# Studies of Symbiotic Microflora and Their Role in the Ecology of Desert Plants

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## Introduction

Microflora in soil greatly influence the ecology of plant roots and consequently the establishment, health, and productivity of plant communities. Among the most common, yet least recognized relationships among plants and microorganisms in desert soils, are the symbioses known as "mycorrhizae." Nearly all plant roots form mycorrhizal associations, some of which are essential and nearly all beneficial to plant growth and development. Most researchers of mycorrhizal fungi agree that the primary benefit to plants appears to be that of improved nutrition, exhibited by a greater rate of growth and higher yields (biomass, fruit, seeds, etc.), compared to non-mycorrhizal associations. The fungal symbiont in turn receives nutrients from the host plant, primarily carbohydrates and other organic nutrients which the fungus can not produce. Although desert soils usually contain adequate quantities of the essential elements for plant growth, certain minerals such as phosphorus and iron are frequently unavailable because of high alkalinity or salinity.

Several major types of mycorrhizae, involving several distinct classes or groups of mycorrhizal fungi, are recognized world wide. Ectomycorrhizae are associations which form between fungi that belong to the fungal classes Ascomycetes or Basidiomycetes and roots of coniferous and hardwood trees and shrubs in the plant families Pinaceae, Fagaceae, Betulaceae, and Salicaceae in temperate climates, Caesalpiniaceae and Dipterocarpaceae in the tropics, and in *Eucalyptus, Tilia,* and *Arbutus* (Meyer, 1973). Endomycorrhizae, particularly those known as vesiculararbuscular (VA) mycorrhizae, form on roots of many broad-leaved shrubs and herbaceous species and are also commonly associated with roots of grasses. VA mycorrhizae occur in numerous species from polar to subtropical regions. They are not commonly found, however, in the Pinaceae, Betulaceae, Orchidaceae, Fumariaceae, Commelinaceae, Ericaceae, Urticaceae, and only rarely in Cruciferae, Chenopodiaceae, Polygonaceae, or Cyperaceae. The families Orchidaceae and Ericaceae form mycorrhizae with other sub-groups of mycorrhizal fungi not related to VA- or ectomycorrhizal fungi. Another interesting association occurs between species in the actinomycete genus *Frankia* and roots of older trees of the genus *Alnus.*

Mycorrhizal fungi share an ecological niche in soil along with a variety of microorganisms, including some which are pathogenic, some commensalistic, and some which are symbiotic with plant roots. Certain bacteria, such as *Azotobacter* and *Rhizobium,* form tripartite systems with roots and mycorrhizal fungi (Smith and Daft, 1977). Other bacteria in soil, such as certain species of fluorescent pseudomonads, have been shown to assist in making phosphorus and perhaps other minerals available to roots (Burr et al., 1978; Kloepper et al., 1980). Research during the past decade has been directed toward clarifying whether the symbiotic bacteria and mycorrhizal fungi need to be added to agricultural soils and whether indigenous populations of these microflora exist and are functional on roots of native plants.

There is a growing world literature on associations between arid land shrubs and VA mycorrhizal fungi (Khan, 1974; Williams and Allen, 1984; Staffeldt and Vogt, 1975;

**Figure 1.** Site A. Molino Basin in the Santa Catalina Mountains, Pima County, Arizona. Elevation 1332 meters (4300 feet).



**Figure 2.** Saguaro (Carnegiea gigantea) growing in association with Palo Verde (Cercidium microphyllum).

Williams and Aldon, 1976) and in natural and disturbed ecosystems in North American deserts (Miller, 1979; Allen, 1983; Schwab and Reeves, 1981; Bethlenfalvay et al., 1984; Moorman and Reeves, 1979; Stahl and Christensen, 1982).

The aims of the present study were to isolate, to identify, and to attempt to culture mycorrhizal fungi (mainly VA mycorrhizal species) from the Upper Sonoran and Lower Sonoran Life Zones in Arizona and to study their role in arid land ecosystems and their significance to both indigenous and introduced species such as Guayule (*Parthenium argentatum* A. Gray) or Plantago (*Plantago ovata* Forsk) (Bloss and Pfeiffer, 1984; Bloss, 1982).

## Collections of Field Samples

Samples of soil and fine roots were collected from several sites in the open oak woodland at Molino Basin in the Upper Sonoran Life Zone and at several sites in the Tucson Valley in the Lower Sonoran Life Zone, as well as from agricultural soils at the University farms at Tucson and Yuma.

Site A, the encinal zone (from Spanish, meaning grove of oaks) of the Santa Catalina Mountains, Pima County, Arizona includes the Molino Basin at 1332m (4300 ft.), an open grass woodland (Whittaker and Niering, 1965). The area is characterized by riparian forest comprised primarily of Mexican Blue Oak (*Quercus oblongifolia* Torr.), Emory Oak (*Quercus emoryi* Torr.), Arizona White Oak (*Quercus arizonica* Sargent), Arizona Ash (*Fraxinus velutina* Torr.), Arizona Sycamore (*Platanus wrightii* S. Wats.), and Alligator Juniper (*Juniperus deppeana* Steud.). Conspicuous plants on xeric slopes are Golden Flowered Agave (*Agave palmeri* Engelm.), Amole (*Agave schottii* Engelm.), Beargrass (*Nolina microcarpa* S. Wats.), Ocotillo (*Fouquieria splendens* Engelm.), Point Leaf Manzanita (*Arctostaphylos pungens* H.B.K.), Sotol (*Dasylirion wheeleri* S. Wats.), Silktassel Bush (*Garrya wrightii* Torr.), Arizona Rosewood (*Vauquelinia californica* (Torr.) Sargent), Catclaw (*Mimosa biuncifera* Benth.), Fairy Duster (*Calliandra eriophyla* Benth.), and a few Saguaro (*Carnegiea gigantea* (Engelm.) Britt. and Rose).

