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Microbial dynamics in arid ecosystems: desertification and the potential role of mycorrhizas

Dinámica de microbios en ecosistemas áridos: desertificación y la posible función de las micorrizas

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ABSTRACT

In semiarid and arid ecosystems, structure and functioning of plant communities is regulated by the timing of moisture inputs and the abiotic factors affecting nitrogen availability. Soils of these regions support a large diversity of belowground microflora and microfauna which have a significant role in the functioning and stability of these ecosystems. Plants that have been studied from these habitats have very often been found to be mycorrhizal (89% of 61 plant families surveyed in arid and semi-arid regions world-wide were found to be mycorrhizal). This paper discusses mycorrhizal-plant interactions and their synergistic effects on plant growth and nutrient dynamics, and attempts to link changes in aboveground plant community dynamics in desert system to changes in the temporal and spatial dynamics of the root zone biota. Factors which directly or indirectly determine the occurrence of mycorrhizal propagules, are potentially important in subsequent plant establishment and diversity since various mycorrhizal fungi can have different physiological effects on their hosts. The successful establishment of plants and the maintenance of plant diversity may be also determined in the semiarid and arid environment by the presence of preferred/ appropriate mycorrhizal fungi. Without successful establishment and maintenance of appropriate mycorrhizal fungi, plant species composition and nutrient dynamics within semiarid and arid ecosystems can be altered, and lead to further degradation of these lands.

Key words: Rhizosphere, arid, mycorrhizae, fungi, mutualism.

RESUMEN

En ecosistemas semiáridos y áridos, la estructura y funcionamiento de la comunidad de plantas son reguladas por la humedad y los factores abióticos y bióticos que afectan la disponibilidad de nitrógeno. Los suelos en estas regiones contienen una gran diversidad de microflora y microfauna, las cuales tienen un papel importante en el funcionamiento y estabilidad de estos ecosistemas. Las plantas que han sido estudiadas provenientes de estos hábitat frecuentemente contienen hongos micorrizas. Este artículo tiene dos propósitos. En primer lugar, discute interacciones entre hongos y plantas, y sus efectos sinérgicos en el crecimiento de plantas y flujo de nutrientes. En segundo lugar, intenta asociar cambios en la comunidad de plantas en desiertos con cambios, tanto temporales y espaciales, en la biota de la zona radicular. Factores que determinan directa o indirectamente la presencia de esporas micorrizas, son potencialmente importantes en el futuro establecimiento de plantas, dado que varias micorrizas pueden tener diferentes efectos fisiológicos en sus hospederos. El establecimiento exitoso de plantas también puede estar determinado por la presencia de micorrizas preferidas o apropiadas. Sin el establecimiento exitoso y mantenimiento de micorrizas apropiadas, la diversidad de plantas y flujo de nutrientes en zonas áridas puede ser alterada.

Palabras claves: Rizosfera, árido, micorrizas, hongos, mutualismo.

INTRODUCTION

The process of desertification involves a sequence of events resulting in the impoverishment of and reduction in vegetation cover of a semiarid or arid region. A detailed study of the semiarid region of Coquimbo, Chile, showed that about 50% of the native plant species had disappeared as a consequence of desertification and that several shrub species dominated the deteriorating previously grass dominated landscape (Fig. 1) (Mabbutt & Floret 1980). Changes in vegetation and other biota in this region of Chile were related to altered land use practices (e.g., intensive agriculture, over-grazing, mining) and to a lesser

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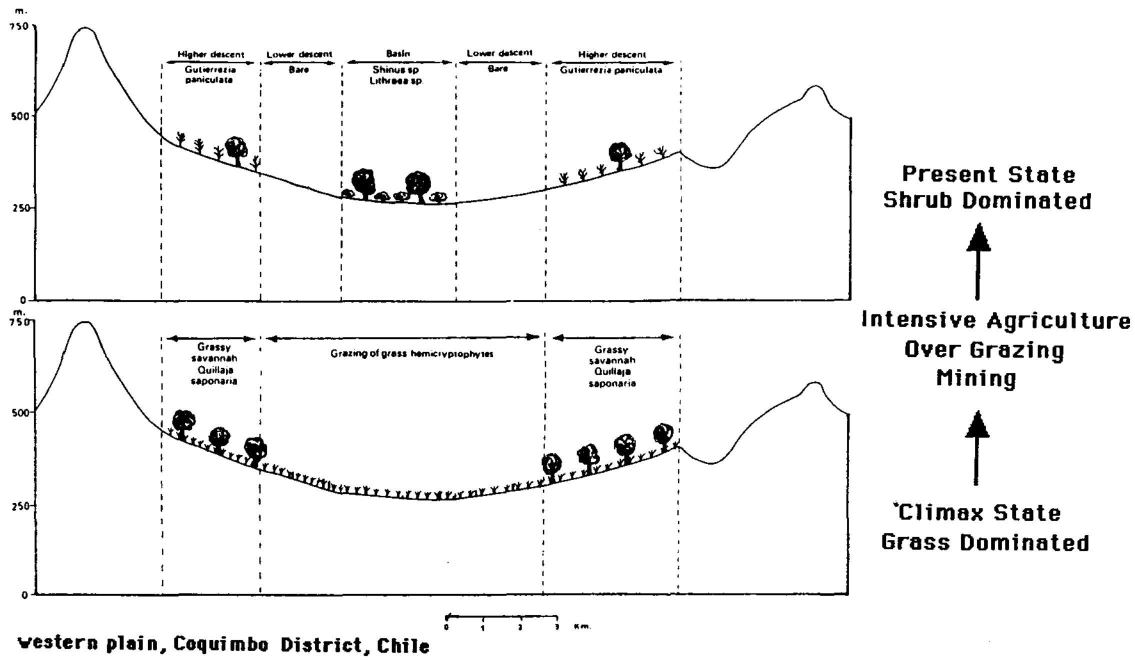

Fig. 1: Changes in vegetation in the semi-arid region of Coquimbo, Chile. Modified from Mabbutt & Floret 1980.

Cambios de la vegetación en la región semiárida de Coquimbo, Chile. Modificado de Mabbutt & Floret 1980.

degree to several drought periods spanning 2-5 years. Comparable deterioration has been documented in Rajastan, India, Eghazer and Azawak regions, Niger, Negev Sand Dunes, Israel, and several other regions of the world (see case studies in Mabbutt & Floret 1980, Heathcote 1983). Evidence from such case studies, some of which can be traced over centuries, demonstrate that the world's semi-arid and arid regions have experienced, and are continuing to undergo, changes towards more desertic conditions (Mabbutt 1984, Helldon 1988, Tsoar 1990). These studies do not provide evidence of a general decline of precipitation as a cause of desertification, although drought or long periods of below-average rainfall may be significant, as in India and the Sahel zone of Niger (Mabbutt & Floret 1980). Research to date has concentrated on anthropogenic effects, and has linked diminution of these semiarid and arid areas to over-exploitation by humans (United Nations 1977, Browman 1984, Karrar & Stiles 1984). The attempts to understand desertification processes and to develop proposals for reclamation and/or restoration have thus far been mainly centered on reverting land back to productive agricultural habitats (Tsoar 1990). Little focus has been placed on native faunal and floral reestablishment.

