ELSEVIER

Applied Soil Ecology 22 (2003) 29–37

Applied Soil Ecology

www.elsevier.com/locate/apsoil

Analysis of the mycorrhizal potential in the rhizosphere of representative plant species from desertification-threatened Mediterranean shrublands

C. Azcón-Aguilar [a], J. Palenzuela [a], A. Roldán [b], S. Bautista [c], R. Vallejo [c], J.M. Barea [a,*]

[a] *Departamento de Microbiología del Suelo y Sistemas Simbióticos, Estación Experimental del Zaidín, CSIC, Profesor Albareda 1, 18008 Granada, Spain*

[b] *Centro de Edafología y Biología Aplicada del Segura (CEBAS-CSIC), Campus Espinardo, 30100 Murcia, Spain*

[c] *Centro de Estudios Ambientales del Mediterráneo (CEAM), Parque Tecnológico, C/Charles R. Darwin 14, 46980 Paterna, Valencia, Spain*

Received 19 March 2002; received in revised form 20 July 2002; accepted 22 July 2002

Abstract

An evaluation of the mycorrhizal status of desertification-threatened ecosystems has been recommended as a first step in rehabilitation/restoration approaches based on revegetation strategies using arbuscular mycorrhizal (AM) technology. Representative desertified semiarid areas were selected from southeast Spain where the vegetation is dominated by grasses, with *Stipa tenacissima* usually present, and with some patches of the shrubs *Pistacia lentiscus*, *Rhamnus lycioides*, *Olea europaea* subsp. *sylvestris* and *Retama sphaerocarpa*. The objective of this study was to evaluate the mycorrhizal potential in these soils, the contribution of the different species established to the mycorrhizal potential of the soils and to assess the main mycorrhizal propagules involved. There were more AM fungal propagules in the rhizospheres of all the shrub species studied compared with adjacent fallow soils, suggesting that AM propagules can be considered as a functional component of the resource islands developing around plant roots. *R. sphaerocarpa* and *O. europaea* had a higher capacity to enhance the development of mycorrhizal propagules in their rhizospheres than *R. lycioides* and *P. lentiscus*. Correlation analyses showed that the number of spores of the most representative AM fungal species, i.e. *Glomus constrictum*, and the total length of extraradical AM mycelium are the propagule sources which were best correlated with the mycorrhizal potential in terms of the number of "infective" AM propagules in the rhizosphere of the target plant species. The contribution of AM symbiosis to the potentiality of *S. tenacissima* as nurse plant was site dependent. Diversity of AM fungi present in the test area is rather low, indicating the high degree of degradation of the ecosystem. At most, only four AM fungal spore morphoecotypes were consistently detected in the rhizosphere of the target plant species.

Keywords: Arbuscular mycorrhiza; Degraded Mediterranean ecosystems; Diversity; Restoration ecology; Revegetation strategies

1. Introduction

Well-developed, fully functional, "internal symbioses" were already recognised in pioneering studies to be fundamental for ecosystem stability and sustain-

* Corresponding author. Tel.: +34-958-121011; fax: +34-958-129600.
E-mail address: jmbarea@eez-csic.es (J.M. Barea).

0929-1393/02/$ – see front matter
PII: S0929-1393(02)00107-5

ability (Odum, 1959). Research carried out in recent decades corroborates such a statement and emphasises the role of mycorrhizal symbioses in sustaining a vegetation cover in natural habitats (Harley, 1971; Jeffries and Barea, 2001). In fact, the mycorrhizal symbioses enhance the ability of the plant to become established and to cope with stress situations, such as nutrient deficiency, drought, soil disturbance, etc. (Barea et al., 1997; Schreiner et al., 1997; Bethlenfalvay and Linderman, 1992).

In semiarid Mediterranean ecosystems, scarce and irregular rainfall, a long dry and hot summer and man-mediated degradative activities may synergistically act as driving-forces able to promote desertification processes. Degradation of natural plant communities, in terms of population structure, successional patterns or species diversity, is known to occur concomitantly with degradation of physico-chemical and biological soil properties (Skujins and Allen, 1986; García et al., 1997; Albaladejo et al., 1998; Requena et al., 2001). In particular, reductions in the belowground microbial diversity and/or activity are usually associated with land degradation (Kennedy and Smith, 1995). Mycorrhizal symbioses and their propagules usually suffer from degradative processes (Brundrett, 1991; Jasper et al., 1991; McLellan et al., 1995), and it has been demonstrated that mycorrhizal activity, among other biological processes within the soil–plant system, is clearly diminished by desertification in Mediterranean ecosystems (Requena et al., 1996). Because of the key ecological functions of mycorrhizal symbioses, loss or diminution of the mycorrhizal potential in degraded areas may limit the successful reestablishment of native plants (Herrera et al., 1993; Sylvia, 1990; Roldán et al., 1997).