The rocky slopes and rolling hills among the oaks are covered by a mixture of grasses, cacti, and annuals. The grasses include Texas Bluestem (*Andropogon cirratus* Hack.), Cone Beardgrass (*Andropogon barbinodis* Lag.), Beggartick Grass (*Aristida orcuttiana* Vasey), Spidergrass (*Aristida ternipes* Cav.), Sideoats Grama (*Bouteloua curtipendula* (Michx.) Torr.), Hairy Grama (*Bouteloua hirsuta* Lag.), Curly Mesquite Grass (*Hilaria belangeri* (Steud.) Nash), and Bullgrass (*Muhlenbergia emersleyi* Vasey). Several species of cacti occur scattered among the grasses and on rocky slopes, including Barrel Cactus (*Ferocactus wislizeni* (Engelm.) Britt. and Rose), Bush Opuntia (*Opuntia phaeacantha* Engelm.), and the foothills chollas *Opuntia spinosior* (Engelm. and Bigel.) Toumey and *Opuntia fulgida* Engelm.

Two other collection sites included Site B: the eastern edge of the Tucson Valley, along the edge of the Lower Sonoran Life Zone, north of Saguaro National Monument, east to the lower reaches of the Santa Catalina Mountains to 762m (2,500 ft.), and Site C: the western edge of the desert floor extending to 915m (3,000 ft.) southeast of

Saguaro National Monument West, in the foothills of the Tucson Mountains.

Site B consisted of mixed species of cacti, Plains Prickly Pear (*Opuntia macrorhiza* Engelm.), Jumping Cholla (*Opuntia fulgida* Engelm.), Saguaro (*Carnegiea gigantea*) Ocotillo (*Fouquieria splendens*) Creosote Bush (*Larrea tridentata* (DC.) Coville), and two grama grasses, *Bouteloua barbata* Lag. and *Bouteloua curtipendula* (Michx.) Torr.

Site C, the lower foothills of the Tucson Mountains, consisted of major species such as Saguaro (*Carnegiea gigantea*) Jumping Cholla (*Opuntia fulgida*) Barrel Cactus (*Ferocactus wislizeni*) Foothills Palo Verde (*Cercidium microphyllum* (Torr.) Rose and Johnston), Desert Broom (*Baccharis sarothroides* Gray), Creosote Bush (*Larrea tridentata*) Catclaw (*Acacia greggii* Gray), Honey Mesquite (*Prosopis juliflora* (Swartz) DC.), Arizona Poppy *(Kallstroemia grandiflora* Torr.), Unicorn Plant (*Proboscidea parviflora* (Woot.) Woot. and Standl.), and numerous annual composites including Paperflower (*Psilostrophe cooperi* (Gray) Green), Desert Marigold (*Baileya multiradiata* Harv. and Gray), and Desert Zinnia (*Zinnia pumila* Gray).

## Verification of Mycorrhizae in Roots

Roots were collected by removing young specimens of plant species from the soil and excising small roots with a pair of pruning shears. Fine feeder roots and root-hairs were most easily cleared and stained for microscopic examination. Wet sieving of collected soil yielded spores and sporocarps that were identifiable to species using microsopic characteristics such as size, color, wall constituents, and other distinctive morphology.

## Isolation of Fungi From Soil

Rhizosphere soil samples at 0-20cm depth were collected monthly from May to October in 1983. Samples were collected at random, primarily under Manzanita, Agave and Sotol, for example, in Site A and under the appropriate dominant species in sites B and C. Roots of small annuals such as White Clover (*Trifolium repens* L.), Slimleaf Bursage (*Ambrosia confertiflora* DC.) or the grama grasses *Bouteloua hirsuta* and *Bouteloua curtipendula* were frequently among the soil samples. Soil samples were sieved for spores using the procedure of Gerdemann and Nicolson (1963). Spores were collected on 400-mesh sieves (37um holes) and collected in tap water in 9-cm Petri dishes for examination under a dissecting microscope (20-70X). Spores were removed from fine debris by means of microforceps or microspatulas and mounted in polyvinyl lactophenol (PVL) for observation on a compound microscope. Attempts were made to culture the representative spore types collected, by placing one chlamydospore on rootlets of 1-week-old Sorghum (*Sorghum bicolor* L.) or Alfalfa (*Medicago sativa* L.) seedlings in pasteurized sand. Although roots of certain plants from the field were cleared and stained to verify the presence of vesicles and hyphae in the plant roots, no attempt was made to associate specific endogonaceous fungi with specific plant hosts.

