ORIGINAL PAPER

Sara Lucía Camargo-Ricalde · Shivcharn S. Dhillion

Endemic *Mimosa* species can serve as mycorrhizal "resource islands" within semiarid communities of the Tehuacán-Cuicatlán Valley, Mexico

Received: 7 May 2002 / Accepted: 10 September 2002 / Published online: 16 October 2002 © Springer-Verlag 2002

Abstract This paper explores if *Mimosa* species (Fabaceae-Mimosoideae) can serve as arbuscular mycorrhizal (AM) and nutrient "resource islands" in six plant communities in the semiarid valley of Tehuacán-Cuicatlán, Mexico. Spatial heterogeneity related to the occurrence of *Mimosa* species results in temporal differences in AM-fungal spore numbers and soil nutrients. A higher number of AM-fungal spores were found in the soil below the canopies of six endemic *Mimosa* species than in the soil from non-vegetated areas. For four species, Mimosa adenantheroides, Mimosa calcicola, Mimosa luisana and Mimosa polyantha, the soil below their canopies had more AM-fungal spores than the soil in non-vegetated areas during the wet season than during the dry season. Two species, Mimosa lacerata and Mimosa texana var. filipes, however, had more spores under their canopies during the dry season than during the wet season. Although physical differences are present within and between sites, in general the soil below the canopies of Mimosa species had significantly higher nutrient levels than the soil from non-vegetated areas. Mimosa species thus form "resource islands" that are not only rich in nutrients but also in mycorrhizal propagules. Mimosa species can serve as mycorrhizal "resource islands" by directly affecting AM-fungal spore dynamics and/or by serving as spore-traps. A range of plants associated with Mimosa species may benefit from the higher number of AM propagules. We believe that the use of Mimosa resource islands as an option for biodiversity conservation and for land restoration ought to be considered in the Valley.

S.L. Camargo-Ricalde () S.S. Dhillion Agricultural University of Norway, Department of Biology and Nature Conservation, P.O. Box 5014, 1432, Ås, Norway e-mail: slcr@xanum.uam.mx Fax: +52-55-58044688

S.L. Camargo-Ricalde
Universidad Autónoma Metropolitana-Iztapalapa,
Div. Ciencias Biológicas y de la Salud, Depto. Biología,
A. Postal 55–535, 09340, México, D.F., México

Keywords Arbuscular-mycorrhizal fungi · Conservation · Resource island · Seasonality · Semiarid

Introduction

In arid and semiarid ecosystems, particular shrubs and trees such as Acacia gregii Gray, Cassia armata S. Wats [= Senna armata (S. Wats) Irwin & Barneby] (García-Moya and McKell 1970), *Prosopis juliflora* (Swartz. DC) (Tiedemann and Klemmedson 1973), Larrea tridentata (Sessé & Mociño ex D.C.) Coville and Prosopis glandulosa Torr. (Reynolds et al. 1999) can serve as reservoirs for soil fertility. These shrubs and trees contribute to desert fertility by protecting understory vegetation and the soil against wind erosion, and by serving as nutrient reservoirs through the storage of nitrogen in roots, stems, and leaves. The potential contribution of nitrogen from a shrub when it dies, the accumulated litter and organic matter under the shrub, and the nitrogen in the surface layer of soil under the shrub canopy all create "islands of fertility" within plant communities (García-Moya and McKell 1970). Fertility islands are not only areas of nitrogen accumulation, but also the sites of highest nutrient and moisture concentration, greatest shade, and lowest daytime temperature (Garner and Steinberger 1989; Reynolds et al. 1999). In addition, such islands form the major source of food for most herbivores, and hence the animals that prey on them (Garner and Steinberger 1989). Furthermore, their occurrence is highly correlated with the spatial variation in soil microbial populations and soil microfauna that promotes nutrient cycling in shrub deserts (Coleman et al. 1983; Dhillion and Zak 1993). Thus, such sites have recently been given the name "resource islands" (Reynolds et al. 1999).

Arbuscular mycorrhizae (AM), as part of the soil microbe community, can play an important role in the maintenance of desert vegetation, since water stress and nutrient deficiencies are the most common constraints of plant growth in arid and semiarid ecosystems, (Allen et al.

1981; Bethlenfalvay et al. 1984; Allen and Allen 1986; Allen 1991; Dhillion and Zak 1993; Tarafdar and Praveen-Kumar 1996). The positive effects of AM are associated with changes in plant-water relationships and low availability of inorganic nutrients, especially phosphorus and nitrogen. Mycorrhizal plants thus have greater tolerance to drought stress, and higher rates of photosynthesis, biomass production and inorganic nutrient accumulation than non-mycorrhizal plants of the same species. In fact, AM have a structuring effect on plant species composition, thus affecting plant biodiversity, ecosystem variability and productivity (Zobel et al. 1997; Van der Heijden et al. 1998).