Dwarf shrub and grass communities are characteristic of degraded semiarid Mediterranean ecosystems, particularly in southeast Spain (López-Bermúdez and Albaladejo, 1990), and it is recognised that re-establishing adapted native tall shrub species is a key step in restoration strategies (Francis and Thornes, 1990; Vallejo et al., 1999). As Requena et al. (1996) have found, most of the native tree and shrub species in these communities are known to form arbuscular mycorrhiza with microscopic fungi of the order Glomales (Morton and Benny, 1990).

Within the framework of revegetation programmes currently being developed in southeast Spain, a number of drought-tolerant, deep-rooting model shrub species are being assayed. These programs include the use of mycorrhizal inoculation technologies to increase revegetation success. However, little is known about the potential of the species actually present in the target ecosystems for providing mycorrhizal propapules or as a basis to produce arbuscular mycorrhizal (AM) inoculum for selected plant species to be used in the revegetation strategies.

Shrub and tall-grass species in degraded semiarid ecosystems typically grow following a patchy distribution, with very low values of plant cover. The vegetation patches commonly constitute “fertility islands” (Garner and Steinberger, 1989), or “resource islands” (Reynolds et al., 1990; Schlesinger et al., 1996), where facilitation among plants may be highly fostered (Callaway, 1995, 1997).

Stipa tenacissima L. is a nearly omnipresent species in the target semiarid areas. Recent studies have described the improving effect of *S. tenacissima* tussocks on their own microenvironment through self-promoting changes in microclimate, soil structure, water infiltration, and organic matter inputs in relation to between-tussock areas (Cerdà, 1997; Bochet et al., 1999; Valladares and Pugnaire, 1999). In addition, it has been recently reported that *S. tenacissima* tussocks could facilitate the introduction of tall shrub species (Maestre et al., 2001), thus acting as “nurse plants”, as termed by Carrillo-García et al. (1999). However, there is no previous assessment of the mycorrhizal potential contribution of this species to the overall improvement of tussock microsites and thus its potential to benefit plant–plant interactions.

The general objective of the current study was to assess the AM status in the rhizosphere of selected model plants so that the natural mycorrhizal potential could be considered as a functional component of such resource islands to be exploited as a source of AM inoculum.

2. Materials and methods

2.1. Study areas and target plant species

The experimental area is located in the neighbouring Murcia and Alicante provinces, southeast Spain.

The climate is semiarid Mediterranean, with extremely hot and dry summers and with rainfall occurring mostly in autumn. The vegetation in these areas is dominated by grasses, with *S. tenacissima* usually present, and with some patches of slow-growing shrubs.

Two surveys were carried out. Survey 1 was developed at the El Picarcho experimental site located in Murcia (1°10′W, 38°23′N, 320 m above sea level). The predominant soils are *Haplic Calcisols* and *Petric Calcisols* developed from limestone with a sandy loam texture (FAO, 1988). The average annual precipitation is 280 mm, the mean annual temperature is 16.5 °C, and potential evapotranspiration reaches 900 mm per year. The topography of the area is mainly flat and slopes do not exceed 6%. The plant cover is sparse and degraded due to ancient grazing. Four representative shrub species from this site, and in general from semiarid shrublands in southeastern Spain, namely *Pistacia lentiscus* L., *Rhamnus lycioides* L., *Olea europaea* L. subsp. *sylvestris* L. and *Retama sphaerocarpa* (L.) Boiss., were selected as target species. A comprehensive analysis of the mycorrhizal status (number of infective AM propagules) and the types of propagules (spores, extraradical AM mycelium or AM root fragments) was carried out in the rhizosphere of the four test shrub species.

The aim of survey 2 was to assess the potential role of the nearly omnipresent *S. tenacissima* as nurse plants facilitating the establishment of other key species. This experiment was carried out in four experimental sites, including El Picarcho and three other sites located in the province of Alicante: Aguas (0°21′W, 38°31′N, 460 m above sea level), Campello (0°23′W, 38°30′N, 380 m above sea level) and Ballestera (0°22′W, 38°28′N, 140 m above sea level). These areas represent open degraded steppe sites, with plant cover ranging from 45 (Aguas site) to 59% (Ballestera site) and slope angles ranging from 12 (Aguas) to 21° (Ballestera). All these three sites have loamy-silty loam *Lithic Calciorthid* soils derived from marls and limestone. The climatic conditions range from 258 mm average annual precipitation and 18 °C average annual temperature at the Ballestera site to 288 mm average annual precipitation and 16 °C of average annual temperature at the Aguas site.

