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, Comelinaeae, 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; Kloeper 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.), Siltkassel Bush (Garrya wrightii Torr.), Arizona Rosewood (Vauquelinia californica (Torr.) Sargent), Catclaw (Mimosa biuncifera Benth.), Fairy Duster (Calliandra etiophyla 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 cirratum Hack.), Cone Beardgrass (Andropogon barbinodis Lag.), Beggartick Grass (Aristida ocatricula Vasey), Spidertass (Aristida ternipes Cav.), Sideoats Grama (Bouteloua curtipendula (Michx.) Torr.), Hairy Grama (Bouteloua hisutla 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) Foothills Palo Verde (Cercidium microphyllum) (Torr.) Creosote Bush (Larrea tridentata) Coville, and two gramas 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 (Accacia 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 microscopic 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 Bur-sage (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...
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 var-
Figure 4. Site C west of Tucson included clonally reproduced 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 situations 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 tendency of such arid land plants to aggregate is attempted below in relationship to the theorized passage of mycorrhizal fungi in a ubiquitous [non-specific] manner from species to species. A further ubiquity seems to have been demonstrated 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-end types of fungi, such as Pezizella ericae [Read, 1974].

The presence of indigenous populations of VA mycorrhizal fungi, which are capable of forming symbiotic relationships 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 attributed 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 nutrient 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 increasingly important relative to diffusion of nutrients in controlling 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).

<table>
<thead>
<tr>
<th>Plant-Soil Association</th>
<th>Date of Collection</th>
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<tbody>
<tr>
<td><em>Manzanita—Arctostaphylos pungens H.B.K.</em></td>
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<tr>
<td>Gigaspora calospora [Nicol. &amp; Gerd.] Gerdemann &amp; Trappe</td>
<td></td>
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<tr>
<td>Acaulospora sp.</td>
<td></td>
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<tr>
<td>Acaulospora laevis Gerdemann &amp; Trappe</td>
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<tr>
<td>Acaulospora scrobiculata Trappe</td>
<td></td>
</tr>
<tr>
<td>Glomus constrictum Trappe</td>
<td></td>
</tr>
<tr>
<td>Glomus geosporum [Nicol. &amp; Gerd.] Walker</td>
<td></td>
</tr>
<tr>
<td>Glomus deserticola Trappe, Bloss &amp; Menge</td>
<td></td>
</tr>
<tr>
<td>Glomus etunicatum Becker &amp; Gerdemann</td>
<td></td>
</tr>
<tr>
<td>Glomus rigidicaulis Walker</td>
<td></td>
</tr>
<tr>
<td>Entrophospora infrequens Ames &amp; Schneider</td>
<td></td>
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<tr>
<td>16-IV-83</td>
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</table>

| Amole—Agave schottii Engelm. |
| Acaulospora scrobiculata Trappe |
| Entrophospora infrequens Ames & Schneider |
| Gigaspora sp. |
| Glomus etunicatum Becker & Gerdemann |
| Glomus geosporum [Nicol. & Gerd.] Walker |
| Glomus constrictum Trappe |
| Glomus deserticola Trappe, Bloss & Menge |
| Glomus mosseae Gerdemann & Trappe |
| 30-VI-83 |

| Weeping Lovegrass—Eragrostis curvula (Schrad.) Nees |
| Acaulospora sp. |
| Acaulospora scrobiculata Trappe |
| Glomus mosseae Gerdemann & Trappe |
| Glomus butleri Walker |
| Glomus geosporum [Nicol. & Gerd.] Walker |
| Glomus etunicatum Becker & Gerdemann |
| Gigaspora sp. |
| 12-VII-83 |

*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 mycorrhizal fungi on their roots. Mycorrhizal 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.

<table>
<thead>
<tr>
<th>Plant-Soil Association</th>
<th>Date of Collection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Under Grape Vitis vinifera L. (cultivated)</td>
<td>25-X-83 Tucson, AZ</td>
</tr>
<tr>
<td>Acaulospora scrobiculata Trappe</td>
<td></td>
</tr>
<tr>
<td>Gigaspora calospora (Nicol. &amp; Gerd.) Gerdemann &amp; Trappe</td>
<td></td>
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<tr>
<td>Glomus constrictum Trappe</td>
<td></td>
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<tr>
<td>Glomus etunicatum Becker &amp; Gerdemann</td>
<td></td>
</tr>
<tr>
<td>Glomus geosporum (Nicol. &amp; Gerd.) Walker</td>
<td></td>
</tr>
<tr>
<td>Glomus microcarpum Tul. &amp; Tul.</td>
<td>15-VIII-84 Tucson, AZ</td>
</tr>
<tr>
<td>Sclerocytis rubiformis Gerd. &amp; Trappe</td>
<td></td>
</tr>
<tr>
<td>Sclerocystis sinuosa Gerd. &amp; Bakshi</td>
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Mycorrhizal with roots of:
- Alfalfa: Medicago sativa L.
  - Glomus mosseae (Nicol. & Gerd.) Gerdemann & Trappe Yuma, AZ
- Gopher Weed: Euphorbia lathyris L.
  - Glomus intraradices Schenck & Smith Tucson, AZ
- Mariola: Parthenium incanum H.B.K.
  - Glomus deserticola Trappe, Bloss, & Menge Tucson, AZ
  - Glomus deserticola Trappe, Bloss, & Menge Tucson, AZ
- Soybean: Glycine max (L.) Merrill
  - Gigaspora calospora (Nicol. & Gerd.) Gerdemann & Trappe Yuma, AZ
  - Glomus geosporum (Nicol. & Gerd.) Walker
  - Glomus microcarpum Tul. & Tul.

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 visible 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, mallows, filamentous 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 produces 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 al., 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
Bloss Symbiotic Microflora 127