It is known that AM fungal activity is related to several soil conditions, such as depth (Virginia et al. 1986), fertility and moisture (Anderson et al. 1984), and compaction (Nadian et al. 1998), but within the arid and semiarid ecosystems, intermittent periods of favorable temperature and moisture, called "windows of opportunity", strongly regulate the mechanisms that control fungal activity and dynamics (Dhillion and Zak 1993; Zak et al. 1995). Moisture is the main limiting factor in desert ecosystems: organism adaptation and functioning is primarily attributed to surviving the long dry periods and responding rapidly and effectively to moisture inputs (Jacobson 1997). Not only total moisture is important but the temporal and spatial patterning of moisture inputs may determine the extent of fungal activity and, possibly, fungal species composition (Dhillion et al. 1995; Zak et al. 1995). In desert ecosystems, temporal and spatial heterogeneity are thus mainly driven by climate and topography (Allen 1991).

Although the idea of "resource island" formation has surfaced in the literature from time to time, relatively few plant species have been studied in this regard. Nutrient and microclimatic conditions have been the main focus of most studies, with few investigations on associated microbes (see Carrillo-García et al. 1999). The objective of this study was to explore if Mimosa species could serve as mycorrhizal and nutrient "resource islands" in the semiarid valley of Tehuacán-Cuicatlán, Mexico. Mimosa species were focused on due to their growing dominance in several threatened plant communities in the Tehuacán-Cuicatlán Valley (Camargo-Ricalde et al. 2002a), their endemism (Martínez-Bernal and Grether 2002), restoration considerations, and their considerable local agrosilvopastoral and cultural value (Casas et al. 2001; S.L. Camargo-Ricalde and S.S. Dhillion, unpublished data). In addition, the presence of the "nurse-nursling" association between Mimosa luisana Brandegee and the columnar cactus Neobuxbaumia tetetzo (F.A.C. Weber) Backeb. (Valiente-Banuet and Ezcurra 1991; Valiente-Banuet et al. 1991) has also been demonstrated. Furthermore, it is the genus with the highest number of species (100-110)of all the Mexican Mimosoideae members (Sousa and Delgado 1993), and where 60% are endemic to the country (Grether et al. 1996).

Materials and methods

Species and the study sites

The Tehuacán-Cuicatlán Valley (part of it a Biosphere Reserve since 1998) is located between 17° 20'-18° 53' N, and 96° 55'-97° 44' W, with a surface of ca. 10,000 km², within the states of Puebla and Oaxaca, Mexico. The Valley has a complex topography, where altitudes range from 500 to 3,200 m.a.s.l. The mean annual precipitation varies between >400 mm and <600 mm with summer rain, and the mean annual temperature is 20°C. Soils are rocky, shallow and well-drained, and texture varies from sandy loam to clay loam, being classified as aridsols (Zavala-Hurtado and Hernández-Cárdenas 1998). Six *Mimosa* species were studied in the Tehuacán-Cuicatlán Valley (Table 1; for details of specific plant community composition and sites, see Camargo-Ricalde et al. 2002a). The communities studied were representative of the area and were available for research in the Valley.

AM fungal spores and soil samples

Two quadrats of $10m \times 10m (200m^2)$ were sampled for each site during both the dry (January) and the wet (July) seasons of 1999. For each quadrat, two Mimosa individuals were randomly chosen for collection of the soil below their canopies (BC). Two nonvegetated areas (open areas, OA) were also sampled. Soil samples were collected at 10-15 cm depth; four samples adjacent to Mimosa species stem-roots (BC), and four samples in open areas (OA); 48 soil samples (8 per site) were collected in total. Soil samples were sealed in polythene bags and brought into the laboratory. Three sub-samples per soil sample were analyzed for AM fungal spores (decanting aliquots of 100 g dry weight each) using the wet sieving (44-, 105-µm sieve openings) and decanting method (Gerdemann and Nicolson 1963). Spores were examined and their number recorded under a dissecting microscope. Permanent slides and a photographic record have been deposited at the Laboratory of Legume Biosystematics, Department of Biology, Autonomous Metropolitan University-Iztapalapa. Spores are in the process of being identified (Schenck and Perez 1990); Glomus and Acaulospora form the dominant genera. Soils were analyzed for pH, electric conductivity (EC), organic matter (OM), total nitrogen (TN), phosphorus (P), calcium (Ca), magnesium (Mg) and texture [Mexican Society of Soil Science, Manual of analytical procedures for soil and plant analysis of the Soil Fertility Laboratory (in Spanish). IRENAT-Colegio de Postgraduados, Mexico; Vázquez-Alarcón and Bautista-Aroche 1993; for details of soil analyses and relationships with plant communities, see Camargo-Ricalde et al. 2002a].

The non-parametric Kruskal-Wallis test (P < 0.05) was used and means were compared by the chi-square test, χ^2 , ($\alpha = 0.05$) to determine whether differences in AM-fungal spore number were significant between the soil BC of *Mimosa* species vs that of OA, during both the dry and the wet seasons. The non-parametric Student *t*-test ($\alpha = 0.05$) was used to determine whether differences in AM-fungal spore number were significant in the soil BC of *Mimosa* species and in OA soil in dry/wet seasons.