2.2. Mycorrhiza determinations in the rhizosphere of the target species

For survey 1, 20 individual plants similar in size (five replicates for each of the four target shrub species) were randomly chosen in a homogenous area from the El Picarcho site measuring approximately 4 ha. One soil sample from around the roots of each individual plant was collected, each sample consisting of five bulked subsamples (200 cm^3 soil cores) randomly collected at a depth of 10–20 cm. For *Stipa* plants, samples were taken from the four experimental sites as before. In all cases, soil samples from bare soil microsites away from plant influence were also taken.

The mycorrhizal potential in these soil samples was measured by the dilution technique (Sieverding, 1991). This method allows calculation of the most probable number (MPN) of mycorrhizal propagules able to develop colonisation units on the root of a test plant.

The mycorrhizal root length in the rhizosphere soil samples was microscopically assessed in a representative root aliquot by using the gridline intersect method of Giovannetti and Mosse (1980), after clearing and staining the root samples with trypan blue (Phillips and Hayman, 1970). The length of the extraradical AM mycelium was measured by a combination of the filtration-gridline methods of Jones and Mollison (1948), Newman (1966) and Miller et al. (1995), using trypan blue for staining the AM hyphae.

AM fungal spores were extracted from rhizosphere soil by wet sieving and decanting, followed by sucrose centrifugation (Sieverding, 1991). After centrifugation, the supernatant was poured through a 50 μm mesh and quickly rinsed with tap water. Spores were counted using a Doncaster dish under the dissecting microscope, and grouped according to morphological characteristics. Permanent slides were prepared for each different spore morphotype using both polyvinyl alcohol and polyvinyl alcohol plus Melzer's solution (1:1). After confirming the uniformity of the morphological groups under the optical microscope, the different morphotypes were identified to genus and, when possible, to species. Spore identification was mainly based on spore size and colour, wall structure and hyphal attachment (Walker, 1983; Morton and Benny, 1990; Schenk and Perez, 1990; INVAM, 1997).

Richness and relative abundance of each fungal species in the rhizosphere of each target plant were

calculated. Mycorrhizal fungal diversity was then calculated by using the Shannon–Wiener index, which combines two components of diversity: species richness and evenness of individuals among the species (Krebs, 1985).

2.3. Statistical analysis

Analyses of variance (ANOVA) were used to test differences and, when appropriate, Fisher's protected least significant differences test was used for comparison of means. Correlation coefficients were generated to examine the relationships between the studied components of the AM population and the number of mycorrhizal propagules (MPN) in the soil. Multiple stepwise regression with a forward selection procedure was performed to determine the relationship between the number of mycorrhizal propagules and selected mycorrhizal parameters. All analyses were performed using SPSS statistical software.

3. Results

3.1. Survey 1

All of the four shrubs formed AM symbiosis. Mycorrhiza formed by *P. lentiscus* and *R. lycioides* were of the *Paris*-type, showing exclusively intracellular hyphal development with a cell-to-cell passage, and producing many coiled hyphae and arbuscules. Roots of *O. europaea* and *R. sphaerocarpa* showed *Arum*-type mycorrhiza, characterised by the abundant intercellular hyphae and arbuscules.

The four test shrub species maintain a population of infective mycorrhizal propagules in soil affected by their roots (Table 1). The capability of the different target plant species to enrich the soil with "infective" mycorrhizal propagules was in the order *R. sphaerocarpa* > *O. europaea* > *R. lycioides* > *P. lentiscus*.

Table 1
Most probable number (MPN) of mycorrhizal propagules in soil from around the root system of the target shrub species and from open sites ($N = 5$)

Plant species	MPN of mycorrhizal propagules (g^{-1} dry soil)
Open sites	0.24 a
Pistacia lentiscus	0.41 a
Rhamnus lycioides	1.65 b
Olea europaea subsp. *sylvestris*	2.97 c
Retama sphaerocarpa	3.78 c

Data sharing a letter in common do not differ significantly ($P < 0.05$) by the Fischer's least significant difference test.

Analysis of soil samples with regard to the type of AM fungal propagules present in the rhizospheres of either *P. lentiscus*, *O. europaea*, *R. lycioides* or *R. sphaerocarpa*, shows that the length of extraradical mycelium, number of fungal spores and mycorrhizal root length, were highest in soil from around *R. sphaerocarpa* roots and lowest in that from *P. lentiscus* (Table 2).