## Results

Sampling of roots and soil from plants at Site A in the Molino Basin (Figure 1) in 1983 yielded sixteen species of
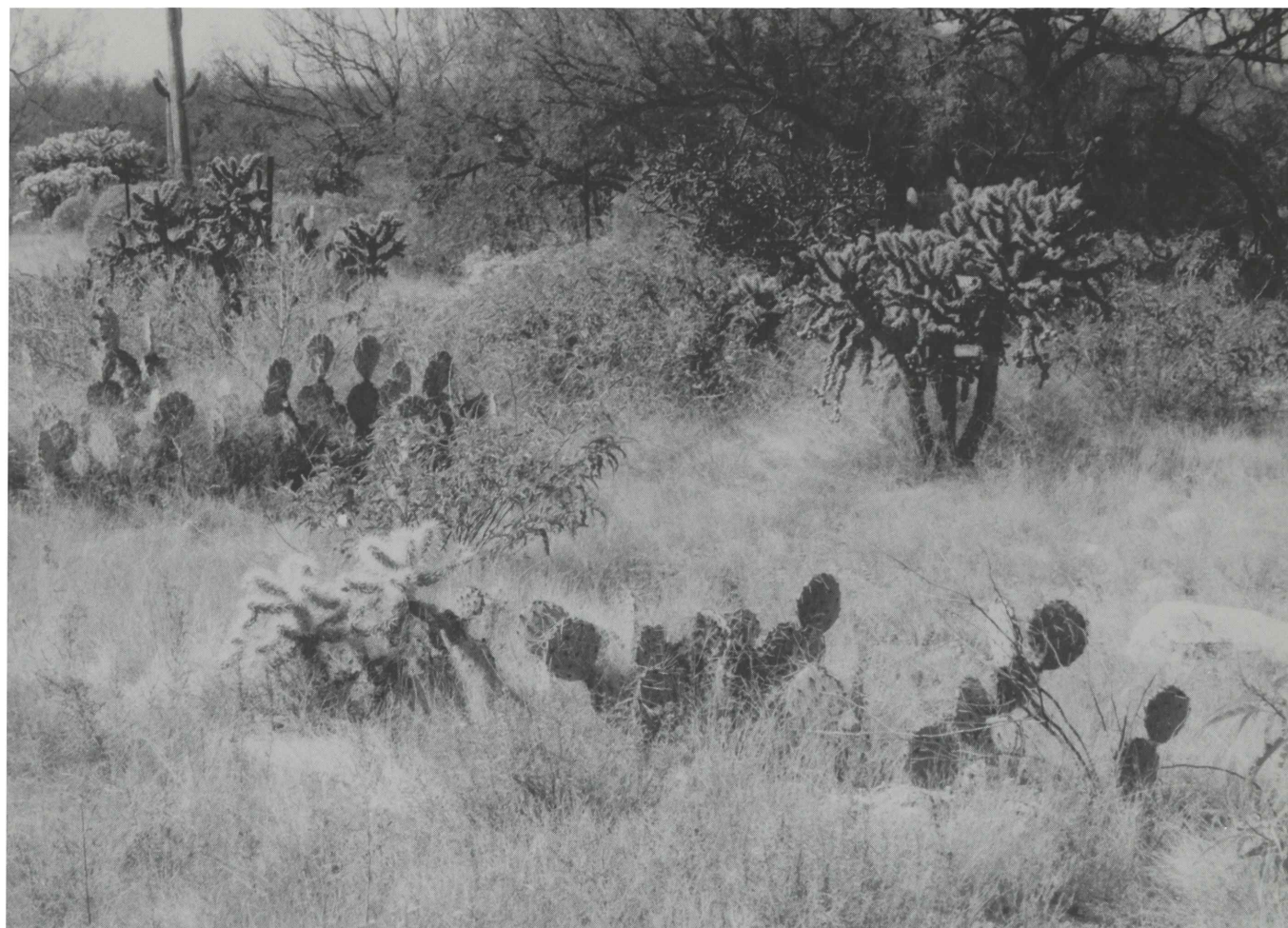
**Figure 3.** Site B east of Tucson included Jumping Cholla (Opuntia fulgida), Prickly Pear (Opuntia sp.), and Saguaro (Carnegiea gigantea) with abundant grasses (Bouteloua spp.) and ephemerals.

VA mycorrhizal fungi (Table 1). Ten species, including one undescribed species each in the genera *Acaulospora* and *Gigaspora*, were isolated from the Point Leaf Manzanita (*Arctostaphylos pungens*) association, eight species from under Amole (*Agave schottii*) and seven species from under Weeping Lovegrass (*Eragrostis curvula*).

The loamy soil beneath *Manzanita* and *Agave* plants contained low quantities of nutrients, N = 5.33 ppm, P = 0.53 ppm, K = 4.44 meg/L, Na = 0.74 meg./L, 462 ppm soluble salts, and pH = 5.40.

Many of the same species of fungi were isolated from the soil at the University of Arizona farms at Tucson and Yuma (Table 2), as well as from Sites B and C in the desert. Populations of mycorrhizal fungi, based on numbers of spores collected of each species, varied with the season at all sites where collections were made. For example, *Gigaspora* species were collected in higher numbers during the warmer months, April to July, at the site in the Catalina Mountains and at the campus farm site in Tucson, but numbers declined rapidly from September to February. Some fluctuations in populations of specific fungi were observed under Grape (*Vitis vinifera* L.), Soybeans (*Glycine*

*max* (L.) Merrill) and Alfalfa *(Medicago sativa* L.) at the locations in the desert Lower Sonoran Life Zone as well.

VA mycorrhizal fungi were prominent in the Creosote Bush association as well as the Palo Verde and Saguaro association of Sites B and C. Endomycorrhizal fungi occurred throughout the sampling from ephemerals to Palo Verde and Saguaro where Saguaro cohabited with Palo Verde (Figure 2).

Creosote Bush was found to be mycorrhizal, with the roots in clonal situations fostering high populations of VA mycorrhizal fungi. Figure 4 shows a clonal group of Creosote Bush arising from a single parent plant at Site C, with a high percentage of open space surrounding the clone. The fungal populations were associated with the network of roots in marked contrast to the "deserted" spaces having no Creosote Bush roots. Grasses and other ephemerals were generally negatively associated with Creosote Bush (Figure 4) as opposed to their positive association with Palo Verde and Saguaro.