Results and discussion

Although AM-fungal spore numbers do not necessarily always correlate with AM-fungal colonization of roots (Walker et al. 1982), and they do not represent either the real abundance or the ecological contribution of whole organisms of species present (Stürmer and Bellei 1994), they are an indicator of the inoculum potential present in the soil (Brundrett 1991; Dhillion and Anderson 1993; Merryweather and Fitter 1998). In this study, AM-fungal

Sites	Municipality	Location	Altitude (m.a.s.l.) and precipitation (x/y) (mm) ^a	Community type	Mimosa species	IV $(x/y)^d$	Disturbance ^e and slope ^f
S1	Chapulco	18° 41' 31" N 97° 24' 01.3" W	2,232 2.1/74.5	Matorral xerófilo (arid tropical scrub)	<i>Mimosa lacerata</i> Rose ^b	56/289	Farming Medium
S2	Coxcatlán	18° 15' 23.7" N 97° 09' 03.3" W	1,140 3.7/75.5	Matorral xerófilo	<i>Mimosa polyantha</i> Benth. ^b	40/270	Goat grazing flat
S3	Caltepec	18° 10' 31.3" N	1,890	An ecotone between the selva baja caducifolia	<i>Mimosa adenantheroides</i> (M. Martens & Galeotti) Benth. ^b	13/222	Urban pressure
		97° 28' 45.8" W	5/54.5	(deciduous tropical forest) and the oak (Quercus) forest			Medium
S4	Tehuacán	18° 24' 09.8" N 97° 26' 19.2" W	1,720 2.1/74.5	Matorral xerófilo	Mimosa calcicola B. L. Rob. ^c	7/249	Salt mining Medium
S5	Caltepec	18° 12' 0.46" N	2,050	An ecotone between the selva baja caducifolia	Mimosa texana (A. Gray) Small var. filines (Britton & Rose) Barnehv ^c	117/280	Farming
		97° 31' 28.6" W	5/54.5	(deciduous tropical forest) and the oak (Quercus) forest			Flat
S6	Caltepec	18° 16' 29.4" N 97° 30' 12.9" W	1,670 11.7/44.7	Matorral xerófilo	Mimosa luisana Brandegee ^c	98/278	Roads Medium
^a Precip	itation records w	ere taken from the n	earest climatological	station in relation to species occurrence,	values are the average of at least 16 year	rs; for x/y , x	ndicates January (dry

Table 1 Mimosa species and characteristics of the study sites within the Tehuacán-Cuicatlán Valley, Mexico

season) mean monthly precipitation and y indicates July (wet season) mean monthly precipitation

^b Endemic to Mexico

^c Endemic to the Valley ^dImportance value within their communities; for *x/y*, *x* indicates the IV of *Mimosa* species and *y* indicates the sum of the partial IV of the species occurring in the site, respectively; in total we registered 24 plant families, 51 genera and ca. 70 species, comprising 5% of the total flora estimated for the Valley (for details, see Camargo-Ricalde et al. 2002a) ^e Faming, goat grazing, deforestation, urban pressure with concomitant road construction, salt mining extraction, and commercial poultry are the major factors of environmental disturbance within both the "matorral xerofflo" and the "selva baja caducifolia"; though environmental disturbance is caused by the simultaneous action of diverse agents; for the table, we mention only the main disturbance factor for each site ^f Flat (0°–15°), medium (15°–30°), and steep (30°–45°)

Table 2 Mean number of arbuscular mycorrhiza (AM)-fungal spores (in 100 g soil dry weight) under different conditions in six study sites within the Tehuacán-Cuicatlán Valley, south-central Mexico: soil below the canopy (BC) of *Mimosa* species and soil of non-vegetated areas (open areas, OA), during both the wet (W, July) season and the dry (D, January) season of 1999. The *Mimosa*

species studied form resource islands within their communities; the species examined for each site were: site 1 (S1) Mimosa lacerata, site 2 (S2) Mimosa polyantha, site 3 (S3) Mimosa adenantheroides, site 4 (S4) Mimosa calcicola, site 5 (S5) Mimosa texana var. filipes, and site 6 (S6) Mimosa luisana

Site	Wet Season	Spore number	Dry season	Spore number	BC	Spore number	OA	Spore number
S1	BC	219±27*	BC	585±146*	W	219±47*	W	124 ±47
	OA	124±27*	OA	101±35*	D	585±146*	D	101±35
S2	BC	204±22*	BC	112±51	W	204±38	W	117±27
	OA	117±15*	OA	69±13	D	112±51	D	69±13
S3	BC	41±3*	BC	26±2	W	41±5*	W	18±5
	OA	18±3*	OA	22±3	D	26±2*	D	22±3
S4	BC	148±8*	BC	115±15*	W	148±14*	W	119 ±6*
	OA	119±3*	OA	47±21*	D	115±15*	D	47±21*
S5	BC	29±6	BC	50±25	W	29±11	W	23±3
	OA	23±1	OA	24±1	D	50±25	D	24 ±1
S6	BC OA ± Standard de	165±10* 71±12* viation; χ^2 (α =0.0)	BC OA 5), *significant	24±6 14±6 difference	W D ± Standard difference	165±16* 24±6 deviation; Student	W D <i>t</i> -test (α=0.0)	71±20* 14±6* 5), *significant

spores were present in all the soil samples analyzed. In general, there were significantly more AM-fungal spores both in the soil BC of *Mimosa* species than in the non-vegetated OA, and during the wet vs the dry season (Table 2).