Although, in general, species diversity declines with increasing aridity (Noy-Meir 1973, 1985) the diversity of the fauna and flora of deserts is comparable to that observed in grasslands and temperate forests (see reviews in Polis 1991). Plant community structure of semiarid and arid regions is influenced by spatial and temporal variability of abiotic (e.g., soil physical characteristics, nutrients, organic matter, moisture, water holding capacity) and biotic (fauna, flora, seed bank, microbes) components of the ecosystem. This variability has been related to moisture and temperature patterns, and the availability of soil nitrogen (Gutiérrez & Whitford 1987a, b, Fisher *et al.* 1988). Several of these studies have suggested that desert biota (e.g., desert annuals, microarthropods) experience relatively rapid changes in patterns of distribution and abundance in relation to the variability in available N, moisture and temperature. For example, shifts from grassland to shrubland in Chihuahuan Desert watersheds resulted in increased temporal and spatial variability of essential resources (nitrogen and moisture) for plant production (Whitford *et al.* 1987). Such heterogeneity in resources influences first the distribution, abundance of particular taxa, then secondly the species composition and trophic relationships, and finally food web structures, community dynamics and landscape patterns (Coleman *et al.* 1988, Polis 1991) (Fig. 2).

In a paper on desertification and global implications of climate change, Schlesinger *et al.* (1990) focused attention on environmental heterogeneity of soil resources as the main determinant of the desertification process. They showed that for desert grasslands, any process which would concentrate water and available nitrogen promotes the invasion of the area by shrubs and leads to increased resource heterogeneity and further environmental degradation. The role that soil biota have in this degradation and the establishment of plants remains unclear, the study of soil biota constituting one of the largest gaps in our knowledge of degraded land reconstruction (Allen 1988). The need to understand the role and management of microorganisms is important, for example, Allen (1988) demonstrated the inoculation with mycorrhizal fungi can affect reestablishment of plant species and alter the outcome of succession trajectories. Few studies have attempted to link changes in above ground plant community dynamics in desert systems to changes in the temporal and spatial dynamics of the soil microflora and microfauna.

The focus of this paper is two fold. First, we will develop an argument for incorporating

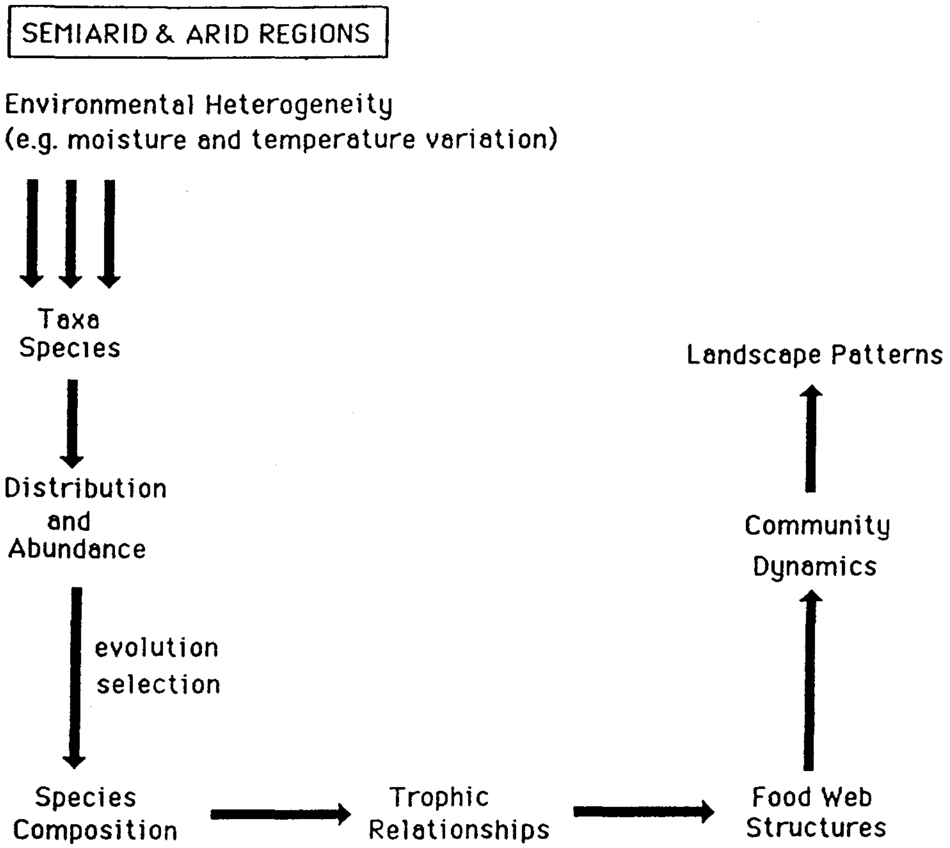

Fig. 2: The hierarchical integration of environmental heterogeneity and microfloral dynamics in structuring desert ecosystems. Influences of environmental heterogeneity on distribution, and abundance of the soil microflora and microfauna and of particular taxa ultimately affecting landscape patterns (developed from ideas presented by Coleman *et al.* 1988 and reviews in Polis 1991).

Integración jerárquica de variación ambiental y dinámica de la microflora en el desarrollo de ecosistemas desérticos. Las influencias de la variación ambiental en la distribución y la abundancia de microbiota del suelo (desarrollado de ideas presentadas por Coleman *et al.* 1988, Polis 1991).

plant-fungal interactions into discussions of desertification. Secondly, we will provide evidence for the feasibility and significance of such research esearch. We will concentrate on mycorrhizal-plant interactions and their synergistic effects on plant growth and nutrient dynamics. By discussing specific case studies, we will focus on fine scale processes and the extrapolation of these up the ecological hierarchy (Fig. 2) with an emphasis on developing potential mechanisms for understanding plant community dynamics and landscape patterns in semiarid and arid environments.

OVERVIEW OF BELOWGROUND PARAMETERS AND INTERACTIONS

Coleman *et al.* (1983) stressed the need for considering soil characteristics both on a macro-scale, landscape (catena), and on a micro-scale, soil aggregate, in order to understand ecosystem dynamics. The primary arena of biotic and abiotic interactions is the soil solution and pore space, which provide for diffusion of gases and liquids and movement of microbes and fauna (Skujins 1984, Foster 1988). Interactions among individual organisms and their immediate environments (fine-scale) might be modeled to predict the behavior of populations/communities (coarse-scale). Although difficult, it is important to identify the level of resolution where processes are occurring, and then attempt to identify and quantify the major biotic components involved in various processes. Spatial heterogeneity not only governs the aboveground or large scale phenomenon but also nutrient dynamics in belowground systems (e.g., Coleman *et al.* 1988). For example, Coleman *et al.* (1983) postulated that nutrient changes, via immobilization and mineralization, may occur in a temporal sequence along the rhizoplane (root surface) (see Fig. 3 for details). By establishing a nutrient translocating network of hyphae reaching spatially heterogenous nutrient pools, decomposing detritus/humus, root-zone fungi may assist plants in overcoming the restrictions to plant growth imposed by the spatial and teporal heterogeneity in nutrient availability (Fig. 3) (Coleman *et al.* 1983, 1988).

