California (elevation 200 m). Some locations may receive only a trace of precipitation two instances of rain were reported in the Mountain Palm Springs area in the 2 years preceding this survey (September 1981). During the year of this study (1981), air temperatures varied between the annual extremes of 48 and 3°C (high:low) and averaged 43 and 25°C (high:low) in the summer.

Vegetation assessment

All perennial plants were counted in four quadrats (each 50 × 50 m) selected at random at each site. The density of plants of a species at each site was based on the total area of the four quadrats (1 ha). To avoid overemphasis of large density values owing to many small plants in describing vegetational patterns, an additional parameter, "biovolume" (BV), was computed as a measure of plant size. This value was based on the generally spherical configuration of the crowns of most plants encountered, and was calculated from the estimated average radius of a sphere encompassing the foliage. Volumes so calculated for individual plants of average size were multiplied by the density value to determine BV per hectare. Photosynthetic activity was estimated by inspection. Plants whose aboveground parts were entirely dry were adjudged inactive while green plants were called active. Plants with leaves partially abscised or discolored were classified as having limited photosynthetic activity.

VAM mycoflora

A representative specimen from each perennial plant species, spatially well-separated from adjacent plants, was selected at each of the four sites. Roots of each plant were carefully freed of the surrounding soil to reach the depth where fine secondary or tertiary roots were present free of the root systems of adjacent plants. Root fragments and soil were collected from a depth of 0.3 to 0.6 m. The extent of colonization of the root specimens by VAM fungi was determined according to Bethlenfalvay and Yoder (1981) and was classified as light, medium, or heavy, indicating the presence of VAM fungi in 1/4, 1/2, or >1/2 of the roots by length.

Sudan grass (*Sorghum bicolor* L.) was grown in pot cultures in a

TABLE 1. Flora of a sandy outwash plain (*Acacia* site) near Mountain Palm Springs, Anza-Borrego Desert State Park, California

Flora	D ^a	BV ^b	EPA ^c	FC ^d	VAM fungus (<i>Glomus</i>)
Chenopodiaceae					
<i>Atriplex polycarpa</i>	32	16.8	3	3	Sp. A
Compositae					
<i>Hymenoclea salsola</i>	42	11.3	2	2	Sp. A
Labiatae					
<i>Hyptis emoryi</i>	6	25.1	2	2	Sp. A
Leguminosae					
<i>Acacia greggii</i>	84	180.2	2	3	Sp. A
<i>Prosopis juliflora</i>	4	16.8	2	2	Sp. A
<i>Psoralea spinosa</i>	20	28.7	1	1	Sp. A

^aDensity (plants per hectare).

^bBiovolume (cubic metres).

^cEstimated photosynthetic activity (1, inactive; 2, limited; 3, active).

^dFungal colonization (1, light; 2, medium; 3, heavy).

sterile sand-perlite medium mixed with soil and root fragments from each desert plant as VAM-fungal inoculum. Plants were grown for 5 months. Spores were collected by wet sieving, mounted in water, and classified according to Trappe (1982).

Soil characteristics

At each of the four sites, four soil samples were collected from under plants, air dried, and separated into two fractions using a sieve of 2-mm opening. The geometric mean diameter of the soil agglomerates was calculated from the fraction smaller than 2 mm according to Kemper and Chepil (1965). The moisture content of unseparated soil at -1.5 MPa was measured gravimetrically according to Richards (1965) using a 15-bar (1 bar = 100 kPa) ceramic plate extractor¹ (Soil Moisture Equipment Co., Santa Barbara, CA). Available (NaHCO₃-extractable) P was determined according to Murphy and Riley (1962) as modified by Watanabe and Olsen (1965), total P according to Shelton and Harper (1941), and total N according to Bremner (1965). The pH in water and the electrical conductivity of a 1:5 soil-water suspension were determined according to Peach (1965) and Bower and Wilcox (1965), respectively.

Results

The vegetation at the four sites was distinct in its species composition, except for some marginal overlap (Tables 1-4). All species were mycorrhizal, including *Atriplex polycarpa* (Table 1), and *Eriogonum fasciculatum* and *Eriogonum nodosum* (Table 3), members of families not usually mycorrhizal (Malloch *et al.* 1980). In most cases, the level of photosynthetic activity corresponded to the degree of VAM-fungal colonization. The roots of cacti or of plants with green leaves were heavily colonized by VAM fungi (Tables 1-4).