**Discussion and Conclusions**

The extensive sampling at Site A uncovered a wide vari-

**Figure 4.** *Site C west of Tucson included clonally repro-
duced Creosote Bush (Larrea tridentata) with surrounding
open spots deserted of grasses and ephemerals.*

ety of arid land VA mycorrhizal fungi which proved to occur
at numerous other sites as well, including agricultural situ-
ations in Pima and Yuma Counties, Arizona as well as
natural desert sites both east and west of Tucson. Situations
where several species of plants were clustered together,
such as the association of grasses and ephemerals with Palo
Verde and Saguaro, yielded numerous VA mycorrhizal
fungi; an analysis of the ecological significance of the ten-
dency of such arid land plants to aggregate is attempted
below in relationship to the theorized passage of mycorrhi-
zal fungi in a ubiquitous (non-specific) manner from species
to species. A further ubiquity seems to have been dem-
onstrated by finding a large number of VA mycorrhizal
fungi in soil under Manzanita, a plant with which they
were not necessarily symbiotic since the genus has been
shown to form mycorrhizae with the ect-endo types of
fungi, such as *Pezizella ericae* (Read, 1974).

The presence of indigenous populations of VA mycorrhi-
zal fungi, which are capable of forming symbiotic relation-
ships with both native and introduced crop plants in the
desert, has significance in regard to plant nutrition, plant
establishment, and plant longevity. Major stresses related
to arid land plants are associated with low precipitation and

high evapotranspiration. Phosphorus is highly immobile in
desert soils and a large portion of phosphorus in fertilizers
added to desert soils reacts with the soil and is unavailable
for plant use (Fuller, 1975). The growth advantages at-
tributed to plants with VA mycorrhizae are believed to be
associated with an increase in the nutritional status of the
plants brought about by increased phosphorus uptake (Daft
and Nicolson, 1966) and enhanced water transport (Safir et
al., 1972).

The seasonal temperature and moisture regimes regulate
mycorrhiza formation and function. Most phosphorus
transformation to the plant occurs during the short nut-
rient flush when moisture is available (Chapin, 1980) and
below ground carbon allocation also requires sufficient
water (Fernandez and Caldwell, 1977).

Nitrogen, phosphorus, and potassium are dilute in the
soil solution and mass flow of soil water meets only a small
part of the plant's total requirements. When concentrations
of nutrients increase, soil temperature becomes increas-
ingly important relative to diffusion of nutrients in con-
trolling the rate at which roots acquire the nutrients.
Highly mobile cations such as calcium and magnesium
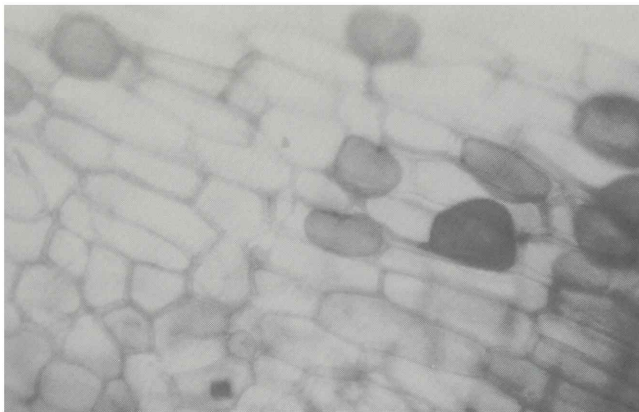move to the root by mass flow and accumulate around

**Figure 5.** *Vesicles and hyphae of a mycorrhizal fungus in root cells of Jumping Cholla (Opuntia fulgida).*
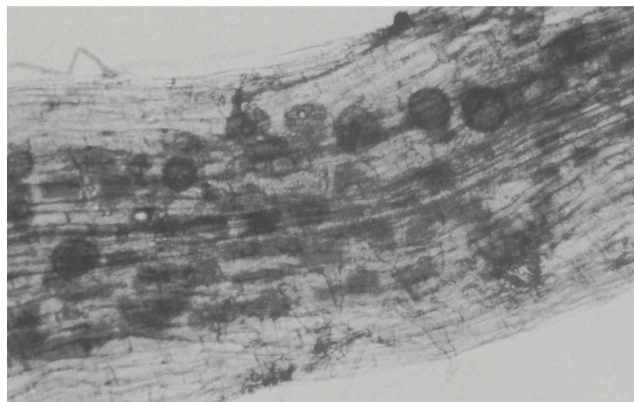


**Figure 6.** *A mycorrhizal association of Glomus intraradices with roots of Guayule (Parthenium argentatum).*
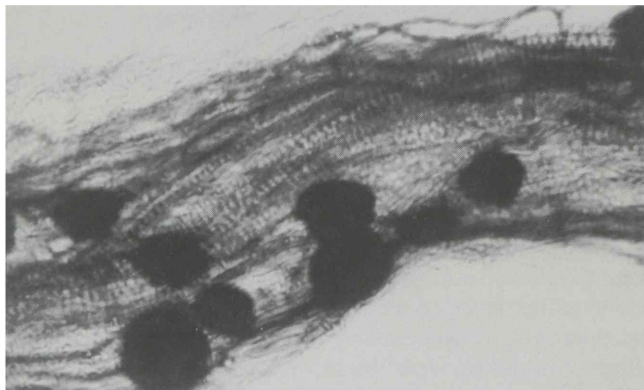