Bacteria, fungi, microarthropods and nematodes play a very important role in the cycling of carbon and nitrogen in desert systems (Whitford 1988, Zak & Whitford 1988, see Zak 1992 for reviews). Nutrient availability is internally coupled to microfloral-microfaunal activity, which in turn is regulated by moisture availability (e.g., Whitford & Freckman 1988, Zak & Whitford 1988). The significance of these interactions in desert soils cannot be over emphasized (see reviews in Polis 1991). In particular, microfloral-microfaunal interactions whithin the root region of desert plants may be crucial when plant demand exceeds mineralization rates by the microflora alone (Ingham *et al.* 1985). Blue grama grass in microcosms with bacteria and amoebae had a significant enhancement of ammonium N uptake (doubled) compared with those with plants with either bacteria or amoebae alone (Elliot *et al.* 1979). Grazing of bacteria and fungi in the root region by microarthropods and nematodes can increase nitrogen mineralization and influence plant growth (e.g., Coleman *et al.* 1984, Clarholm 1985). Several studies have also shown significant change in plant biomass and nutrient uptake in response to alteration of the root region microflora and microfauna (e.g., Coleman *et al.* 1984, Dhillion 1992a). Soil microfauna can alter the rates of substrate utilization and nutrient release by either mechanically processing litter and detritus or by direct grazing of fungi and bacteria. Microfauna can thus influence organic matter distribution and temporal heterogeneity of decomposer sites and ultimately decomposition processes (Coleman *et al.* 1983, see reviews in Polis 1991). Faunal grazing of fungi in soil and along the root surface should be considered an important mechanism determining nutrient flux belowground and in determining the microfloral dynamics. Numerous studies (e.g., Ingham 1988, McGonigle & Fitter 1988, Moore 1988, Moore *et al.* 1988) have shown that saprophytic and mycorrhizal fungi can be grazed by microarthropods and nematodes, and that these interactions can have negative and positive effects on plant growth. Moreover, at certain densities, microarthropod grazing can actually stimulate fungal growth and activity (e.g., Hanlon 1981, Moore *et al.* 1988) thus increasing mineralization rates of nitrogen in the root zone (see Fig. 3).

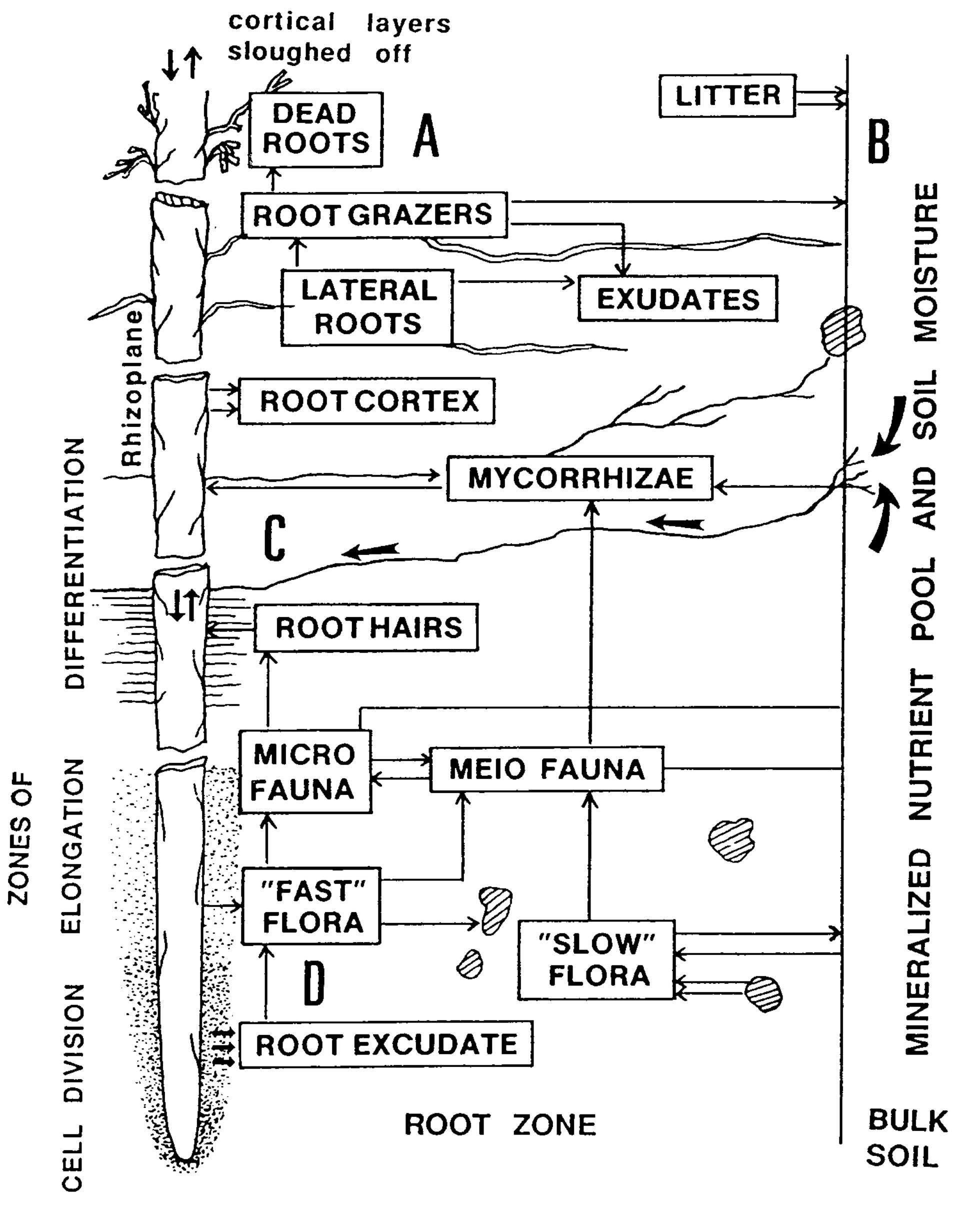

Fig. 3: Conceptual diagram of the interactions and activity occurring in the rhizosphere/ root zone. A: Region where cortical layers from old roots are sloughed off and where activity of root grazers and other soil microflora is high; B: Region beyond the root zone where mycorrhizae can act as extensions of the root system exploiting mineral and moisture pools; C: Region of the root where mycorrhizal penetration can take place and functional internal structures develop (e.g., arbuscules); D: Region of rapid changes among microflora and fauna associated with root exudates and the root tip. Microfauna and meiofauna grazing on microbes affect nutrient availability, for uptake by root and mycorrhizae, and microbes. (Modified by Dhillion (unpublished) from diagrams in Trofyrow & Coleman 1982, Coleman *et al.* 1983, Coleman *et al.* 1988).

Diagrama de las interacciones y actividad que ocurren en la rizosfera. A: región donde capas externas de raíces viejas se desprenden y donde la actividad de microflora es alta; B: región más allá de la zona radical donde las micorrizas pueden actuar como extensiones del sistema radical haciendo uso de los minerales y humedad presente; C: región de la raíz donde puede ocurrir la penetración de micorrizas y desarrollarse estructuras internas funcionales (arbúsculos); D: región de cambios rápidos en microbiota asociada con excreciones y punto de crecimiento de la raíz. Microbiota alimentándose de microbios afectan la disponibilidad de nutrientes. (Modificado por Dhillion (datos no publicados) de diagramas de Trofyrow & Coleman 1982, Coleman *et al.* 1983, Coleman *et al.* 1988).

Given the importance of the root region in nutrient dynamics, particularly in desert and semiarid ecosystems, we would emphasize that research on nutrient dynamics and plant growth include investigations of the microfloral-microfaunal interactions in the root region. Furthermore, the complex interface between the root surface (rhizoplane), root zone soil (rhizosphere) and non-root zone soil (bulk soil) should be viewed as a three dimensional construct (Fig. 3).