This study shows that AM-fungal spore number tends to be higher during the wet season than during the dry season (Table 2). Differences between the soil BC of *Mimosa* species and the soil in OA were larger during the wet season than during the dry season. During the wet season, significant differences were found in AM-fungal spore numbers comparing the soil BC of Mimosa species with the soil collected in OA for *M. lacerata* (S1), *M.* polyantha (S2), M. adenantheroides (S3), M. calcicola (S4) and *M. luisana* (S6), while no significant differences were registered for *M. texana* var. *filipes* (S5). During the dry season, significant differences between the soil BC of Mimosa species and the soil in OA in relation to AMfungal spore number were found for only two species, M. *lacerata* (S1) and *M. calcicola* (S4). Spores function as survival units if germination is delayed; thus, differences in spatial and temporal AM-fungal spore numbers may be related to different AM fungi, which are likely to have different strategies for survival under the stress of a semiarid habitat (McGee 1989). Within arid and semiarid ecosystems, AM fungi can have an opportunistic growth pattern in response to low and variable rainfall amounts ("moisture windows"). The fungi can continue to grow vegetatively as long as the moist layer persists, spore production being associated with declining moisture availability (Jacobson 1997), although it is not clear whether AM-fungal phenology is controlled by the fungus or mediated by the plant symbiont (Sanders and Fitter 1992; Jacobson 1997). Within the six study sites, the amount of rainfall varies enormously between January (mid-dry season) and July (mid-wet season) (Table 1). However, this variation in rainfall can only partly explain the significant differences in the number of AM-fungal spores between seasons.

Similar variations in spore numbers have been reported by other studies, e.g., in an ash plantation (Fraxinus americana L.) and in an old meadow in central Iowa (1-1,837 spores/kg oven-dry soil) (Walker et al. 1982); in a semiarid open scrub dominated by Melaleuca uncinata R. Br. in southern Australia (1-14 spores) (McGee 1989); in Quercus havardii Rydb. communities in semiarid Texas (27–43 spores/100 g dry soil) (Dhillion et al. 1994); in an arid dune field dominated by grasses in the Namibian desert (1-535 spores/150 cm³ soil) (Jacobson 1997); and in a sand dune soil on the island of Santa Catarina in Brazil (168–380 spores/100 g dry soil) (Stürmer and Bellei 1994). Such large variations in AM-fungal spore numbers may be due to seasonal patterns in AM-fungal sporulation, which can vary according to the specific AM fungus or plant species (Mosse and Bowen 1968; Dhillion and Anderson 1993; Jacobson 1997). Distribution of spores within the soil is extremely variable over space and time (Walker et al. 1982). Variation in spore abundance is the result of the non-uniform spatial distribution of spores in the soil, which may also be caused by the threshold of mycorrhizal biomass needed to induce spore production (Gazey et al. 1992; Stürmer and Bellei 1994).

Unexpectedly, soil BC of *Mimosa lacerata* (S1) and *M. texana* var. *filipes* (S5) had a higher number of spores during the dry than the wet season (Table 2). The soil BC of *Mimosa lacerata* had 168% more AM-fungal spores and the soil BC of *M. texana* var. *filipes* had 72% more AM-fungal spores during the dry season than during the wet season. Though spatial and temporal heterogeneity can explain these differences in part, other factors that may be affecting AM-fungal spore production are *Mimosa* species-specific root exudates and the microbial communities developed at each site (Garbaye 1991; Whitford 1996). *Mimosa lacerata* and *M. texana* var.

filipes root exudates may play an important role affecting AM-fungal phenology, creating AM-fungal spore reservoirs in the soil BC of these *Mimosa* species during the dry season. However, there is no information about the type and quality of the root exudates produced by *Mimosa* species.

Though the microbial community of the rhizosphere is defined as a key factor in the development, stability and efficiency of mycorrhiza, little is yet known about it (e.g. Garbaye 1991; Dhillion and Zak 1993; Whitford 1996). For instance, information about AM-fungal spore population dynamics (predation, dispersal and germination) is scarce for arid and semiarid ecosystems. It is known that AM-fungal spores are consumed and dispersed by animals (e.g., nematodes, collembolans, ants, and small mammals) (Warner et al. 1987; Dhillion et al. 1994; Dhillion 1999; Snyder and Friese 2001), and parasitized by other fungi or bacteria (see e.g., Fitter and Garbaye 1994). In addition, some spore-associated bacteria (e.g., Pseudomonas spp. and Corynebacterium spp.) are capable of stimulating the germination of spores of AM fungi [e.g., Glomus versiforme (Karsten) Berch (= Glomus epigaeum Daniels and Trappe)] (Mayo et al. 1986). The population dynamics of these organisms consequently affect AM-fungal spore dynamics; for example, changes in the population of bacteria could provoke changes in the germination rate of AM-fungal spores. There is no information about the biological diversity of the microbial communities within the six study sites. The ecology of microbial communities within these sites, and the type and quality of the root exudates produced by Mimosa species are two examples of research lines that may be explored to understand interactions within the resource islands formed by Mimosa species.