**Figure 7.** *VA mycorrhizal hyphae and vesicles in cortical root tissue of Prickly Pear (Opuntia phaeacantha).*
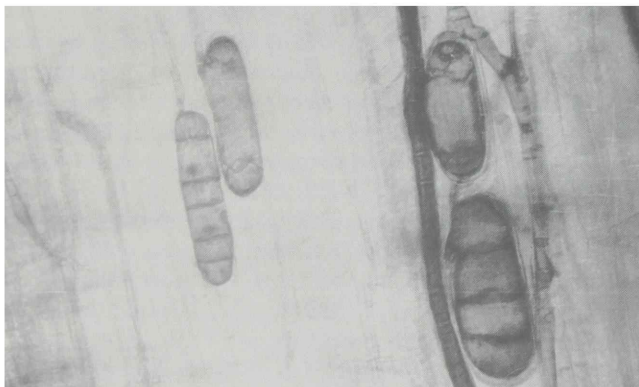


**Figure 8.** *VA mycorrhizal hyphae and vesicles in root cell of Mariola (Parthenium incanum H.B.K.).*

**Table 1.** VA mycorrhizal fungi identified from soil and roots of plants at Molino Basin, Santa Catalina Mountains, Arizona (Upper Sonoran Life Zone).

| Plant-Soil Association | Date of Collection |
|---|---|
| *Manzanita—Arctostaphylos pungens H.B.K. | |
|    *Gigaspora calospora* (Nicol. & Gerd.) | |
|      Gerdemann & Trappe | |
|    *Acaulospora* sp. | |
|    *Acaulospora laevis* Gerdemann & Trappe | |
|    *Acaulospora scrobiculata* Trappe | |
|    *Glomus constrictum* Trappe | 16-IV-83 |
|    *Glomus geosporum* (Nicol. & Gerd.) Walker | |
|    *Glomus deserticola* Trappe, Bloss & Menge | |
|    *Glomus etunicatum* Becker & Gerdemann | |
|    *Glomus rigidicaulis* Walker | |
|    *Entrophospora infrequens* Ames & Schneider | |
| | |
| **Amole—Agave schottii Engelm.** | |
|    *Acaulospora scrobiculata* Trappe | |
|    *Entrophospora infrequens* Ames & Schneider | |
|    *Gigaspora* sp. | |
|    *Glomus etunicatum* Becker & Gerdemann | |
|    *Glomus geosporum* (Nicol. & Gerd.) Walker | 30-VI-83 |
|    *Glomus constrictum* Trappe | |
|    *Glomus deserticola* Trappe, Bloss & Menge | |
|    *Glomus mosseae* Gerdemann & Trappe | |
| | |
| **Weeping Lovegrass—Eragrostis curvula (Schrad.) Nees** | |
|    *Acaulospora* sp. | |
|    *Acaulospora scrobiculata* Trappe | |
|    *Glomus mosseae* Gerdemann & Trappe | |
|    *Glomus butleri* Walker | 12-VII-83 |
|    *Glomus geosporum* (Nicol. & Gerd) Walker | |
|    *Glomus etunicatum* Becker & Gerdemann | |
|    *Gigaspora* sp. | |

*Isolation of fungal spores from soil beneath roots of the dominant species does not indicate necessarily that the fungus was mycorrhizal with roots of the plant species indicated.

roots. These elements limit plant growth only at extremely low bulk soil solution concentration. The amount of available phosphorus in desert soils is generally adequate for native vegetation. Intensive cultivation of soils under irrigation or uses of plants in certain combinations or high densities per unit area may increase the demand for phosphorus as well as other nutrients.

Some root-inhabiting bacteria are capable of dissolving highly insoluble forms of phosphate in soil, making it available for plant absorption (Katznelson et al., 1962), whereas other bacteria such as *Rhizobium* and *Azotobacter* have the capacity to assist roots in assimilating nitrogen. There have been some useful combinations of VA mycorrhizal fungi and soil bacteria (Bagyaraj and Menge, 1978) applied to roots that have resulted in increased nutrient uptake and plant survival particularly on spoiled soils such as mine tailings and eroded soils (Medve et al., 1977; William and Allen, 1984).

Deserts by definition have a low percentage of plant cover. Plants may be highly scattered with significant "deserted" areas intervening. The present study has shown that desert plants foster high populations of VA mycorrizal fungi on their roots. Mycorrizal fungi can not live without plants to provide food, so it is not surprising that open "deserted" or despoiled areas soon lack concentrations of these fungi. When mycorrhizal plant communities are dis-

**Table 2.** VA mycorrhizal fungi identified from soil and roots of plants in the Lower Sonoran Life Zone of Pima and Yuma Counties, Arizona.

| Plant-Soil Association | Date of Collection |
|---|---|
| **Under Grape Vitis vinifera L. (cultivated)** | 25-X-83 Tucson, AZ |
| Acaulospora scrobiculata Trappe | |
| Gigaspora calospora (Nicol. & Gerd.) Gerdemann & Trappe | |
| Glomus constrictum Trappe | |
| Glomus etunicatum Becker & Gerdemann | |
| Glomus geosporum (Nicol. & Gerd.) Walker | |
| Glomus microcarpum Tul. & Tul. | 15-VIII-84 Tucson, AZ |
| Sclerocytis rubiformis Gerd. & Trappe | |
| Sclerocystis sinuosa Gerd. & Bakshi | |
| **Mycorrhizal with roots of:** | |
| **Alfalfa: Medicago sativa L.** | 15-VI-80 Yuma, AZ |
| Glomus mosseae (Nicol. & Gerd.) Gerdemann & Trappe | |
| **Mycorrhizal with roots of:** | |
| **Gopher Weed: Euphorbia lathyris L.** | 25-VII-80 Tucson, AZ |
| Glomus intrardices Schenck & Smith | |
| **Mycorrhizal with roots of:** | |
| **Mariola: Parthenium incanum H.B.K.** | 5-VII-78 Tucson, AZ |
| **Joboba: Simmondsia chinensis (Link) Schneid.** | 5-VII-78 Tucson, AZ |
| Glomus deserticola Trappe, Bloss, & Menge | |
| **Mycorrhizal with roots of:** | |
| **Soybean: Glycine max (L.) Merrill** | 15-VIII-79 Yuma, AZ |
| Gigaspora calospora (Nicol. & Gerd.) Gerdemann & Trappe | |
| Glomus geosporum (Nicol. & Gerd.) Walker | |
| Glomus microcarpum Tul. & Tul. | |



*Figure 9.* Glomus deserticola.