Field observations of roots show that root distribution is not uniform through soil, root biomass generally being greatest close to the surface. In a detailed study of root profiles in the semiarid regions of Rajastan, India, bacterial and fungal numbers and organic matter was closely associated with zones of highest root biomass regardless of depth, unlike earthworms numbers, and P and pH levels which were not related to any particular zone of depth (Table 1). Fungal numbers and organic matter also decreased with depth but had highest values within the root zone soil (Table 1). These bacterial and fungal numbers are comparable to those found in some grassland soils (Risser *et al.* 1981, Dhillion & Anderson 1993a, Dhillion personal observation 1990) and in other ecosystems (see McMahon 1981 for a review). In the Chihuahuan Desert of Southeastern New Mexico, root mass and nematodes numbers associated with mesquite (*Prosopis glandulosa*) decreased with depth (Freckman & Virginia 1989). Nematodes were found to maximum depth of recovered roots only at the playa site (11-12 m) and occurred as deep as 5-6 m at the arroyo, 2-3 m in a dune habitat, and 1-2 m in the blackgrama grassland and creosotebush sites (Freeckman & Virginia 1989). At the playa, 75% of the nematodes and 90% of roots were below 0.5 m, whereas, in the creosote bush system 79% of the roots and 99.7% of the nematodes were recovered in the upper 0.5 m of the soil. Total nematodes across all sites were highly associated with total soil N, NH_4^+, PO_4^{-3} but not NO_3^- or moisture. In a sand desert Virginia *et al.* (1986) reported that mycorrhizae accumulated up to

TABLE 1

Biotic and abiotic soil characteristics of that region of soil within which > 40% of the root biomass occurred for selected plant taxa. Samples were taken from a semiarid region of the Jodhpur district, 10 km south-west of Jodhpur city, Rajastan, India (Dhillion, unpublished data)

Características bióticas y abióticas para esa región del suelo en la cual > 40% de la biomasa de raíz estaba presente. Las muestras provienen de una región semiárida del distrito de Jodhpur, 10 km al suroeste de la ciudad de Jodhpur, Rajastan, India (Dhillion, datos no publicados)

Plant species (numbers of samples observed)	Depth of soil (m) with largest root biomass (> 40%)	Nº of Earthworm per kg of soil[a]	Nº of Collecbolans per 10 g of soil[b]	Bacterial numbers $(x10^6)$ per g of soil[c]	Fungal numbers $(x10^3)$ per of soil[b,c]	P (µg/g)[a]	Organic Matter (%)[b, c]	pH[a]
Prosopis cineraria[1] (5)	1-2	1.2	20	3.6	2.4	7	0.5	6.7
Acacia senega[1] (7)	1-1.75	0.3	8	0.8	1.6	10	0.3	7.2
Acacia nilotica[1] (5)	0.5-1.25	1.4	12	1.9	3.2	4	0.3	6.3
Indigofera oblongifolia[1] (3)	0.75-1.25	0.5	26	1	1.7	3	0.2	5.4
Tephrosia purpurea[1] (12)	1.75-2.5	0.2	5	0.7	1	2	0.2	6.5
Tamarix articulata[2] (10)	0.25-0.50	2	67	3	4.2	2	0.5	6.5
Tecomella undulata[3] (7)	0-0.25	2	18	2	3	2	0.6	6.8
Zizyphys nummularia[4] (5)	0.25-0.75	4	19	1.2	2.1	3	1.4	5.3
Capparis decidua[5] (7)	0.25-0.75	2.3	37	1.1	2.3	5	1.2	6.8
Cenchrus ciliarus[6] (15)	0-0.20	4.3	56	9.3	3.5	11	0.7	7.4
Cenchrus setigerus[6] (15)	0-0.25	10.2	82	6.4	8.3	9	1.2	7.9
Lasiurus sindicus[6] (15)	0-0.50	5.3	59	5.3	7.2	10	1.8	4.6
Sporobolus marginatus[6] (15)	0-0.20	2.6	42	6.2	12	10	0.8	6.9

Family = [1]Fabaceace, [2]Tamarixaceae, [3]Bignoniaceae, [4]Rhamnaceae, [5]Capparidaceae, [6]Poaceae.

All woody plants sampled were of similar age.

[a] Values varied and no trends were detected with increase in depth.

[b] Values decreased with depth in bulk and root zone soil.

[c] Highest values were associated with highest root density (per cm3 of soil) and biomass.

4 m in a nutrient-rich zone immediately above the water table. These studies reveal that root distribution and associated microfloral-microfaunal component are distributed at various depths of the soil with distribution varying according to the plant species. The varying niches/zones occupied by plants belowground reduce interspecific competition for resources and can lead to increase in diversity of coexisting species. Deep roots can provide access to soil moisture and may increase nutrient uptake by the plant, particularly if infected by roots symbionts such as rhizobia and mycorrhizal fungi (Virginia *et al.* 1986). Semiarid and arid soils clearly support a large diversity of organisms, at varying depths, and it is likely that the belowground microflora and microfauna play a significant role in the functioning and stability of these ecosystems.

MYCORRHIZAS

The primary stresses imposed on vegetation in arid environments are the lack of optimum moisture for the majority of the year and low availability of nitrogen during periods of optimal temperature and moisture (see review by Zak & Freckman in Polis 1991). Any organism or life history strategy that is able to help plants ameliorate these stresses, to any degree, will render these plants more successful than those without the association. Mycorrhizas are one example of a plant-fungal association that is found in plants under a range of abiotic conditions (for recent indepth reviews on mycorrhizae see Safir 1987, Allen 1991, Brundrett 1991). Mycorrhizal symbiosis occurs in a vast majority of vascular plants except for members of a few families, including Cruciferae, Brassicaceae and Zygophyllaceae (Newman & Redell 1987, Dhillion & Friese in press). Mycorrhizas are divided into four groups according to external and internal morphology of the root-fungus association, (1) Vesicular-arbuscular mycorrhizal (VAM) fungi (associate with mostly herbaceous and some woody species), (2) Ectomycorrhizae (associate with almost entirely woody species), (3) Ericaceous (associate mainly with members of the Ericaceae) and (4) Orchidaceous (associate with members of the Orchidaceae).

Ectomycorrhizae are formed by plants associated with ascomycetes and basidiomycetes. While this symbiosis is common in mesic environments, ectomycorrhizae are less frequently reported in arid and semi-arid regions (Trappe 1981). For example several desert truffle forming fungi, from Africa and the Arabian peninsular have been found to form ectomycorrhizas (Trappe 1981). Although desert truffles and other basidiomycete members occur in deserts of South Africa, Central America, west-central India and southwest USA (e.g., Trappe 1981, Zak & Whitford 1986) their mycorrhizal associations are unknown (Trappe 1981, Zak & Dhillion-personal observations 1991). Unlike VAM, which are considered to be ecologically obligate biotrophs, ectomycorrhizas are capable of decomposing organic matter and can be important in nitrogen and water transport to the host plant.

Vesicular-Arbuscular Mycorrhizae

Vesicular-arbuscular mycorrhizal (VAM) fungi are found associated with about 90% of the world's herbaceous species (Malloch *et al.* 1980). Eigthty-nine percent of 61 plant families surveyed in arid and semi-arid regions worldwide were found to be mycorrhizal (Table 2), with 84% of the families surveyed forming exclusively VAM associations. However, these data reveal that only 69% of the species sampled (total of 338) were mycorrhizal. This small percentage of mycorrhizal species is due to the large number of species (105 species) that belonged to nonmycorrhizal families, e.g., Chenopodiaceae, Brassicaceas (Table 2). It is, however, imperative to realize that several data presented in Table 2 were extracted from studies where, (1) few samples were examined for mycorrhizae (< 5 samples), and (2) sampling was done only once during the growing season, i.e., not only lacking in the documentation of seasonal variation in VAM colonization, but also questioning the actual mycorrhizal status of species, especially of those classified as nonmycorrhizal. While nonmycorrhizal plants may also be apparently dominant members of plant communities in desert ecosystems, it is clear that mycorrhizas, especially VAM, may potentially play an important role in these ecosystems and warrant detailed study.