All VAM fungi were of the genus *Glomus* of the Endogonaceae (Gerdemann and Trappe 1974): *G. fasciculatum* (Thaxter *sensu* Gerd.) Gerd. & Trappe (Gerdemann and Trappe 1974), *G. epigaeum* Daniels & Trappe (Daniels and Trappe 1979), *G. mosseae* (Nicol & Gerd.) Gerdemann and Trappe (Gerdemann and Trappe 1974), and *G. intraradices* Schenck & Smith (Schenck and Smith 1982). This is the first report of *G. epigaeum* and *G. intraradices* from a desert environment. Two new species, sp. A (*Acacia* and *Chilopsis* sites) and sp. B, (*Opuntia* site), were also found. Species A was characterized

¹Reference to a specific company and (or) product is only for purposes of information and does not imply approval or recommendation of the product or company by the United States Department of Agriculture or the Canadian Journal of Botany nor criticism of others which may also be suitable.

by small (<1.2 mm) irregularly shaped sporocarps, and spores (40-80 µm longest dimension) with two thin (composite thickness 2-4 µm) pale-yellow walls and occluded hyphal attachments of 6-10 µm diameter. The spores of species B had many characteristics of the spores of *G. fasciculatum*, but were distinct in having very thick walls with hyaline warts on the surface.

Species B occurred only at the *Opuntia* site (Table 2) and *G. fasciculatum* and *G. intraradices* occurred only at the *Agave-Yucca* site (Table 3). However, species A occurred in the desert washes of both the *Acacia* and *Chilopsis* sites (Tables 1 and 4), *G. mosseae* at the *Agave-Yucca* and *Chilopsis* sites (Tables 3 and 4), and *G. epigaeum* at the *Opuntia* and *Agave-Yucca* sites (Tables 2 and 3).

The soils at all four sites originated from acid-igneous rock. This was reflected in their coarse texture, with quartz as the predominant mineral species. All soils had a light and a dark component. The dark particles were much less numerous and consisted of mica at the *Acacia* and *Opuntia* sites and of mica and amphiboles at the other two sites. Soil at the *Agave-Yucca* site was apparently subject to more intense weathering than at the other sites. Here, the relatively fine sand particles had heavy ferric sesquioxide coatings giving this soil a reddish appearance. Muscovite was also present at this site. The *Chilopsis* site was most diverse in terms of sample mineralogy. In addition to mica, quartz, and feldspar, a large diversity of other unidentified minerals were observed at the *Agave-Yucca* and *Chilopsis* sites. Fragmented mica particles were found with platelets separated by VAM-fungal hyphae and spores at all sites (Fig. 1).

The soil was moderately acid at the *Agave-Yucca* site. Its pH was significantly lower than that of the other sites which were slightly alkaline (Table 5). The salt concentration at all sites was 5 mS/m or lower (Table 5), values well below the levels which affect the growth of nonhalophytes (Levitt 1980; Bower and Wilcox 1965). Soil-moisture content at -1.5 MPa was significantly higher at the *Agave-Yucca* site than at the *Acacia* and *Opuntia* sites (Table 5).

Both N and P concentrations were extremely low at all four sites (Table 6). The *Acacia* and *Opuntia* sites were lowest in available (NaHCO₃-extractable) P and total N. The *Agave-Yucca* site was significantly higher in available P and lower in total P than the other sites. The *Chilopsis* site was intermediate in available P and highest in total N.

TABLE 2. Flora of a sandy playa (*Opuntia* site) near Mountain Palm Springs, Anza-Borrego Desert State Park, California^a