Within the Mimosa resource island itself, temporal heterogeneity led to differences in the number of AMfungal spores. Comparing the wet season to the dry season, significant differences were reported for M. lacerata (S1), M. adenantheroides (S3), M. calcicola (S4) and M. luisana (S6) resource islands, while no significant differences were observed for M. polyantha (S2) and *M. texana* var. *filipes* (S5) resource islands. In the case of the soil samples from non-vegetated OA, a significant difference in the number of AM-fungal spores between seasons was reported only for sites S4 and S6, whereas the spore numbers in soil from sites S1, S2, S3 and S5 were not significantly different between seasons (Table 2). Differences in soil stability (Jacobson 1997), soil structure and nutrient content (Johnson et al. 1992), and micro-topography (Gibson and Hetrick 1988) affect AM-fungal spore dynamics. Although physical differences are present within and between study sites, the soil BC of Mimosa species in general has a higher nutrient content (OM, P, Ca and Mg) and milder conditions (pH, EC, temperature, shade) than the soil of OA (Table 3). Differences in soil structure are evident when in nonvegetated OA, for example, wind and rain easily erode the soil and disperse spores that may be "trapped" in the areas below the canopy of shrubs and trees. Mimosa resource islands may also function as AM-fungal spore-traps; this effect may also be related to topography, where sites S1, S3, S4, and S6 are of medium slope, and sites S2 and S5 are flat (Table 1). A similar pattern of AM-fungal spore distribution and spore-traps has also been found in plant species such as *Jatropha cuneata* Wiggnis et Roll, *Larrea tridentata* (Sessé & Mociño ex D.C.) Coville, *Lysiloma candida* Brandegee, and *Prosopis articulata* S. Watson, among others (Carrillo-García et al. 1999). However, not all the shrubs and trees that accumulate AM-fungal spores in the soil under their canopies can form resource islands (e.g., members of the Cactaceae, Euphorbiaceae, Lamiaceae and Zygophyllaceae families) as discussed by Carrillo-García et al. (1999).

Mimosa species as resource islands, and their function

As well as plant communities in the Valley (Camargo-Ricalde et al. 2002a), the type, degree and intensity of environmental disturbance is another factor that can affect AM-fungal population dynamics (Allen 1991: Dhillion and Zak 1993; Dhillion et al. 1994; Carrillo-García et al. 1999; Dhillion 1999). Within the Valley, three main forms of ecological degradation have been recognized: an increase in the number of unplanned crop fields, extensive goat grazing, and deforestation (Zavala-Hurtado and Hernández-Cárdenas 1998). Though it is well known that AM-fungal inoculum is reduced when soil is disturbed, little is known about this factor in the study area; this is the first study of its kind in the Valley. Specifically within the study sites (Table 1), goat grazing, deforestation for creation of new agricultural fields, soil and rock extraction for mills (salt mines), and urban growth pressure, mainly through the opening of new dirt roads, are the most common environmental disturbances found in the Valley. More research is needed to understand how disturbance affects the microbial communities established in the resource islands formed by Mimosa species. Modifications of the resource islands may directly affect the associated flora (nurse-nursling association), which belongs mainly to the Agavaceae and Cactaceae families, most of them endemic to Mexico and to the Valley [e.g., Agave marmorata Roezl, A. salmiana Otto & Salm-Dyck, Coryphanta radians (DC) Britton & Rose, Escontria chiotilla (F.A.C. Weber) Rose, Mammilaria carnea Zucc. ex Pfeiffer, Neobuxbaumia tetetzo (F.A.C. Weber) Backeb.] (Camargo-Ricalde et al. 2002a, b). It is important to note that the majority of these species (45 of 50 species examined within the six study sites) are mycorrhizal (Camargo-Ricalde et al. 2002b).

