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S. S. Dhillion · P. E. Vidiella · L. E. Aquilera C. F. Friese · E. De Leon · J. J. Armesto · J. C. Zak

Mycorrhizal plants and fungi in the fog-free Pacific coastal desert of Chile

Abstract The Chilean fog-free Pacific coastal desert, one of the driest desertic regions of the world, is undergoing rapid rates of desertification as a result of intensive agriculture, overgrazing and mining. There is an urgent need to document the mycorrhizal status of Chilean plants, and the role of the symbiosis in rehabilitation and preservation of species diversity. Here we present one of the first reports on the mycorrhizal status of annual and perennial herbs and shrubs from this region. Plants were collected during 1991 when rainfall was close to or above the annual average, providing the opportunity to asses several rare plant species. The plants examined included endemic species and endangered and rare geophytes. More than 90% of 38 species (19 families) were found to form exclusively arbuscular mycorrhizal fungi associations. Six species of mycorrhizal fungi were isolated from the root zones of plants sampled, four of which are undescribed.

Key words Arid · Endemic · Mycorrhizae · Chile · Geophyte · Symbionts

S. S. Dhillion (⊠)

Centre National de la Recherche Scientifique, CEFE, 1919 Route de Mende, BP 5051, F-34033 Montpellier, France

P. E. Vidiella · J. J. Armesto Laboratorio de Sistemática e Ecología Vegetal, Universidad de Chile, Casilla 653, Santiago, Chile

L. E. Aquilera Departamento de Biologia, Universidad de La Serena, La Serena, Chile

C. F. Friese Department of Biology, University of Dayton, Dayton, OH 45469, USA

E. De Leon · J. C. Zak Department of Biological Sciences, Texas Technical University, Lubbock, TX 79409-3131, USA

Introduction

Arid regions comprise about 40% total land cover of the earth (Evenari et al. 1985; Skujins 1992). Much of this land is undergoing desertification as a result of intensive agriculture, overgrazing and mining. For example, a detailed study of the semiarid region of Coquimbo, Chile showed that about 50% of the native plants species had disappeared as a consequence of desertification (Mabbutt and Floret 1980). The arid environments of South America are of fairly recent origin; climatic changes began in the mid-Eocene with a gradual decrease in temperature and an increase in the drying effect of the Andean range (e.g. Arroyo et al. 1982; Ochsenuis 1982). An attempt to rehabilitate these desertified lands requires the in-depth study of species distribution and potentially beneficial associated symbionts (Dhillion and Zak 1993).

The widespread occurrence and importance to plant growth, nutrition and establishment of symbiotic arbuscular mycorrhizal (AM) fungi are well established (Harley and Smith 1983; Allen 1991), and there are many reports on the mycorrhizal status of plants from natural ecosystems (e.g. Brundrett 1991; Allsopp and Stock 1993; Dhillion and Zak 1993; Dhillion and Friese 1994). However, relatively few studies have been published on the mycorrhizas of arid regions (see references in Trappe 1981; Dhillion and Zak 1993), and the documentation of mycorrhizas from arid regions of South America is even more scarce. Of the 61 arid region plant families studied worldwide, 89% were found to have mycorrhizal members (Dhillion and Zak 1993); however, none of these studies included any accounts from South America.

In this paper, we report on the mycorrhizal status of plants and characterize mycorrhizal fungi in Chile. Plants were examined from various locations of the Chilean fog-free desert, one of the driest desertic regions of the world (Skujins 1992).

Materials and methods

Plants were collected on 15–20 November 1991 from the fog-free coastal desert in North-Central Chile, 28–32° lat, at locations along the N-S transect in region IV of the arid regions of Chile (Fig. 1). Atriplex and Acacia spp. plants were sampled in January 1991. This study is the first report on the mycorrhizal status of several plants collected during 1991 when rainfall was close to or, in most collection sites, above the annual average (Fig. 2), thus providing the opportunity to assess several otherwise rarely obtainable species. The year of collection was regarded as a "heavy desert bloom" year. A detailed description of the region and sites has been presented by Armesto and Vidiella (1993). The soil in this region generally has very low organic matter, moderate P (Olsen) and N, and a neutral pH (Table 1). Soils associated with Acacia caven had relatively high P (33 ppm; Table 1).