Flora	D	BV	EPA	FC	VAM fungus (<i>Glomus</i>)
Cactaceae					
<i>Echinocactus acanthodes</i>	1	0.5	3	3	<i>epigaeum</i> , sp. B
<i>Echinocereus engelmannii</i>	11	0.1	3	3	<i>epigaeum</i> , sp. B
<i>Opuntia acanthocarpa</i>	65	58.81	3	3	<i>epigaeum</i> , sp. B
<i>Opuntia bigelovii</i>	184	96.4	3	3	<i>epigaeum</i> , sp. B
Compositae					
<i>Franseria dumosa</i>	9	0.3	2	2	<i>epigaeum</i> , sp. B
<i>Hymenoclea salsola</i>	4	1.1	1	1	<i>epigaeum</i> , sp. B
Euphorbiaceae					
<i>Euphorbia polycarpa</i>	820	1.2	1	1	<i>epigaeum</i> , sp. B
Fouquieriaceae					
<i>Fouquieria splendens</i>	2	8.4	1	1	<i>epigaeum</i> , sp. B
Leguminosae					
<i>Acacia greggii</i>	4	2.1	3	3	<i>epigaeum</i> , sp. B
<i>Cassia armata</i>	4	2.1	2	2	<i>epigaeum</i> , sp. B
<i>Psoralea schottii</i>	9	12.9	3	2	<i>epigaeum</i> , sp. B
Zygophyllaceae					
<i>Larrea divaricata</i>	1	2.1	3	3	<i>epigaeum</i> , sp. B

^aAbbreviations and units as in Table 1.TABLE 3. Flora of a sandy slope (*Agave-Yucca* site) at Box Canyon, Anza-Borrego State Desert Park, California^a

Flora	D	BV	EPA	FC	VAM fungus (<i>Glomus</i>)
Agavaceae					
<i>Agave deserti</i>	172	30.9	3	3	<i>mosseae</i> , <i>epigaeum</i>
<i>Yucca schidigera</i>	65	24.8	3	2	<i>mosseae</i> , <i>intraradices</i>
Cactaceae					
<i>Echinocactus acanthodes</i>	4	2.1	3	3	<i>mosseae</i> , <i>intraradices</i>
<i>Opuntia basilaris</i>	3	0.1	3	3	<i>mosseae</i>
<i>Opuntia echinocarpa</i>	48	1.3	3	3	<i>mosseae</i> , <i>epigaeum</i>
Compositae					
<i>Brickellia frutescens</i>	6	0.2	1	1	<i>mosseae</i> , <i>fasciculatum</i>
<i>Guthierrezia sarothrae</i>	1377	5.8	3	3	<i>mosseae</i> , <i>fasciculatum</i>
<i>Lepidospartum squamatum</i>	24	12.7	1	1	<i>mosseae</i> , <i>fasciculatum</i> , <i>intraradices</i>
Cupressaceae					
<i>Juniperus californicus</i>	13	11.8	3	3	<i>mosseae</i> , <i>epigaeum</i>
Ephedraceae					
<i>Ephedra californica</i>	10	1.1	3	3	<i>mosseae</i> , <i>fasciculatum</i>
<i>Ephedra viridis</i>	17	8.9	3	3	<i>mosseae</i> , <i>fasciculatum</i> , <i>epigaeum</i>
Graminae					
<i>Hilaria rigida</i>	163	18.4	1	1	<i>mosseae</i>
Krameriaceae					
<i>Krameria grayi</i>	3	0.3	2	1	<i>mosseae</i>
<i>Krameria parvifolia</i>	18	2.0	2	2	<i>mosseae</i>
Leguminosae					
<i>Acacia greggii</i>	6	21.5	3	3	<i>mosseae</i> , <i>intraradices</i>
Polygonaceae					
<i>Eriogonum fasciculatum</i>	80	21.5	2	2	<i>mosseae</i> , <i>epigaeum</i>
<i>Eriogonum nodosum</i>	2	0.2	2	1	<i>mosseae</i>
Rhamnaceae					
<i>Simmondsia chinensis</i>	3	6.4	2	3	<i>mosseae</i>
Zygophyllaceae					
<i>Larrea divaricata</i>	8	7.2	1	2	<i>mosseae</i>

^aAbbreviations and units as in Table 1.