Differences in the biological form and age of *Mimosa* species and the plants that establish in the *Mimosa* resource islands (e.g., globular, columnar, arboreous, rosette, shrubs, and trees), as well as the root morphology of each species (Hoffman and Mitchell 1986), may also influence the number of AM-fungal spores recorded in this study. Although Reynolds et al. (1999) report that, despite the different phenological strategies of the two

Mimos species Mimos	a species ar examined a <i>adenanthe</i>	for each sit	f OA, and in the V te were: S1 Mimo Mimosa calcicola,	W and D seasons o sa lacerata, S2 Mi S5 Mimosa texana	of 1999. The Mimos imosa polyantha, 5 i var. filipes, and 5	sa block de S3 were no S6 matter, 2	sign (ANOVA, <i>P</i> <(t enough data for th <i>TN</i> total nitrogen, <i>P</i>	0.05), and on Tukey's ne statistical analysis. phosphorus, <i>Ca</i> calci	s test ($P<0.05$). In the steet ($P<0.05$). In the steet of EC Electric conduction, Mg magnesium	e case of <i>TN</i> , there trivity, <i>OM</i> organic
Sites	BC/OA	W/D	pH (1:2 H ₂ O)	EC (µS/cm)	OM (%)	TN (%)	P (mEq/100 g)	Ca (mEq/100 g)	Mg (mEq/100 g)	Texture
S1	BC	≥C	7.39* 7.18*	0.192* 0.225*	7.59** 7.40**	0.60 0.46	5.03* 5.70*	4.99* 3.24*	0.90	Loamy sand Sandy loam
	OA	n≥∩	7.32*	0.179*	7.00** 7.00**	0.50 0.64	2.85* 4.02*	2.99* 4.13*	0.83	Loamy sand Sandy loam
S2	BC	≥C	6.13* 6.87*	0.123^{**} 0.136^{**}	2.74* 0.89*	0.01	6.7* 4.69*	1.37^{*} 1.00*	0.99*	Sandy loam Sandy loam
	OA	n≽∩	6.25* 6.13*	0.060**	2.04* 1.59*	0.17 0.047	3.55*	0.39*	0.74* 0.38*	Sandy loam Sandy loam
S3	BC	≷Q	6.75* 5.12*	0.190* 0.067*	5.10^{**} 2.61^{**}	0.26 0.20	318* 7.54*	0.04* 1.25*	3.97* 0.81*	Clay loam Sandv clav loam
	OA	D≷D	6.16* 5.32*	0.103* 0.059*	$\frac{3.82}{3.82}$	0.07	3.35*	0.54^{*} 1.80*	2.70* 0.94*	Clay loam Sandy loam
S4	BC	≷Q	7.40* 7.35*	0.265* 0.166*	15.31* 16.59*	$1.16 \\ 0.97$	4.86 4.19	0.03	1.55* 1.50*	Sandy loam Sandv clav loam
	OA	≥D	7.27* 7.46*	0.237 * 0.211 *	13.40*11.74*	$0.85 \\ 1.13$	4.02 5.03	0.03	1.12* 0.93*	Sandy loam Clay loam
S5	BC	≷Q	6.04^{*} 5.18*	0.078^{*} 0.051^{*}	5.74** 5.74**	0.20 0.04	5.03 5.36	0.16^{**} 0.179^{**}	0.68 0.56	Sandy loam Sandy loam
	OA	₽D	6.02* 6.43*	0.036^{*} 0.051^{*}	0.63^{**} 2.42 ^{**}	0.06 0.17	4.19 3.35	0.21^{**} 0.21^{**}	0.53 0.68	Sandy clay loam Sandy loam
S6	BC	≥D	7.39* 7.51*	0.225* 0.198*	5.55* 6.06*	0.01 0.60	3.69 3.85	0.04 0.04	1.15 0.64	Clay loam Clay loam
	OA	₽Q	7.53* 7.48*	0.158^{*} 0.204^{*}	4.78* 5.48*	$0.031 \\ 0.35$	3.52 3.35	0.04 0.04	0.49 1.08	Clay loam Clay loam
* Signi ** Sign	ficant diffe	rence betwee erence only	en both the soil BC between the soil B	C of Mimosa specie C of Mimosa speci	ss and the soil of O. ies and the soil of C	A, and the M OA, but not b	⁷ and D seasons between seasons			

ളാ **Table 3** Comparison of the soil physico-chemical characteristics found in the soil BC of *Mimosa Iuisana*. Statistical assessment was based on an analysis of variance, randomized

shrubs that form resource islands [*Larrea tridentata* (Sessé & Mociño ex D.C.) Coville and *Prospois glandulosa* Torr.], they are similar in function, and the stage of maturity of a resource island complex did not seem to be a significant factor influencing the growth and physiological activity of these shrubs. No attention, however, was paid to mycorrhizal propagules in the soil, where, according to our data, changes can occur.

Mimosa resource islands are rich not only in nutrients, but also in mycorrhizal propagules. Mimosa species can serve as mycorrhizal resource islands in two ways, i.e., by directly affecting AM-fungal spore dynamics, and by serving as spore-traps. The use of Mimosa resource islands as an option for biodiversity conservation and for land restoration ought to be considered in the Tehuacán-Cuicatlán Valley. Several questions in relation to AM in Mimosa resource islands have arisen during this study (e.g., the role of wet and dry seasons, type and quality of root exudates, spore dynamics and microbe-nutrient interactions, nurse plants and AM symbiosis, function of the different Mimosa species, etc.). For a better understanding of the ecological importance of Mimosa resource islands in arid and semiarid ecosystems, more research is needed on interactions within these communities.