TABLE 2

Mycorrhizal status of plant families from semi-arid and arid regions#. The general mycotrophic nature (considering all habitats) of the family is represented as: – Largely nonmycorrhizal, ± Represented by both mycorrhizal species and nonmycorrhizal members, ++ Largely mycorrhizal family, UC-Uncertain status due to too few species observed. The type of mycorrhizas generally found associated with members of the family can be either vesicular-arbuscular (VAM) and/or ectomycorrhizal types (ECM)

Estado de micorrización de familias de plantas provenientes de regiones semiáridas y áridas#. La naturaleza de las micorrizas (considerando todos los hábitat) de la familia está representada por: – Mayormente sin micorrizas, ± Representada por especies con y sin micorrizas, ++ Mayormente familia con micorrizas, UC-Estado desconocido ya que muy pocas especies han sido estudiadas. El tipo de micorrizas asociado con miembros de la familia puede ser vesículo-arbuscular (MVA) y/o ectomicorrizas (ECM)

PLANT FAMILY (Total number of species examined)	Number of mycorrhizal species (*)	Number of nonmycorrhizal species (*)	General mycorrhizal nature of family and predominant type of mycorrhiza found in the family
Agavaceae (5)	3	2	UC, VAM
Amaranthaceae (2)	0	2	±, VAM
Anacardiaceae (3)	3	1	UC, VAM
Apocynaceae (2)	2	0	++, VAM
Asclepiadaceae (3)	3	0	++, VAM
Asteraceae (47)	47 (2)	0	++, VAM
Boraginaceae (6)	5	1	++, VAM
Brassicaceae (16)	0	16	–, VAM
Cactaceae (7)	5	2	±, VAM
Capparidaceae (4)	0	4	–, VAM
Caprifoliaceae (1)	1	0	UC, VAM
Caryophyllaceae (2)	0	2	UC, VAM
Casuarinaceae (1)	1	0	±, VAM & ECM
Chenopodiaceae (36)	5	31 (2)	–, VAM
Cistaceae (2)	2	0	UC, VAM
Convolulaceae (3)	2	1	±, VAM
Cruciferae (10)	0	10	–, VAM
Cucurbitaceae (1)	0	10	–, VAM
Cupressaceae (3)	3	0	±, VAM
Cyperaceae (2)	1	1	–, VAM
Eleagnaceae (3)	2	1	±, VAM
Euphorbiaceae (5)	3 (1)	2	++, VAM
Fabaceae (32)	31 (4)	1 (1)	++, VAM & ECM
Fagaceae (3)	3	0	++, ECM
Fouquieriaceae (2)	2	0	±, VAM
Geraniaceae (1)	1	0	++, VAM
Gnetaceae (1)	1	0	±, VAM
Iridaceae (1)	1	0	++, VAM
Labiatae (1)	1	0	UC, VAM
Liliaceae (3)	3	0	++, VAM
Malvaceae (2)	2	0	++, VAM
Nyctaginaceae (1)	0	1	UC, VAM
Oleaceae (3)	1	2 (2)	UC, VAM
Onagraceae (1)	1	0	++, VAM
Orobanchaceae (1)	1	0	UC, VAM
Oxalidaceae (1)	1	0	±, VAM
Palmae (2)	1	1	UC, VAM
Papaveraceae (1)	0	1	±, VAM
Pinaceae (2)	0	2	++, VAM
Plantaginaceae (5)	5	0	++, VAM
Plumbaginaceae (1)	1	0	++, VAM
Poaceae (38)	38	0	++, VAM
Polemoniaceae (4)	4	0	++, VAM
Polygonaceae (15)	6 (2)	9 (1)	±, VAM
Portulacaceae (1)	0	1	–, VAM
Ranunculaceae (1)	1	0	–, VAM
Rhamnaceae (5)	4	1	±, VAM & ECM
Rosaceae (8)	8 (1)	0	++, VAM
Rubiaceae (1)	0	1	±, VAM

PLANT FAMILY (Total number of species examined)	Number of mycorrhizal species (*)	Number of nonmycorrhizal species (*)	General mycorrhizal nature of family and predominant type of mycorrhiza found in the family
Salicaceae (5)	5	0	++, VAM & ECM
Salvadoraceae (2)	2	0	UC, VAM
Sapindaceae (1)	1	0	UC, VAM & ECM
Saxifragaceae (3)	3	0	±, VAM
Scrophulariaceae (8)	6	2	±, VAM
Solanaceae (6)	5 (2)	1	++, VAM
Tamaricaceae (4)	1	3	–, VAM
Urticaceae (2)	0	2	±, VAM
Verbenaceae (1)	1	0	++, VAM
Yuccaceae (3)	3	0	++, VAM
Zygophyllaceae (8)	2	6	UC, VAM

\# These data are a summary of a complete list of semi-arid and arid mycorrhizal species (Dhillion - unpublished data) compited from Nicholson 1960, Williams & Aldon 1976, Miller 1979, Rose 1981, Trape 1981 (contains a list of references and mycorrhizal taxa of semi-arid and arid regions), Pendleton & Smith 1983, Bloss 1985, Bloss & Walker 1987, Allen & Allen 1986, Newman *et al.* 1986, Newman & Reddell 1987, Neeraj *et al.* 1991, Dhillion & Zak personal observations 1991.

* Number of plant species for which only a single sample was examined for mycorrhizal associations.

Mycorrhizal hyphae, like roots, have important characteristics for the uptake of nutrients e.g., root characteristics such as (1) absorbing power for ions in solution, (2) abundance and distribution, and (3) an effective radius. Different root branch and root diameter (size) classes can be preferentially colonized by mycorrhizas (e.g., In the Chihuahuan Desert-Staffeldt & Vogt 1975, Dhillion & Zak unpublished data. In grassland species - Anderson & Liberta 1987, Miller & Jastrow 1990). Reinhardt & Miller (1990) working on prairie grasses indicated that the proportion of root length colonized by mycorrhizae increased with root diameter, indicative of the increase in the cortical tissue present in the roots for colonization.