Three species of AM fungi, *Scutellospora* sp., *Glomus coronatum* and *G. constrictum* were present in the rhizospheres of the four test plant species, with *Entrophospora* sp. also present in the rhizosphere of *O. europaea* (Fig. 1). The richness and abundance of each AM fungal spore morphotype in soil differed with the host plant. The diversity of the AM fungal species as calculated by the Shannon-Wiener index in samples of soil associated with each of the shrub species, was: 0.856 for *R. sphaerocarpa*, 0.814 for *O. europaea*, 1.080 for *R. lycioides* and 1.081 for *P. lentiscus*.

Regression analyses aimed at assessing which type of AM propagules were most strongly correlated

Table 2
Mycorrhizal propagules in soil from around the root system of the target shrub species ($N = 5$)

Plant species	Length of extraradical AM hyphae (m g^{-1} dry soil)	Number of AMF spores 100 g^{-1} of dry soil	Mycorrhizal root length (cm g^{-1} dry soil)
Pistacia lentiscus	1.19 a	49 a	0.71 a
Rhamnus lycioides	1.67 a	61 ab	0.94 a
Olea europaea subsp. *sylvestris*	2.45 b	83 b	1.36 ab
Retama sphaerocarpa	2.64 b	151 c	2.28 b

Data in the same column sharing a letter in common do not differ significantly ($P < 0.05$) by the Fischer's least significant difference test.

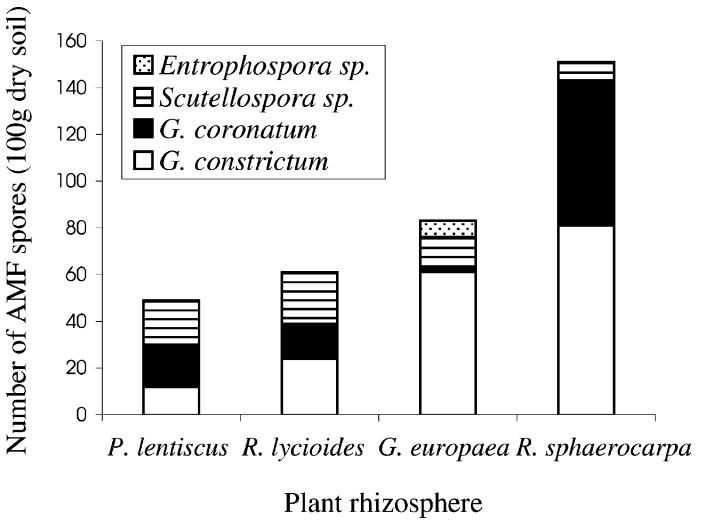

Fig. 1. Abundance of AMF species in the rhizosphere of the plants studied.

with the mycorrhizal inoculum potential in the rhizosphere of the test plant species showed that the highest correlation coefficient corresponded with the length of extraradical AM mycelium (MPN = $-2.114 + 2.172$(length of extraradical AM hyphae), $R^2 = 0.984$) and the number of *G. constrictum* spores, followed by the length of mycorrhizal root fragments (Table 3). The correlation between the total number of AM fungal spores and the total number of infective mycorrhizal propagules was not statistically significant.

3.2. Survey 2

Two-way ANOVA followed by Fisher's protected least significant difference tests shows that the number of mycorrhizal propagules in soil from around the tussocks of *S. tenacissima* was significantly higher than that in the bare soil between *Stipa* plants, when the data for the four sites were and analysed together (Table 4). However, site-by-site analysis shows that the differences were statistically significant only at the El Picarcho site (Table 4).

Table 3
Correlation coefficients for several components of the arbuscular mycorrhizal population and the number of mycorrhizal propagules (MPN) in soil from around the root system of the target shrub species and from open sites ($N = 5$)

Variable	Pearson's correlation coefficient
Total length of extraradical AM hyphae	0.997**
Number of *Glomus constrictum* spores	0.991**
Length of mycorrhizal root fragments	0.948*
Total number of AMF spores	0.897

* Significant at $P < 0.05$.
** Significant at $P < 0.01$.

Table 4
Most probable number (MPN) of mycorrhizal propagules (g^{-1} dry soil) in bare soil or in soil taken from around five *Stipa* tussocks at each of four sites

Site	Bare soil	Rhizosphere soil from *Stipa* tussocks
El Picarcho (Murcia)	0.24 a	1.12 b
Aguas (Alicante)	0.61 ab	1.14 b
Campello (Alicante)	0.61 ab	1.04 ab
Ballestera (Alicante)	0.91 ab	0.75 ab
Average	0.65 a	0.99 b

Data corresponding to the different sites and soils sharing a letter in common do not differ significantly ($P < 0.05$) by the Fischer's least significant difference test.