Acknowledgements We thank Carolina Jiménez Gonzáles and Verónica García García for their assistance in the laboratory and the fieldwork, Rosalva García Sánchez for her logistic support, and two reviewers for their constructive comments. This work was supported in part by the Consejo Nacional de Ciencia y Tecnología (CONACyT, grant 112386 to S.L. C.-R.) and the Universidad Autónoma Metropolitana. This work is part of the Management of Biodiversity Research and TERG group at the Agricultural University of Norway led by S.S.D.

References

- Allen EB, Allen MF (1986) Water relations of xeric grasses in the field: interactions of mycorrhizas and competition. New Phytol 104:559–571
- Allen MF (1991) The ecology of mycorrhizae. Cambridge University Press, New York
- Allen MF, Smith WK, Moore TS, Christensen M (1981) Comparative water relations and photosynthesis of mycorrhizal and non-mycorrhizal *Bouteloua gracilis*. New Phytol 88:683–693
- Anderson RC, Liberta AE, Dickman LA (1984) Interaction of vascular plants and vesicular-arbuscular mycorrhizal fungi across a soil moisture-nutrient gradient. Oecologia 64:111–117
- Bethlenfalvay GJ, Dakessian S, Pacovsky RS (1984) Mycorrhizae in southern California desert: ecological implications. Can J Bot 62:519–524
- Brundrett M (1991) Mycorrhizas in natural ecosystems. Adv Ecol Res 21:171–313
- Camargo-Ricalde SL, Dhillion SS, Grether R (2002a) Community structure of endemic *Mimosa* species and environmental heterogeneity in a semi-arid Mexican valley. J Veg Sci 13 (in press)
- Camargo-Ricalde SL, Dhillion SS, Jiménez-González C (2002b) Mycorrhizal perennials of the "matorral xerófilo" and the "selva baja caducifolia" communities in the semiarid Tehuacán-Cuicatlán Valley, Mexico. Mycorrhiza (in press)
- Carrillo-García A, León de la Luz JL, Bashan Y, Bethlenfalvay GJ (1999) Nurse plants, mycorrhizae, and plant establishment in a disturbed area of the Sonoran Desert. Rest Ecol 7:321–335

- Casas A, Valiente-Banuet A, Viveros JL, Caballero J, Cortés L, Dávila P, Lira R, Rodríguez I (2001) Plant resources of the Tehuacán-Cuicatlán Valley, Mexico. Econ Bot 55:129–166
- Coleman DC, Reid CPP, Cole CV (1983) Biological strategies of nutrient cycling in soil systems. Adv Ecol Res 13:1–55
- Dhillion SS (1999) Environmental heterogeneity, animal disturbances, microsite characteristics, and seedling establishment in a *Quercus havardii* community. Rest Ecol 7:399–406
- Dhillion SS, Anderson RC (1993) Seasonal dynamics of dominant species of arbuscular mycorrhizae in burned and unburned sand prairies. Can J Bot 71:1625–1630
- Dhillion SS, Zak JC (1993) Microbial dynamics in arid ecosystems: desertification and the potential role of Mycorrhizas. Rev Chil Hist Nat 66:253–270
- Dhillion SS, McGinley MA, Friese CF, Zak JC (1994) Construction of sand shinnery oak communities of the Llano Estacado: animal disturbances, plant community structure and restoration. Rest Ecol 2:51–60
- Dhillion SS, Vidiella PE, Aquilera LE, Friese CF, De León E, Armesto JJ, Zak JC (1995) Mycorrhizal plants and fungi in the fog-free Pacific coastal desert of Chile. Mycorrhiza 5:381–386
- Fitter AH, Garbaye J (1994) Interactions between mycorrhizal fungi and other soil organisms. Plant Soil 159:123–132
- Garbaye J (1991) Biological interactions in the mycorrhizosphere. Experentia 47:370–375
- García-Moya E, McKell CM (1970) Contribution to the nitrogen economy of a desert-wash plant community. Ecology 51:81–88
- Garner W, Steinberger Y (1989) A proposed mechanism for the formation of "Fertile Islands" in the desert ecosystem. J Arid Environ 16:257–262
- Gazey C, Abbott LK, Robson AD (1992) The rate of development of mycorrhizas affects the onset of sporulation and production of external hyphae by two species of *Acaulospora*. Mycol Res 96:643–650
- Gerdemann JW, Nicolson TH (1963) Spores of mycorrhizal *Endogone* species extracted from soil by wet sieving and decanting. Trans Br Mycol Soc 46:235–244
- Gibson DJ, Hetrick BAD (1988) Topographic and fire effects on the composition and abundance of VAM-mycorrhizal fungi in a tallgrass prairie. Mycologia 80:433–441
- Grether R, Camargo-Ricalde SL, Martínez-Bernal A (1996) Species of genus *Mimosa* (Leguminosae) in Mexico (in Spanish with English summary). Bol Soc Bot Mex 58:149–152
- Hoffman MT, Mitchell DT (1986) The root morphology of some legume spp. in the south-western Cape and the relationship of vesicular-arbuscular mycorrhizas with dry mass and phosphorus content of Acacia saligna seedlings. S Afr J Bot 52:316– 320
- Jacobson KM (1997) Moisture and substrate stability determine VA-mycorrhizal fungal community distribution and structure in an arid grassland. J Arid Environ 35:59–75
- Johnson NC, Tilman D, Wedin D (1992) Plant and soil controls on mycorrhizal fungal communities. Ecology 73:2034–2042
- Martínez-Bernal A, Grether R (2002) Mimosa (in Spanish). In: Kelly L, Medina-Lemos R (eds) Flora del Valle de Tehuacán-Cuicatlán. Number 33, Biology Institute, National Autonomous University of Mexico (UNAM) (in press)
- Mayo K, Davis RE, Motta J (1986) Stimulation of germination of spores of *Glomus versiforme* by spore-associated bacteria. Mycologia 78:426–431
- McGee P (1989) Variation in propagule numbers of vesiculararbuscular mycorrhizal fungi in a semi-arid soil. Mycol Res 92:28–33
- Merryweather J, Fitter AH (1998) The arbuscular mycorrhizal fungi of *Hyacinthoides non-scripta*. II. Seasonal and spatial patterns of fungal populations. New Phytol 138:131–142
- Mosse B, Bowen GD (1968) The distribution of *Endogone* spores in some Australian and New Zealand soils, and in an experimental field soil at Rothamsted. Trans Br Mycol Soc 51:485–492
- Nadian H, Smith SE, Alston AM, Murray RS, Siebert BD (1998) Effects of soil compaction on phosphorus uptake and growth of