Plants associated with VAM fungi show a varied response, ranging from mutualistic to parasitic, to colonization by these fungi. The type of response observed in mycorrhizal plants can depend on one or several factors including available soil moisture, inorganic nutrient availability, substrate pH, VAM fungal species, type of host plant root system, plant host species, age of host plant, time of year, irradiance and soil associated microorganisms (e.g., Buwalda & Goh 1982, Fitter 1985, Hetrick *et al.* 1988, Anderson & Liberta 1992, Dhillion 1992a, 1992b, Dhillion & Ampornpan 1992, Dhillion & Anderson in press, 1993, Meredith & Anderson 1992). In mutualistic associations, the host plant receives inorganic nutrients and water in exchange for carbohydrates. The host plant is generally considered the sole source of carbohydrates for the fungus. Plants benefitting from this association have greater tolerance to drought stress, higher photosynthetic rates, biomass production and inorganic nutrient accumulation (uptake) than nonmycorrhizal plants of the same species (e.g., Safir *et al.* 1971, Allen & Allen 1986, Dhillion & Ampornpan 1992). VAM may be of special importance in arid regions because of the impact of this symbiosis on plant drought tolerance and nutrient uptake (Allen & Allen 1986, Allen 1991). The fungal hyphae extend beyond the root hair zone and exploit nutrient rich regions and/or bridge these high nutrient microsites to nutrient depleted regions near the root (Fig. 3). The fungi thus function as a supplemental root system for the plant and increase the volume of soil that would normally be available for nutrient extraction to the plant. The positive effects of mycorrhizae are associated with low availability of inorganic nutrients, especially phosphorous and nitrogen. Colonization levels of roots by VAM fungi are generally inversely related to the availability of these inorganic nutrients (e.g., Miller *et al.* 1986, Dhillion & Ampornpan 1992). A negative response to VAM fungi and lower colonization levels may thus be expected if nutrient availability is high. Even when nutrient availability is low, a mycorrhiza well ramified through soil could be significantly important in relation to competition for nutrients and/or moisture by other microorganisms. Both field and laboratory studies have demonstrated that proliferation of VAM hyphae occurs in microsites high in organic matter and nutrients (Jackson & Caldwell 1989). Although the number of species studied is small, studies have shown that mycorrhizal links can occur between annuals, herbaceous perennials or tree species, and not even be restricted to the same taxon or family (see Newman 1988 for a review). By aiding in the extraction of soil nutrients by an individual plant mycorrhiza (or sharing between plants) can alter plant population and community dynamics affecting plant-plant interactions and ultimately succession trajectories (Allen & Allen 1990)

The role that mycorrhizas play in structuring plant communities is thought to be important through processes such as plant competition, phenology and interspecific nutrient transport through hyphal links, although there are accounts of null or negative mycorrhizal effects (e.g., Allen 1991, Brundrett 1991). The successful invasion of South Africa by *Acacia saligna* was associated with mycorrhizal activity (Hoffman & Mitchell 1986). There is growing evidence both from laboratory and field data suggesting that VAM may be important in maintaining and promoting plant species diversity. Gange *et al.* (1990) demonstrated that the reduction of mycorrhizal infection (using a fungicide, iprodione) in the field resulted in a decrease in plant species diversity. Furthermore, mycorrhizae can increase plant diversity in early succession communities by allowing nonmycotrophic (do not form mycorrhizas) species to exist where inoculum is low or not present and mycotrophic species to predominate where inoculum is high (Allen 1988). The most likely ways in which increase in species diversity can might occur are, at the seedling stage when mycorrhizal infection can occur rapidly, through effects on seedling establishment and/or competition (Gange *et al.* 1990). Seedlings face a problem of resource allocation between shoot and root growth, mycorrhizal infection could alleviate this problem and thus be of benefit (competitive advantage) to a plant (Fitter 1985). In field studies several plant species have been shown to exhibit host-endophyte preference or 'ecological specifity' when associated with indigenous mycorrhizae (Giovannetti & Hepper 1985, Henkel *et al.* 1989, McGonigle & Fitter 1990, Dhillion 1992b, 1992c, Sanders & Fitter 1992). The degree of plant-VAM specificity (measured as colonization and sporulation levels and/or fungal morphology) has been related to plant dependence on native VAM species (e.g., Giovanetti & Hepper 1985, Henkel *et al.* 1989, Dhillion 1992b, 1992c, Sanders & Fitter 1992). It has been hypothesized that in native plant communities, endophyte preference and dependence suggest that selection favoring certain fungus-plant combinations occurs (McGonigle & Fitter 1990, Dhilion 1992b, 1992c, Sanders & Fitter 1992). It is therefore likely, if this apparent preference exists, that in plant communities, VAM may affect aspects of plant establishment and growth dynamics. However, we caution that phenomenon such as degree of specificity/preference or ecological specificity can only be adequately investigated under natural conditions when we are able to identify with certainty specific VAM fungi within roots of plants.

Animal disturbances at a variety of scales can influence the occurrence of mycorrhizal propagules, which in turn may preferential increase or decrease seedling establishment. McIlveen & Cole (1976) found viable mycorrhizal spores in ant and earthworm casting materials on the soil surface and identified viable spores in the gut contents of earthworms. Allen *et al.* (1984) noted in soils that were not deeply buried by the volcanic ash from Mount St. Helens, gopher mounds contained old soils, which introduced mycorrhizae and other residual organisms to the tephra surface. These mounds became sites of enhanced plant establishment because of both improved nutrient status and the presence of beneficial mycorrhizal fungi capable of initiating a mutualistic association with the invading plants (Andersen & MacMahon 1985). On sand shinnery-oak (*Quercus havardii*) sites in west Texas, rabbit mounds soils were found to have greater root material, higher mycorrhizal spore densities, numbers of microorganism and fungal hyphal lengths than non-mound soils (Dhillion *et al.* in press) (Table 3). Burrowing by porcupines in Israel (Shachak *et al.* 1991) and a herbivorous rodent in Chile (Contreras & Gutiérrez

TABLE 3

Comparisons of selected constituents of mound and off mound soils of western cottontail (*Sylvilagus auduboni*) burrows in sand shinnery-oak (*Quercus havardii*) sites in west Texas*

Comparaciones de constituyentes seleccionados en montículos de cuevas de conejos (*Silvilagus auduboni*) y fuera de los montículos en sitios con robles (*Quercus havardii*) en Texas*

Mound characteristics	Mound	Off Mound	Significance
Root pieces - g per 100 g of soil	5.8	2.6	***
VAM spores - counts per 100 g of soil	43	27	ns
Hyphal lengths - cm per 100 g of soil	1,669	1,035	**
Total bacteria - colony forming units per 10 g of soil	16×10^7	12×10^7	**
Total fungi - colony forming units per 10 g of soil	21×10^3	14×10^3	***

* Dhillion *et al.* in press.

** $p < 0.01$.

*** $p < 0.001$.

1991) was found to increase plant biomass, propagule number and germination. Species composition and plant cover on kangaroo rat mounds in a Chihuahuan Desert grassland differed from those on intermound soils, and soil nitrogen content was consistently higher in mound soils than in intermound soils (Moorhead *et al.* 1988). Ant nests can also represent and important disturbance that may significantly affect mycorrhizal dynamics in the immediate vicinity of the nest. The ant mount nest enrichment hypothesis (Culver & Beattie 1983, Friese & Allen 1993) states that ant activity creates sites higher in nutrients and microbes than the surrounding soils and that these nutrient rich sites are beneficial to the establishment and fitness of any undamaged, relocated seeds once the mounds are abandoned. Mounds built by *Lasius flavus* were found to maintain a range of short-lived plant species in a calcareous grassland community in England which would otherwise probably become extinct (Woodell & King 1991). For instance, seeds of *Arenaria serpyllifolia* exhited 41% germination on ant mounds and only 5% on off mound areas (Woodell & King 1991). Within the mounds of the western harvester ant (*Pogonomyrmex occidentalis*), in Wyoming, USA, root proliferations was observed, and the resultant root mats produced by ant clipping had higher mycorrhizal inoculum levels than the surrounding soils (Friese & Allen 1993). It is, therefore, reasonable to assume that in the above cases, mycorrhizal propagules present in these displaced soils could influence the plant species establishment, composition and ultimately plant community diversity.