*Figure 10.* Glomus albidum.
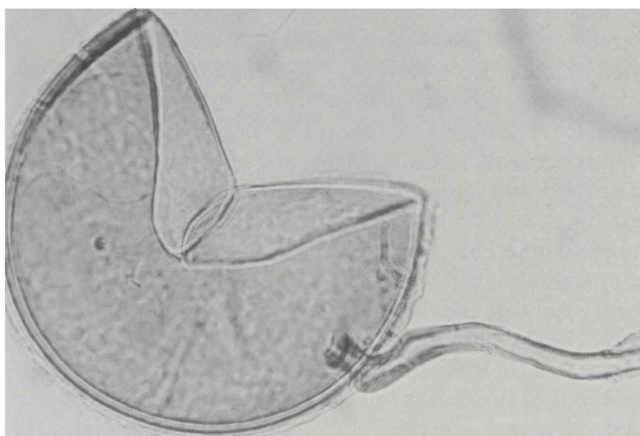


*Figure 11.* Glomus intraradices.



*Figure 12.* Gigaspora calospora.

turbed, nonmycorrhizal plant species come to predominate (Reeves et al., 1979). A difficulty in reestablishing native plants on disturbed soils can be traced to the lack of VA mycorrhizal fungi. Daft, Hacskaylo, and Nicolson (1975) have established the need for VA mycorrhizal fungi in the establishment of pioneer plants on coal mine wastes. Aldon (1975) showed that endomycorrhizae increased the height, dry weight, and percentage survival of Fourwing Saltbush (*Atriplex canescens* (Pursh) Nutt.), transplanted on coal mine spoils in New Mexico and with Rabbitbrush (*Chrysothamnus nauseosus* (Pall.) Britton) grown on the same material (Lindsey, Cress and Aldon, 1977). Moorman and Reeves (1979) have used endomycorrhizal fungi to bioassay effects of soil disturbance at a given site. The bioassay consists of determining the percentage infection in roots of maize grown for 30 days in soil from disturbed and undisturbed sites in which numbers of visable propagules, spores and infected roots are counted. The greater the disturbance, the fewer the mycorrhizal fungi.

The open or "deserted" area between plants in the desert would be similar to despoiled sites in that they are not favorable for native plant growth unless VA mycorrhizal fungi are introduced as well.
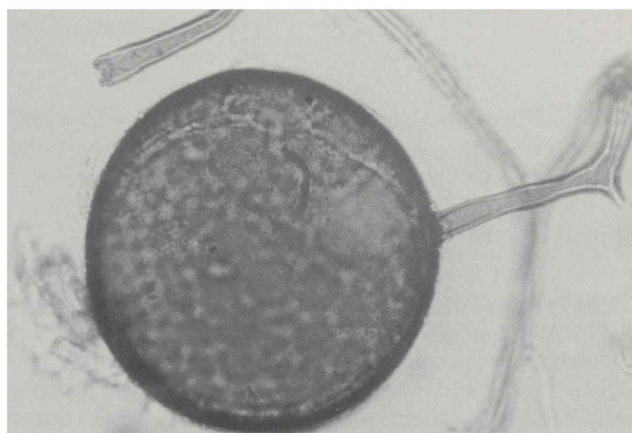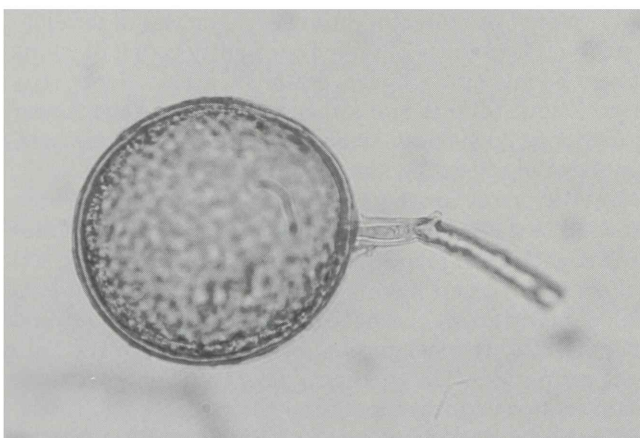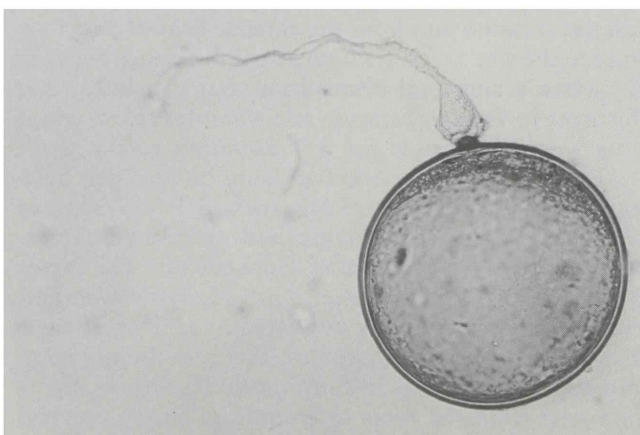
A number of desert plants such as Barrel Cactus, Saguaro, and Ocotillo produce multitudes of seeds but relatively few grow to maturity. In non-desert regions, competition has often been implicated as an important factor in non-establishment. Only one in a million seeds of Saguaro actually produces a giant cactus. Is this due to competition? Although ecologists often single out competition as a factor limiting plant establishment and growth in mesic and tropical regions, in the desert some plants seem often to establish better and to thrive in conjunction with other already established plants. Indeed, in the Sonoran Desert there are several examples of a plant species cohabiting in close proximity with a different species using the latter as a "nurse plant" or protector during early phases of development. Such frequently observed contiguity is that of young Saguaro cactus and a larger, established Palo Verde tree. Desert Zinnia (*Zinnia pumila*) and the yellow Paperflower (*Psilostrophe cooperi*) are frequently found in close association, particularly on highly alkaline, caliche soils.