Discussion

The distribution of VAM-fungal species at the four sites was not random. Site preference was demonstrated by the occurrence of some of the species at one site only, while none of the

species were found at more than two sites. The data were not sufficient to establish causal relationships between the conditions prevailing at a site and the composition of its VAM mycoflora, but the vegetational, edaphic, and climatic (precip-

TABLE 4. Flora of a sandy wash (*Chilopsis* site) at Yaqui Flat, Anza-Borrego Desert State Park, California^a

Flora	D	BV	EPA	FC	VAM fungus (<i>Glomus</i>)
Bignoniaceae					
<i>Chilopsis linearis</i>	40	565.6	3	3	<i>mosseae</i> , sp. A
Capparidaceae					
<i>Isomeris arborea</i>	17	8.9	2	2	<i>mosseae</i>
Leguminosae					
<i>Prosopis juliflora</i>	4	1.8	3	2	<i>mosseae</i>
<i>Psoralea argophylla</i>	8	11.5	3	3	<i>mosseae</i> , sp. A
Loasaceae					
<i>Petalonix thurberi</i>	3	0.1	2	2	<i>mosseae</i> , sp. A
Tamaricaceae					
<i>Tamarix pentandra</i>	1	4.2	2	2	<i>mosseae</i> , sp. A

^aAbbreviations and units as in Table 1.

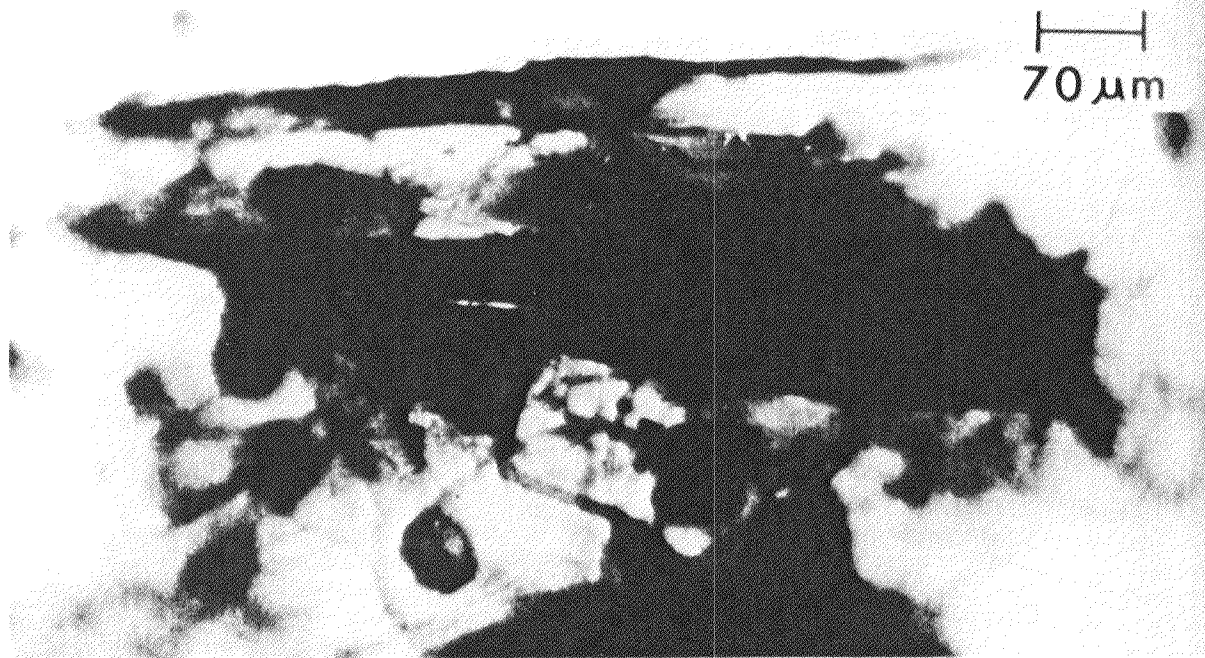


FIG. 1. Hyphae and spores of a vesicular-arbuscular mycorrhizal fungus which have penetrated the cleavage planes of a mica particle.

itation) factors available suggest patterns which are of interest in the study of VAM-fungal adaptation.