A number of anthropogenic and natural disturbances, including tillage, drought, erosion and fire, can influence fungal diversity substantially by the reduction or elimination of mycorrhizal propagules (Pendleton & Smith 1983, Allen 1988, Allen 1991, Brundrett 1991). A serious problem related to the loss of mycorrhizal propagules in arid lands is that a large proportion of the early colonizing species are nonmycotrophic annual species belonging to families such as the Brassicaceae and Chenopodiaceae (Allen & Allen 1988, Allen 1989). These plants, abundant in semiarid and arid regions, are adapted to growth in desertified soil. The continued presence of nonmycotrophic annuals precludes mycorrhizal establishment (Allen 1989) and can take several years (6-15) before mycorrhizal species start establishing (Allen & Allen 1988). Several studies have shown that it is the harshness of the site (e.g., characterized by its position on the landscape, topsoil application or burn condition) which determine whether annuals act as facilitators of or competitors to colonizing/invading mycotrophic species (e.g., Pendleton & Smith 1983, Allen & Allen 1988, Allen 1989). It is therefore essential that the heterogeneity of the landscape is understood before any changes are suggested for reclamation or restoration (Allen 1989). In semiarid and arid regions, the patchy distribution of fungal propagules in roots, soils and plant communities, activities of other organisms transporting or consuming these propagules, and local and seasonal environmental fluxes affecting abundances of propagules and the lack of well documented studies of seasonal dynamics of mycorrhizas also add to the complexity of and hinder efforts to the implementation of successful remedies for degraded arid systems (Allen 1991, Brundrett 1991).

Mycorrhizal dynamics - VAM case studies

To effectively ascertain the roles of VAM in desert and semi-arid ecosystems, the dynamics of the symbiosis should be followed in relation to the life history strategy of each choosen plant taxa. For annual plants, root samples should be collected over the life of the plant, with particular attention given to the seedling stage and periods when plants may experience physiological stress. Sampling of perennial plants should also correspond to important phenological events (e.g., periods of active root growth; leaf production and flowering) and follow moisture inputs that would be sufficient to activate belowground activity. Detailed sampling for annuals and perennials throughout the growing season will provide the most comprehensive details of the mycorrhizal-plant growth dynamics, which can be used to determine the role of mycorrhizas in plant survival strategies, patterns of plant establishment and distributions at a variety of scales.

In this last section of the paper we present the mycorrhizal data for four plant species adapted to xeric conditions; one from a dry-mesic sand prairie in Illinois and three from the Chihuahuan Desert, in order to indicate the types of information that can be obtained with the suggested approaches. Prickly pear cactus (*Opuntia humifusa* (Raf.) Raf.) was sampled on two sand prairie sites in west-central Illinois during the 1987 growing season. Sand prairies comprise of the dry and dry-mesic regions of the North American tallgrass prairie and are dominated by plant species (e.g., *Schizachyrium scoparium* (Michx.) Nash, *O. humifusa*) adapted to xeric conditions (Dhillion *et al.* 1988, Dhillion & Anderson 1993). Twelve cactus pads were sampled on each site per sampling date to obtain root length and VAM colonization (field sampling and laboratory techniques are similar to thus reported in Dhillion 1991). *Opuntia humifusa* root lengths increased rapidly, peaking in June, suggesting extensive root growth during this period and declined towards the end of the growing season (Fig. 4). Specific root length data (cm/g) showed that the rapid increase in late spring to early summer (April-June) and the subsequent decline was due to a decrease in fine root biomass (Dhillion unpublished data). VAM colonization on the other hand gradually increased towards August and declined through October. Mycorrhizal colonization apparently does not seem to be related to spore densities associated with the root zone of *O. humifusa*, which increased towards the end of the growing season (Dhillion unpublished data). The low colonization by VAM may be due to the fungi not keeping up with the rapid fine root growth early in the growing season (May-June). The results suggest that *O. humifusa* plants support lower levels of mycorrhizal fungal biomass during the period of extensive root growth (April-June), but higher levels when warmer temperature and lower moisture availability may significantly stress these plants (late June onwards). The VAM association may be beneficial to these plants, the fungi being able to assist in water and nutrient uptake during harsh periods (periods of high physiological demands) (Dhillion & Anderson 1993). In contrast, however, it is possible that under similar conditions, plants with higher VAM colonization levels may experience greater stress, and thus have lower water- and nutrient-use-efficiencies, than plants with low or no VAM colonization, due to their larger loss of photosynthates to the fungal symbionts (Dhillion & Anderson 1993).

The three plant species choosen to represent VAM dynamics in the Chihuahuan Desert; *Bouteloua eriopoda* (Torr.) Torr.; *Larrea tridentata* (D.C.) Cov. and *Xanthocephallum sarothrae* (Pursh.) Shinners. were sampled over one growing season along an elevational gradient at the Jornada Long Term Ecological

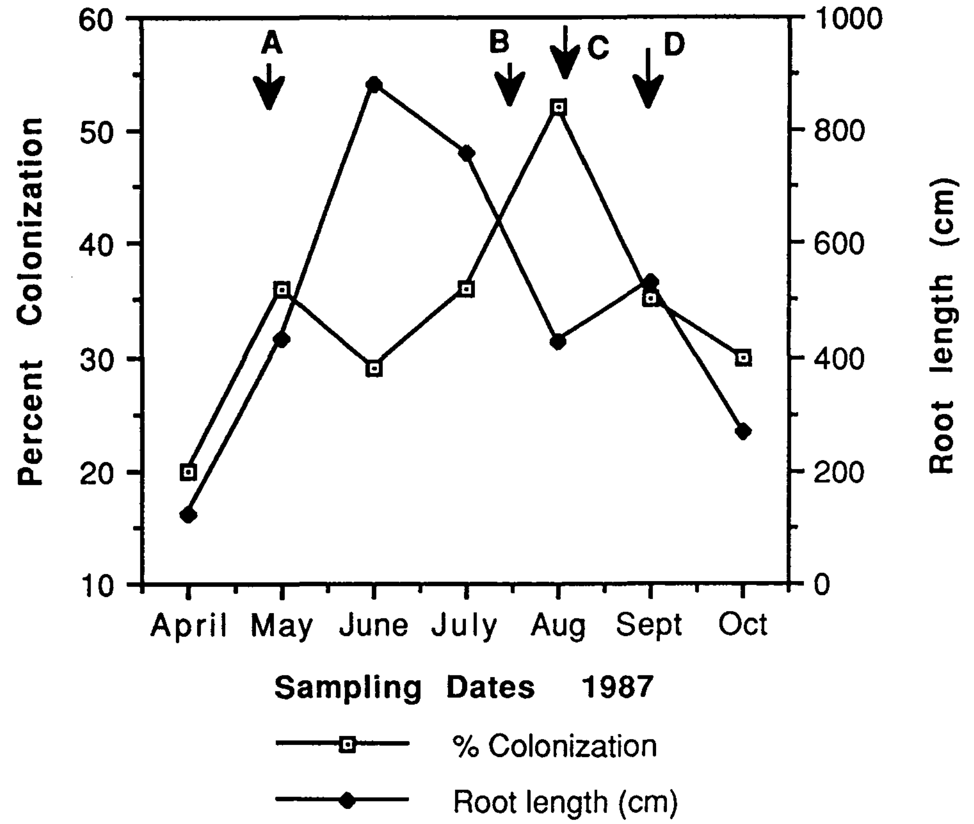

Fig. 4: Mean total root length (cm) and proportion of root length colonized (%) by VAM fungi of prickly pear cactus (*Opuntia humifusa* var *humifusa*) on sand prairie in west-central Illinois, USA. The arrows indicate the phenological stage of *O. humifusa* during the sampling period. A: New growth of cladodes and roots; B: Peak Biomass; C: Flowering; D: Fruit formation and seed dispersal (Dhillion unpublished data).