Mortality rates among Palo Verde seedlings have been shown to be determined by soil moisture and not by competition with other plants (Shreve, 1917). Interestingly, soil pockets in the desert having enough soil moisture for Palo Verde establishment also have enough for grass growth and generally already have grasses established when the Palo Verde germinates. The successful new Palo Verde seems to obtain its mycorrhizal fungi from the grasses. The desert, with its brief periods of winter rainfall and alternating intervals of warm and cool air temperatures, favors growth of short-lived plants over extensive interconnecting areas, including some areas which are otherwise seasonally deserted of plant life. The short-lived plants seem to serve as bridges for passage of VA mycorrhizal fungi from one spot favorable for perennials to another. These ephemerals, such as winter grasses, mallow, filaree and others not only foster the growth and reproduction of endomycorrhizal fungi in their roots, but leave viable populations of spores in soil pockets where Palo Verde and other perennials eventually become established.

In a study of the Palo Verde and Saguaro association, Shreve (1931), working at the Desert Botanical Laboratory of the Carnegie Institution on Tumamoc Hill near Tucson, reported that the two species were frequently in contiguity and that in every case the Palo Verde was the older plant. He believed the relationship was due to better conditions for the young Saguaro which derived protection from mechanical injury and from the intense heat of direct exposure to the sun's rays. He found little difference between soil moisture and total evaporation, but concluded that differences in soil temperature and water loss from young cactus were responsible for its adaptation to the shade provided by Palo Verde. Another factor to consider, however, is that the association of Saguaro with Palo Verde may relate in part to the tree supplying the fungus for the cactus.

As opposed to the association of ephemerals, Palo Verde and Saguaro together, Creosote Bush (*Larrea tridentata*) occurs frequently in nearly pure stands, as does Triangle Leaf Bursage (*Franseria deltoides* Torr.), excluding competitive species of plants by forming clonal rings of plants which arise from the roots in a circle as large as several meters (Vasek et al., 1975). In addition, Creosote Bush pro-

duces an allelopathic response by excreting substances from its roots and leaves which preclude the establishment of other plants nearby (Adams et al., 1970). The progeny of the plant arise from roots of one plant forming clonal rings of plants up to several meters in diameter (Vasek et el., 1975). Sternberg (1975) has reported that genetically controlled peroxidase and acid phosphatase enzyme systems in each ring are the same, lending credence to the clonal system of dense stand formation. The finding cited above of VA mycorrhizal fungi in association with Creosote Bush is significant. In these clonal communities, where seed reproduction is less important, the relaying of mycorrhizal fungi along the network of roots is apparently sufficient without the complex passage from grass to tree to cactus which seems to operate in the association of ephemerals, Palo Verde and Saguaro.

In the case of the Palo Verde and Saguaro association, the Saguaro generally outlives the Palo Verde. When the Saguaro finally dies it rots and leaves a rich pocket of decomposed organic material. This soil pocket is quickly colonized by grasses and various ephemerals. Next comes Palo Verde, followed by another Saguaro. There is no reason to suppose that favorable sites have not had thousands of repeated cycles. The passage of VA mycorrhizal fungi through the succession of plants at such sites appears to be efficient and seems to have become an integral part of the succession phenomenon. Repeated seasonal growth, sporulation, and re-infection in cyclical fashion has significance for agriculture: just as native desert plants have been shown to benefit from high populations of VA mycorrhizal fungi and to serve as reservoirs for passing these fungi from plant to plant, so too have these natives served as reservoirs for passing fungi to introduced crop plants of agriculture as shown in Table 2. The fertility of desert soils for these agricultural crops is certainly enhanced by these indigenous populations of symbiotic microflora.

**References**

Adams, S., B. R. Strain, and M. S. Adams. 1970. Water-repellent soils, fire, and annual plant cover in a desert scrub community of southeastern California. *Ecology* 52: 696-700.

Allen, M. F. 1983. Formation of vesicular-arbuscular mycorrhizae in *Atriplex gardneri* (Chenopodiaceae): seasonal response in a cold desert. *Mycologia* 75: 773-776.

Bagyaraj, D. J., and J. A. Menge. 1978. Interaction between a VA mycorrhiza and *Azotobacter* and their effects on rhizosphere microflora and plant growth. *New Phytol.* 80: 567-573.

Bethlenfalvay, G. J., S. Dakessian, and R. S. Pacovsky. 1984. Mycorrhizae in a southern California desert: ecological implications. *Can. J. Bot.* 62: 519-524.