4. Discussion

All the target plants examined in this study were heavily mycorrhizal, indicating a high level of mycotrophy of the existing vegetation within the test

ecosystems. Survey studies carried out as other desertified area of the southeast of Spain (Requena et al., 1996, 1997), involving different plant species, also showed a considerable mycotrophic habit for most of the plant species actually present.

It is known that a patchy distribution of individual plant species from the natural succession is characteristic of arid and semiarid ecosystems (Halvorson et al., 1994). In addition, some perennial plants are known to create resource islands and behave as "ecosystem engineers" (Jones et al., 1997). Plants analysed in the present study, currently grown dispersed in patches, develop an AM mycelial network colonising soil microhabitats surrounding the roots. The AM mycelium is connected with the root system of plants growing nearby and allows an exchange of nutrients between them (Allen and Allen, 1992; Bethlenfalvay and Schüepp, 1994) as found in the present study. This extramatrical AM mycelium can, therefore, be a functional component for the development and functions of the resource islands to enhance an early integration of mycotrophic seedlings into the system, as corroborated by Carrillo-García et al. (1999, 2000). Results from the present study, therefore, suggest an important ecosystem function for the mycotrophic target plant species in providing available AM propagules as a source of inoculum for plant seedlings in either natural or directed revegetation processes.

As was to be expected (Eom et al., 2000), the four target shrub species differed in their capabilities to enrich the soil in mycorrhizal propagules, with *R. sphaerocarpa* and *O. europaea* having a higher capacity to enhance the development of AM propagules in their rhizospheres than *R. lycioides* and *P. lentiscus*. This can be explained considering that the first two species form *Arum*-type mycorrhizas while *R. lycioides* and *P. lentiscus* form those of the *Paris*-type. *Paris* mycorrhizas, common in Mediterranean ecosystems (Bedini et al., 2000), allocate most of their carbon to intraradical rather than extraradical development and sporulation.

It is noteworthy that *Stipa*, despite having a fibrous root system, is strongly mycotrophic, probably an adaptation for multiple (drought, nutrient deficit, etc.) stresses This study suggests that AM propagules in the rhizosphere of *Stipa* plants can contribute to the nurse role of this species, as reported by Maestre et al. (2001). However, this potential is dependent on the site; thus, further work is needed to support a generalised contribution of AM symbiosis to the role of *Stipa* as nurse plant.

Correlation analysis showed that the number of spores of the most representative AM fungal species, i.e. *G. constrictum*, and the total length of extraradical AM mycelium are the propagule sources which were best correlated with the total mycorrhizal potential in the rhizosphere of the target plant species. These findings agree with previous observations showing that the mycelium extending from mycorrhizal roots is usually the main source of inoculum in semiarid and arid ecosystems, while the importance of soilborne spores is less recognised (McGee, 1989; Brundrett and Kendrick, 1991; Requena et al., 1996; Bashan et al., 2000). Although the total number of AM fungal spores was relatively low in the ecosystem, and not significantly correlated with the mycorrhizal potential of the rhizosphere soil studied, the number of spores of a particular AM fungal species (*G. constrictum*) was correlated. This indicates some contribution of AM fungal spores to the mycorrhizal potential of the area.

Different AM fungal species have different effects on plant performance and nutrient cycling (Allen et al., 1995; Newsham et al., 1995; Jeffries and Barea, 2001). Furthermore, AM fungal communities have been shown to have the potential to determine plant community structure (van der Heijden et al., 1998a,b). Thus, concepts such as "functional diversity" (Allen, 1996) and "successional pattern" (Aziz et al., 1995; Gould and Hendrix, 1998) must be considered in ecological studies involving mycorrhizal symbioses. In fact, particular AM fungal species, and not all the components of the AM fungal population, appear to play a key ecosystem role at a given stage of the AM fungal succession and mycorrhizal functionality (Jeffries and Barea, 2001). These statements could explain why in the reported experiments the number of infective mycorrhizal propagules in the rhizosphere of the target plant species was not correlated with the total number of AM fungal spores but was for a particular species, i.e. *G. constrictum*. Probably this fungus is better adapted to germinate and colonise plant roots under the conditions of the test soils. In fact, this AM fungal species has been demonstrated to be an effective mycorrhizal inoculum in other experimental area in the same region (Requena et al., 2001), and could be a relevant component of the resource islands.