A relationship between the occurrence of VAM fungi and the distribution of vegetation was apparent at the *Acacia* and *Opuntia* sites. These sites were adjacent and alike in edaphic and climatic characteristics, but differed in their vegetational composition. This difference was reflected in the distinct VAM mycoflora of the sites. Although VAM fungi showed no host specificity (Tinker 1978) by colonizing all plants at all sites, the occurrence of different VAM-fungal species at these two sites may have been influenced by host preference (Mosse 1973). Such a capability of plants to selectively influence VAM-fungal colonization has been demonstrated in agricultural situations (Schenck and Kinloch 1980). However, the diversity in the floristic composition of the vegetation and the relative uniformity of the VAM mycoflora at all sites indicated that host effects may be only one of the mechanisms which determine VAM-fungal species distribution. The *Agave-Yucca* site was different from the others in its edaphic characteristics and in a greater incidence of precipitation. The VAM mycoflora at this

site was distinct in its relative diversity and was dominated by *G. mosseae* which colonized all plants at the site. *Glomus mosseae* also occurred at the *Chilopsis* site which showed similarities with the *Agave-Yucca* site in soil texture, available P, moisture levels, and precipitation patterns. A preference of *G. mosseae* for these conditions may explain its distribution. No such explanation can be offered for the cooccurrence of *G. epigaeum* at the *Agave-Yucca* and *Opuntia* sites, which were different in vegetation, edaphic conditions, and rainfall patterns. The occurrence of species A in the two desert washes (*Acacia* and *Chilopsis* sites) may be linked to a tolerance of, or preference for, periodic abrasion as a result of running water in sand at those sites.

One can conclude that a complex interaction of factors (Hayman 1983; Lambert *et al.* 1980) is responsible for the distribution of the VAM mycoflora at these sites. That such distributional patterns vary with the climatic and edaphic environment, as well as with land use, has been recognized, but causal relationships are poorly understood (Abbott and Robson 1982). Information is particularly lacking from desert environments

TABLE 5

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TABLE 5. Soil characteristics at four sites in the Colorado Desert of southern California^a

Soil parameters	Site			
	<i>Acacia</i>	<i>Opuntia</i>	<i>Agave-Yucca</i>	<i>Chilopsis</i>
pH	7.4a	7.5a	6.0b	7.3a
EC ^b (mS/m)	2.2b	3.7c	1.2a	5.0d
GMD ^c (μm)	682a	486b	370bc	331c
MC ^d (% g/g)	2.5a	2.5a	3.4b	2.9ab

^aNumbers followed by the same letter were not significantly different ($P < 0.05$) by Tukey's multiple range test.

^bElectrical conductivity (EC) was measured in a 1:5 soil-water suspension.

^cGeometric mean diameter (GMD) was calculated as $GMD = \left(\frac{\sum W_i \log \bar{x}_i}{\sum W_i} \right)^{1/2}$ where W_i is the aggregate mass in the fraction with an average diameter \bar{x}_i .

^dMoisture content (MC) was determined at -1.5 MPa and represents soil water at the permanent wilting point for most plants.

TABLE 6. Phosphorus and nitrogen concentrations (micrograms per gram of soil) at four sites in the Colorado Desert of southern California^a

Site	Phosphorus		Nitrogen (total)
	Available	Total	
<i>Acacia</i>	1.4a	199a	93a
<i>Opuntia</i>	1.5a	218a	151ab
<i>Agave-Yucca</i>	4.5c	131b	235bc
<i>Chilopsis</i>	3.1b	218a	510c

^aNumbers followed by the same letter in one column are not significantly different ($P < 0.05$) by Tukey's multiple test.

(Rose 1981; Trappe 1981), where VAM fungi may be of particular importance to the vegetation by imparting special adaptive advantages for the survival to their hosts (Williams and Aldon 1976). Such advantages are the increased uptake of P and water (Allen 1982; Nelsen and Saphir 1982) by VAM plants. In the soils under consideration these uptake processes may be further enhanced by the role of VAM fungi in weathering mica (Fig. 1). This process may result in an important increase in the capacity of soils rich in mica to retain water and to provide nutrients for uptake by microorganisms (Berthelin and Leyval 1982) and VAM fungi. As the availability of water is one of the main factors controlling CO₂ exchange (Farquhar and Sharkey 1982), it would be of interest to establish whether VAM colonization levels vary with precipitation patterns as a result of changes in photosynthate availability. A relationship between photosynthesis and the extent of VAM colonization has been demonstrated elsewhere (Bethlenfalvay and Pacovsky 1983; Johnson *et al.* 1982) and is suggested by the present findings.

Agricultural applications of mycorrhizal research requires the proper selection of VAM fungi for both host and environment (Trappe 1982). An elucidation of the factors which control VAM-fungal distribution in natural environments (Mosse *et al.* 1981) is a necessary step towards fulfillment of this requirement.

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