Trifolium subterraneum colonized by four species of vesiculararbuscular mycorrhizal fungi. New Phytol 139:155–165

- Reynolds JF, Virginia RA, Kemp PR, de Soyza AG, Tremmel DC (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource islands development. Ecol Monogr 69:69–106
- Sanders IR, Fitter AH (1992) The ecology and functioning of vesicular-arbuscular mycorrhizas in co-existing grassland species. I. Seasonal patterns of mycorrhizal occurrence and morphology. New Phytol 120:517–524
- Schenck NC, Perez Y (1990) Manual of the identification of VA mycorrhizal fungi. Synergistic Publications, Gainesville, Fla.
- Snyder R, Friese CF (2001) A survey of arbuscular mycorrhizal fungal root inoculum associated with harvester ants nests (*Pogonomyrmex occidentalis*) across the western United States. Mycorrhiza 11:163–165
- Sousa M, Delgado A (1993) Mexican Leguminosae: phytogeography, endemism, and origins. In: Ramamoorthy TP, Bye R, Lot A, Fa J (eds) Biological diversity of Mexico: origins and distribution. Oxford University Press, Oxford, pp 459–511
- Stürmer SL, Bellei MM (1994) Composition and seasonal variation of spore populations of arbuscular mycorrhizal fungi in dune soils on the island of Santa Catarina, Brazil. Can J Bot 72:359– 363
- Tarafdar JC, Praveen-Kumar (1996) The role of vesicular arbuscular mycorrhizal fungi on crop, tree and grasses grown in an arid environment. J Arid Environ 34:197–203
- Tiedemann AR, Klemmedson JO (1973) Effect of mesquite on physical and chemical properties of the soil. J Range Manage 26:27–29
- Valiente-Banuet A, Ezcurra E (1991) Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. J Ecol 79:961–971

- Valiente-Banuet A, Vite F, Zavala-Hurtado JA (1991) Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*. J Veg Sci 2:11–14
- Van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72
- Vázquez-Alarcón A, Bautista-Aroche N (1993) Soil and water chemical analysis interpretation guide (in Spanish). Universidad Autónoma Chapingo, Department of Soils, Mexico
- Virginia RA, Jenkins MB, Jarrel WM (1986) Depth of root symbiont occurrence in soil. Biol Fertil Soils 2:127–130
- Walker C, Mize CW, McNabb HS Jr (1982) Populations of endogonaceous fungi at two locations in central Iowa. Can J Bot 60:2518–2529
- Warner NJ, Allen MF, MacMahon JA (1987) Dispersal agents of vesicular-arbuscular mycorrhizal fungi in a disturbed arid ecosystem. Mycologia 79:721–730
- Whitford W (1996) The importance of the biodiversity of soil biota in arid ecosystems. Biodivers Conserv 5:185–195
- Zak JC, Sinsabaugh R, MacKay WP (1995) Windows of opportunity in desert ecosystems: their implications to fungal community development. Can J Bot 73:S1407–S1414
- Zavala-Hurtado JA, Hernández-Cárdenas G (1998) Characterization and diagnosis study of the area proposed as Tehuacán-Cuicatlán Biosphere Reserve (in Spanish). Universidad Autónoma Metropolitna-Instituto Nacional de Ecología (SE-MARNAP), México
- Zobel M, Moora M, Haukioja E (1997) Plant coexistence in the interactive environment: arbuscular mycorrhiza should not be out of mind. Oikos 78:202–208