Longitud de raíz promedio (cm) y porcentaje del largo de radicular colonizado por hongos MVA (%) de *Opuntia humifusa* var *humifusa* en praderas arenosas de Illinois, USA. Las flechas indican el estado fenológico de *O. humifusa* durante el período de muestreo. A: Nuevo crecimiento de cladodios y raíces; B: Máxima producción biomasa; C: Floración; D: Formación de frutos y dispersión de semillas. (Dhillion datos no publicados).

Research site near Las Cruces, New Mexico, USA. Ten plants were sampled per collection date. Given that these three taxa are C_4 species common to semiarid and arid regions, root growth, not unexpectedly, was found to peak from summer to early autumn. This time period also corresponds to the end of the rainy season for this part of the Chihuahuan Desert (see McMahon 1981). The pattern in root growth observed for *L. tridentata* was consistent with the data presented by Fisher *et al.* 1988. Using root-in-growth tubes, Fisher *et al.* (1988) found the greatest root growth occurred from August to October. While there were definite peaks in root growth, VAM development did not vary substantially over the growing season for either *B. eriopoda* or *L. tridentata* (Fig. 5). Moreover, VAM development of these two species was low with only a minor component of the root system colonized. In contrast, VAM root lengths of *X. Sarothrea* were highest in January and subsequently declined through May remaining constant for the remainder of the year. However, like the VAM status of *B. eriopoda* and *L. tridentata*, VAM development in *X. sarothrea* was low. The low but consistent levels of VAM in these three species suggests that for perennials in desert environments, an efficient strategy for optimizing the benefits of VAM relationships would be to maintain low but consistent levels of the endophyte. With plant growth highly limited by moisture availability, a low but active VAM biomass would be able to take advantage of random, moisture inputs and not impose a significant carbon drain on the plant during periods of suboptimal moisture when soils are event too dry for VAM to be a benefit. Similarly, plants with a low but consistent levels of VAM colonization would not be constrained by a lag in VAM development if the symbiosis had to reestablish each time there was sufficient moisture for plant growth. Therefore the periodic benefits of the VAM association may outweight the consistent but low carbon drain to VAM, and may in fact have a net gain to these plants. Also, over the long term, the low level of VAM, but low carbon cost strategy would be more effective for a perennial plant species. Annual plants on the other hand may be expected to maximize mycorrhizal development during that part of their life cycle when the benefits of VAM would significantly increase their fitness, either during the seedling stage or during seed development.

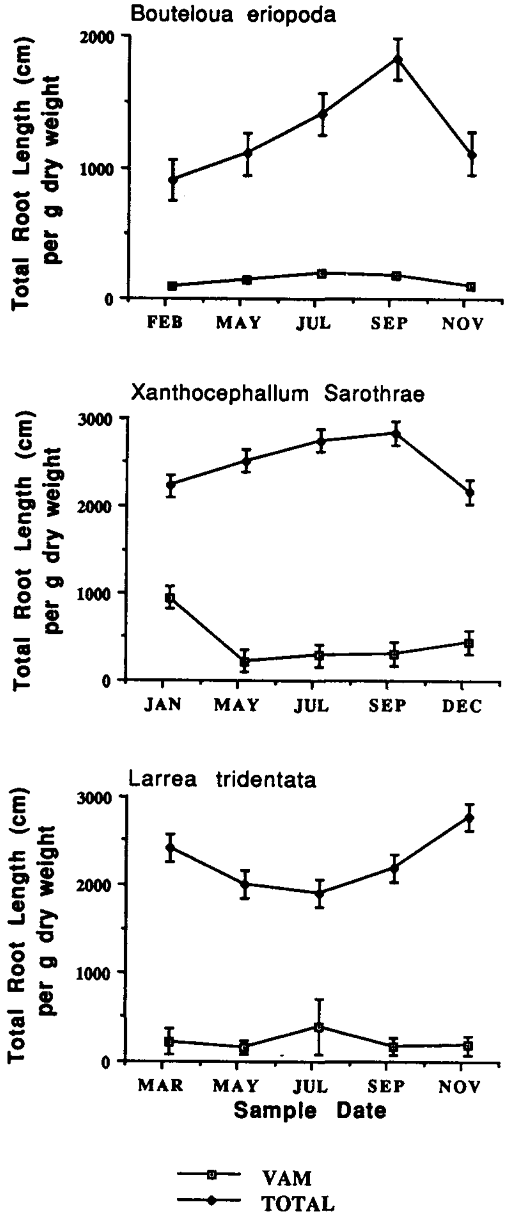

Fig. 5: Mean (± SD) total and VAM root length (cm) per g dry weight of roots of *Bouteloua eriopoda* (Torr.) Torr., *Xanthocephallum sarothrae* (Pursh) Shinners., and *Larrea tridentata* (D.V.) Cov. These plants were sampled over one growing season along an elevation gradient at the Jornada Long Term Ecological Research site near Las Cruces, New Mexico, USA. (Dhillion, Zak & Whitford unpublished data).

Longitud total promedio (±DE) y largo de raíz con MVA (cm), por g de peso seco de raíces de *Bouteloua eriopoda* (Torr.) Torr., *Xanthocephallum sarothrae* (Pursh) Shinners., & *Larrea tridentata* (D.C.) Cov. Estas plantas fueron muestreadas durante una temporada de crecimiento a lo largo de un gradiente de elevación en Jornada Long Term Ecological Research Site cerca de Las Cruces, Nuevo México, USA. (Dhillion, Zak & Whitford, datos no publicados).

POTENTIAL ROLE OF MYCORRHIZAS IN SEMI-ARID AND ARID REGIONS

In semiarid and arid ecosystems, structure and functioning of plant communities is highly regulated by the timing of moisture inputs and the abiotic and biotic factors affecting nitrogen availability, which are in turn regulated by belowground interactions of roots, microflora, microfauna and soils. The study of soil biota constitutes one of the largest gap in our knowledge of restoration and reclamation of desertified ecosystems. Plants that have been examined from arid habitats have very often been found to be mycorrhizal during the entire growing season or at least to form mycorrhizal associations during some part of their life cycle. In natural ecosystems, plants that are dependent on mycorrhizas require them to supply nutrients and water (especially during periods of high physiological demands) to sustain growth ('normal') and reproduction. Given the potential benefits of the mycorrhizal symbiosis, plant establishment and plant community dynamics on arid soils can be influenced by the presence or absence of mycorrhizal populations. Factors which directly or indirectly determine the occurrence of mycorrhizal propagules, for example, animal-mediated disturbances and the presence or absence of mycotrophic and nonmycotrophic species, are potentially important in subsequent plant establishment since various mycorrhizal fungi can have different physiological effects on their hosts. The successful establishment of seedlings may be determined by the presence of mycorhizal fungi, which may be specific to particular host i.e., exhibit 'ecological specificity'. Without successful establishment of appropriate mycorrhizal fungi, the plant species composition and nutrient dynamics within semiarid and arid communities will also be altered, and lead to the further degradation of these lands. At present, ongoing anthropogenic exploitation through mining, over-grazing and extensive agriculture, and cultural activities, the patchy distribution of mycorrhizal propagules in roots, soils and plant communities, activities of other organisms affecting these propagules, and local and seasonal environmental fluxes affecting abundances of propagules, and the lack of well documented studies of seasonal dynamics of mycorrhizas add to the complexity of the implementation of sucessful remedies for degraded arid ecosystem restoration and reclamation.

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