Diversity studies showed that, at most, only four AM fungal spore morphotypes were consistently detected in the rhizosphere of the target plant species. These have been isolated, multiplied and their monospecific cultures established. Diversity of AM fungi present in the test area seems, therefore, rather low, indicating the high degree of degradation of the ecosystem (Margalef, 1974; Krebs, 1985). Interestingly, and in spite of the fact that the test ecosystem was situated about 300 km apart from that previously studied by Requena et al. (1996), based on the shrub legume *Anthyllis cytisoides*, the same AM fungal species characterised as colonising the rhizospheres of *R. sphaerocarpa*, *R. lycioides*, *O. europea* and *P. lentiscus* in the present study, were also present in the rhizosphere of *Anthyllis* plants (Requena et al., 1996). Clearly, these AM fungal strains can be considered "ecotypes" (Jeffries and Barea, 2001), which are physiologically and genetically adapted to the whole environment of the desertification-threatened Mediterranean ecosystems in the southeast of Spain. Functional compatibility tests also demonstrate the effectiveness of the ecotypes isolated to improve the performance of the target plant species. Accordingly, it is logical to propose the exploitation of such AM fungal propagules in revegetation strategies with indigenous plant-fungal symbioses.

In conclusion, our results support the importance of the natural mycorrhizal potential associated with patchily distributed woody species from the natural succession in degraded ecosystems. The native AM fungi seem to be a functional component of the resource islands created by the perennial woody species, which seem able to act as a source of inoculum to improve nursing seedling performance. An AM mycelial network, either growing out from roots or arising from germinating spores, appears to guarantee effective mycorrhizal development in the ecosystem.

Acknowledgements

This research was supported by the EC + CICYT co-financed FEDER Programme (1FD97-0507 FOREST) and the EU Environment and Climate Research Programme (ENV4-CT97-0682 REDMED, Climate and Natural Hazards). We thank Mrs. Custodia Cano for her excellent technical assistance.

References

Albaladejo, J., Martinez-Mena, M., Roldan, A., Castillo, V., 1998. Soil degradation and desertification induced by vegetation removal in a semiarid environment. Soil Use Manage. 14, 1–5.

Allen, M.F., 1996. The ecology or arbuscular mycorrhizas: a look back into the 20th century and a peek into the 21st. Mycol. Res. 7, 769–782.

Allen, M.F., Allen, E.B., 1992. Development of mycorrhizal patches in a successional arid ecosystem. In: Read, D.J., Lewis, D.H., Fitter, A.H., Alexander, I.J. (Eds.), Mycorrhizas in Ecosystems. CAB International, Wallingford, UK, pp. 154–170.

Allen, E.B., Allen, M.F., Helm, D.J., Trappe, J.M., Molina, R., Rincon, E., 1995. Patterns and regulation of mycorrhizal plant and fungal diversity. In: Collins, H.P., Robertson, G.P., Klug, M.J. (Eds.), The Significance and Regulation of Soil Biodiversity. Kluwer Academic Publishers, Amsterdam, The Netherlands, pp. 47–62.

Aziz, T., Sylvia, D.M., Doren, R.F., 1995. Activity and species composition of arbuscular mycorrhizal fungi following soil removal. Ecol. Appl. 5, 776–784.

Barea, J.M., Azcón-Aguilar, C., Azcón, R., 1997. Interactions between mycorrhizal fungi and rhizosphere micro-organisms within the context of sustainable soil–plant systems. In: Gange, A.C., Brown, V.K. (Eds.), Multitrophic Interactions in Terrestrial Systems. Backwell Science, Cambridge, pp. 65–77.

Bashan, Y., Davis, E.A., Carrillo-García, A., Linderman, R.G., 2000. Assessment of VA mycorrhizal inoculum potential in relation to the establishment of cactus seedlings under mesquite nurse-trees in the Sonoran Desert. Appl. Soil Ecol. 14, 165–175.

Bedini, S., Maremmani, A., Giovannetti, M., 2000. *Paris*-type mycorrhizas in *Smilax aspera* L. growing in a Mediterranean sclerophyllous wood. Mycorrhiza 10, 9–13.

Bethlenfalvay, G.J., Linderman, R.G., 1992. Mycorrhizae in Sustainable Agriculture. ASA Special Publication, Madison, WI, 124 pp.

Bethlenfalvay, G.J., Schüepp, H., 1994. Arbuscular mycorrhizas and agrosystem stability. In: Gianinazzi, S., Schüepp, H. (Eds.), Impact of Arbuscular Mycorrhizas on Sustainable Agriculture and Natural Ecosystems. Birkhäuser Verlag, Basel, Switzerland, pp. 117–131.

Bochet, E., Rubio, J.L., Poesen, J., 1999. Modified topsoil islands within patchy Mediterranean vegetation in SE Spain. Catena 38, 23–44.

Brundrett, M.C., 1991. Mycorrhizas in natural ecosystems. In: Macfayden, A., Begon, M., Fitter, A.H. (Eds.), Advances in Ecological Research. Academic Press, London, pp. 171–313.