Bloss, H. E. 1982. Formation of mycorrhizae in *Plantago ovata*. *Mycologia* 74: 505-508.

Bloss, H. E., and C. M. Pfeiffer. 1984. Latex content and biomass increase in mycorrhizal guayule (*Parthenium argentatum*) under field conditions. *Ann. Appl. Biol.* 104: 175-183.

Burr, T. J., M. N. Schroth, and T. Suslow. 1978. Increased potato yields by treatment of seedpieces with specific strains of *Psuedomonas fluorescens* and *P. putida. Phytopathology* 68: 1377-1383.

Chapin, F. S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecological Systems* 11: 233-260.

Daft, M. J., E. Hacskaylo, and T. H. Nicolson. 1975. Arbuscular mycorrhizas in plants colonising coal spoils in Scotland and Pennsylvania. pp. 561-580 in F. E. Sanders, B. Mosse, and P. B.

Tinker (eds.), *Endomycorrhizas.* Academic Press. New York.

Fernandez, O. A., and M. M. Caldwell. 1977. Root growth of *Atriplex confertifolia* under field conditions. pp. 117-122 in J. K. Marshall (ed.), *The Below Ground Ecosystem: A Synthesis of Plant-associated Processes.* Colorado State University, Fort Collins, Colorado.

Fuller, W. H. 1975. *Management of Southwestern Soils.* University of Arizona Press. 195 pp.

Katznelson, H., E. A. Peterson, and J. W. Rovatt. 1962. Phosphate-dissolving microorganisms on seed and in the root zone of plants. Can. J. Bot. 40: 1181-1186.

Khan, A. G. 1974. The occurrence of mycorrhizas in halophytes, hydrophytes, and xerophytes, and of endogene spores in adjacent soils. J. Gen. Microbiol. 81: 7-14.

Kloepper, J. W., J. Leong, M. Teintze, and M. N. Schroth. 1980. Enhanced plant growth by siderophores produced by plant growth-promoting rhizobacteria. Nature 286: 885-886.

Lindsey, D. L., W. A. Cress, and E. F. Aldon. 1977. *The Effects of Endomycorrhizae on Growth of Rabbitbrush, Fourwing Saltbush, and Corn in Coal Mine Spoil Material.* U. S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. Research Note RM-343. 6 pp.

Medve, R. J., F. M. Hoffman, and T. W. Gaither. 1977. The effects of mycorrhizal-forming amendments on the revegetation of bituminous stripmine spoils. *Bull. Torrey Bot. Club* 104: 218-225.

Meyer, F. H. 1973. Distribution of ectomycorrhizae in nature and man-made forests. pp. 79-105 in T. G. Marks and T. T. Kozlowski (eds.), *Ectomycorrhizae–Their Ecology and Physiology.* Academic Press. New York.

Miller, R. M. 1979. Some occurrences of vesicular-arbuscular mycorrhizae in natural and disturbed ecosystems of the Red Desert. Can. J. Bot. 57: 619-623.

Moorman, T., and F. B. Reeves. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal population. *Am. J. Bot.* 66: 14-18.

Read, D. J. 1974. *Pezizella ericae* sp. nov. the perfect stage of a typical mycorrhizal endophyte of Ericaceae. *Trans. Brit. Mycol. Soc.* 63: 381-383.

Reeves, T. B., D. Wagner, T. Moorman, and J. Kiel. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural ecosystems. *Am. J. Bot.* 66: 6-13.

Safir, G. R., J. S. Boyer, and J. W. Gerdemann. 1972. Nutrient status and mycorrhizal enhancement of water transport in soybean. *Plant Physiol.* 49: 700-703.

Schwab, S. M., and F. B. Reeves. 1981. The role of endomycorrhizae in revegetation practices in the semi-arid west. III. Vertical distribution of vesicular-arbuscular (VA mycorrhiza inoculum potential. *Am. J. Bot.* 68: 1293-1297.

Shreve, F. 1917. The establishment of desert perennials. *J. Ecol.* 5: 210-216.

Shreve, F. 1931. Physical conditions in sun and shade. *Ecology* 12; 96-104.

Smith, S. E., and M. J. Daft. 1977. Interactions between growth, phosphate content and nitrogen fixation in mycorrhizal and nonmycorrhizal *Medicago sativa. Aust. J. Plant Physiol.* 4: 403-413.

Staffeldt, E. E., and K. B. Vogt. 1975. Mycorrhizae of desert plants. Progress Report of the Desert Biome. 1974 Progress Report pp. 61-69. Utah State University, Logan, Utah.

Stahl, P. D., and M. Christensen. 1982. Mycorrhizal fungi associated with *Bouteloua* and *Agropyron* in Wyoming sagebrush-grasslands. *Mycologia* 74: 877-885.

Sternberg, L. 1975. Growth forms of *Larrea tridentata. Madrono* 23: 408-417.

Vasek, F. C., H. B. Johnson, and D. H. Eslinger. 1975. Effects of pipeline construction on creosote bush scrub vegetation of the Mojave Desert. *Madrono* 23: 1-13.

Whitaker, R. H., and W. A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona. A gradient analysis of the south slope. *Ecology* 46: 429-452.

Williams, S. E., and E. F. Aldon. 1976. endomycorrhizal associations of some arid zone shrubs. *Southwest. Nat.* 20: 437-444.

Williams, S. E., and M. F. Allen. 1984. *VA Mycorrhizae and Reclamation of Arid and Semi-arid Lands.* Wyo. Agric. Exp. 8th. Rept. SA1261. 91 pp.