Brundrett, M.C., Kendrick, B., 1991. The mycorrhizal status, root anatomy, and phenology of plants in a sugar maple forest. Can. J. Bot. 66, 1153–1173.

Callaway, R.M., 1995. Positive interactions among plants. Bot. Rev. 61, 306–349.

Callaway, R.M., 1997. Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112, 143–149.

Carrillo-García, A., León de la Luz, J.L., Bashan, Y., Bethlenfalvay, G.J., 1999. Nurse plants, mycorrhizae, and plant establishment in a disturbed area of the Sonoran desert. Res. Ecol. 7, 321–335.

Carrillo-García, A., Bashan, Y., Bethlenfalvay, G.J., 2000. Resource island soils and the survival of the giant cactus, cardon, of Baja California Sur. Plant Soil 218, 207–214.

Cerdà, A., 1997. The effect of patchy distribution of *Stipa tenacissima* L. on runoff and erosion. J. Arid Environ. 36, 37–51.

Eom, A.-H., Hartnett, D.C., Wilson, G.W.T., 2000. Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. Oecologia 122, 435–444.

FAO, 1988. FAO–UNESCO soil map of the world. Revised legend. World Soil Resources Report 60. FAO, Rome.

Francis, D.F., Thornes, J.B., 1990. Matorral: erosion and reclamation. In: Albaladejo, J., Stocking, M.A., Díaz, E. (Eds.), Soil Degradation and Rehabilitation in Mediterranean Environmental Conditions. Consejo Superior de Investigaciones Científicas, Murcia, Spain, pp. 87–115.

García, C., Hernandez, T., Roldán, A., Albaladejo, J., 1997. Biological and biochemical quality of a semiarid soil after induced revegetation. J. Environ. Qual. 26, 1116–1122.

Garner, W., Steinberger, Y., 1989. A proposed mechanism for the formation of fertile islands in the desert ecosystem. J. Arid Environ. 16, 257–262.

Giovannetti, M., Mosse, B., 1980. An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infections in roots. New Phytol. 84, 489–499.

Gould, A.B., Hendrix, J.W., 1998. Relationship of mycorrhizal activity to time following reclamation of surface mine land in western Kentucky. II. Mycorrhizal fungal communities. Can. J. Bot. 76, 204–212.

Halvorson, J.J., Bolton Jr., H., Smith, J.L., Rossi, R.E., 1994. Geostatistical analysis of resource islands under *Artemisia tridentata* in the shrub-steppe. Great Basin Nat. 54, 313–328.

Harley, J.L., 1971. Fungi in ecosystems. J. Appl. Ecol. 8, 627–642.

Herrera, M.A., Salamanca, C.P., Barea, J.M., 1993. Inoculation of woody legumes with selected arbuscular mycorrhizal fungi and rhizobia to recover desertified Mediterranean ecosystems. Appl. Eviron. Microbiol. 59, 129–133.

INVAM, 1997. http://www.invam.caf.wvu.edu/.

Jasper, D.A., Abbot, L.K., Robson, A.D., 1991. The effect of soil disturbance on vesicular-arbuscular mycorrhizal fungi in soils from different vegetation types. New Phytol. 118, 471–476.

Jeffries, P., Barea, J.M., 2001. Arbuscular mycorrhiza—a key component of sustainable plant–soil ecosystems. In: Hock, B. (Ed.), The Mycota. IX. Fungal Associations. Springer, Berlin, pp. 95–113.

Jones, P.C.T., Mollison, J.E., 1948. A technique for the quantitative estimation of soil micro-organisms. J. Gen. Microbiol. 2, 54–69.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Kennedy, A.C., Smith, K.L., 1995. Soil microbial diversity and the sustainability of agriculture soils. Plant Soil 170, 75–86.

Krebs, C.J., 1985. Species diversity. In: Krebs, C.J. (Ed.), Ecology: The Experimental Analysis of Distribution and Abundance, 3th ed. Harper & Row, New York, pp. 507–534.

López-Bermúdez, F., Albaladejo, J., 1990. Factores ambientales de la degradación del suelo en el area mediterránea. In: Albaladejo, J., Stocking, M.A., Díaz, E. (Eds.), Soil Degradation and Rehabilitation in Mediterranean Environmental Conditions. Consejo Superior de Investigaciones Científicas, Murcia, Spain, pp. 15–45.

Maestre, F.T., Bautista, S., Cortina, J., Bellot, J., 2001. Potential of using facilitation by grasses to establish shrubs on semiarid degraded steppe. Ecol. Appl. 12, 1641–1655.

Margalef, R., 1974. Ecologia. Omega, Barcelona, Spain, 951 pp.

McGee, P., 1989. Variation in propagule numbers of vesicular-arbuscular mycorrhizal fungi in a semiarid soil. New Phytol. 92, 28–33.

McLellan, A.J., Fitter, A.H., Law, R., 1995. On decaying roots, mycorrhizal colonisation and the design of removal experiments. J. Ecol. 83, 225–230.

Miller, R.M., Reinhardt, D.R., Jastrow, J.D., 1995. External hyphal production of vesicular-arbuscular mycorrhizal fungi in pasture and tallgrass prairie communities. Oecologia 103, 17–23.

Morton, J.B., Benny, G.L., 1990. Revised classification of arbuscular mycorrhizal fungi (Zygomycetes): a new order, Glomales, two new suborders, Glomineae and Gigasporineae, and two new families, Acaulosporaceae and Gigasporaceae, with an emendation of Glomaceae. Mycotaxon 37, 471–491.

Newman, E.I., 1966. A method of estimating the total length of root in a sample. J. Appl. Ecol. 3, 139–145.

Newsham, K.K., Fitter, A.H., Watkinson, A.R., 1995. Multi-functionality and biodiversity in arbuscular mycorrhizas. Tree 10, 407–411.

Odum, E.P., 1959. Fundamentals of Ecology. Saunders, Philadelphia, 546 pp.

Phillips, J.M., Hayman, D.S., 1970. Improved procedures for clearing and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of the infection. Trans. Br. Mycol. Soc. 55, 158–161.

Requena, N., Jeffries, P., Barea, J.M., 1996. Assessment of natural mycorrhizal potential in a desertified semiarid ecosystem. Appl. Environ. Microbiol. 62, 842–847.

Requena, N., Jimenez, I., Toro, M., Barea, J.M., 1997. Interactions between plant-growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi and *Rhizobium* spp. in the rhizosphere of *Anthyllis cytisoides*, a model legume for revegetation in Mediterranean semiarid ecosystems. New Phytol. 136, 667–677.

Requena, N., Pérez-Solis, E., Azcón-Aguilar, C., Jeffries, P., Barea, J.M., 2001. Management of indigenous plant-microbe symbioses aids restoration of desertified ecosystems. Appl. Environ. Microbiol. 67, 495–498.

Reynolds, J.F., Virginia, R.A., Cornelius, J.M., 1990. Resource island formation associated with the desert shrubs, creosote bush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) and its role in the stability of desert ecosystems: a simulation model. Suppl. Bull. Ecol. Soc. Am. 70, 299–300.

Roldán, A., García, C., Albaladejo, J., 1997. AM fungal abundance and activity in a chronosequence of abandoned fields in a semiarid Mediterranean site. Arid Soil Res. Rehabil. 11, 211–220.

Schenk, N.C., Perez, Y., 1990. Manual for the Identification of VA Mycorrhizal Fungi. Synergistic Publications, Gainesville, FL, 286 pp.

Schlesinger, W.H., Raikes, J.A., Hartley, A.E., Cross, A.F., 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77, 364–374.

Schreiner, R.P., Mihara, K.L., McDaniel, H., Bethlenfalvay, G.J., 1997. Mycorrhizal fungi influence plant and soil functions and interactions. Plant Soil 188, 199–209.

Sieverding, E., 1991. Vesicular-Arbuscular Mycorrhiza Management in Tropical Agrosystems. GTZ, Eschborn, Germany, 371 pp.

Skujins, J., Allen, M.F., 1986. Use of mycorrhizae for land rehabilitation. MIRCEN J. 2, 161–176.

Sylvia, D.M., 1990. Inoculation of native woody plants with vesicular-arbuscular mycorrhizal fungi for phosphate mine land reclamation. Agric. Ecosyst. Environ. 31, 253–261.

Valladares, F., Pugnaire, F.I., 1999. Tradeoffs between irradiance capture and avoidance in semiarid environments assessed with a crown architecture model. Ann. Bot. 83, 459–469.

Vallejo, V.R., Bautista, S., Cortina, J., 1999. Restoration for soil protection after disturbances. In: Trabaud, L. (Ed.), Life and Environment in Mediterranean Ecosystems. Advances in Ecological Sciences. Wit Press, Wessex, pp. 301–343.

Heijden, M.G.A., Boller, T., Wiemken, A., Sanders, I.R., 1998a. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79, 2082–2091.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R., 1998b. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396, 69–72.

Walker, C., 1983. Taxonomic concepts in the Endogonaceae. I. Spore wall characteristics in species descriptions. Mycotaxon 18, 443–455.