Plant samples were excavated so as to minimize root loss. The root system of each plant along with associated root-zone soil was carefully placed in a vial of 10:35:10:5 formalin-water-ethanolacetic acid (FAA) and kept for further processing. Roots in FAA were rinsed in water and placed for clearing in 10% KOH at room temperature for 7 days. The roots were then stained with trypan blue to assess percentage AM colonization using the gridline intersection method (Giovannetti and Mosse 1980). The presence of arbuscules, and mycorrhizal vesicles and hyphae were used to determine colonization. Hyphae were scored as mycorrhizal when attached to arbuscules or mycorrhizal vesicles or both. AM spores were isolated from a 20-ml soil sample employing a wet-sieving density gradient procedure (Anderson and Liberta 1989). Only intact, cytoplasm-filled spores were counted and identified following Schenck and Perez (1990).

Results and discussion

Plant species and mycorrhizal colonization

This study showed that 84% of the 38 plant species sampled, and 95% of the families, were mycorrhizal (Table 2). All species endemic to the Chilean arid regions had relatively high colonization levels, in most cases with the presence of arbuscules and vesicles, except for some species of Atriplex, which belong to a typically nonmycorrhizal family, Chenopodiaceae (Table 2; Newman and Reddell 1987). Atriplex spp. had varying levels of AM. Similar trends were reported among Atriplex spp. in South Africa (Allsopp and Stock 1993). Geophytes (e.g. Leontochir ovallei, Hippeastrum bagnoldii, Sisyrinchium graminifolium), many of which are either endangered or rare (CONAF 1989; Hoffmann 1989), were found to be highly mycorrhizal. In South Africa, Mesembryanthemum sp. (classified as belonging to the family Mesembryanthemaceae in South Africa; Allsopp and Stock 1993) was found to be nonmycorrhizal, unlike in this study, which showed Mesembryanthemum cristallinum (Aizoaceae) to have relatively high levels of colonization (Table 2). Samples of Helenium aromaticum collected at different sites showed a wide range of colonization levels of 0-23% (Table 2). It is likely that site-specific edaphic factors influence the degree of colonization in these plants. No ectomycorrhizas were observed in any of the plants.

Families regarded as nonmycorrhizal, e.g. Portulaceae, Chenopodiacea (Newman and Reddell 1987), had

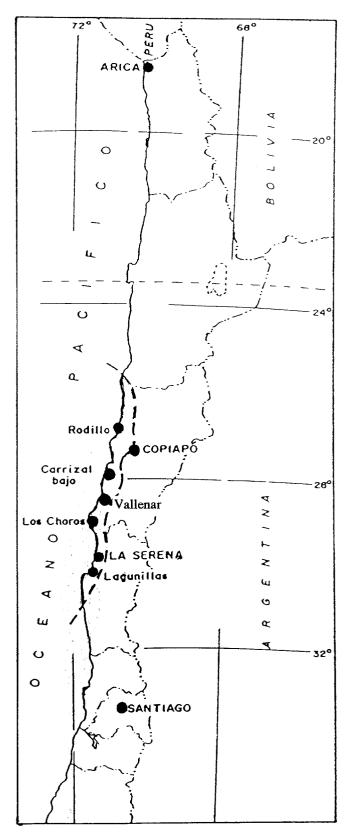


Fig. 1 The location of the fog-free Pacific coastal desert and collection sites in Northern Chile (adapted from Armesto and Vadiella 1993)

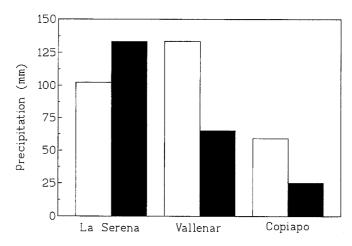


Fig. 2 Mean annual precipitation for 1991 (□) and the past 15 years (■) occurring in the fog-free Pacific coastal desert of Chile (adapted from Munoz 1991)

either no mycorrhizal associations or very low colonization levels (Table 2), and no spores were found in the root-zone soil of these plants (Table 2). Of 61 plant families surveyed in arid and semi-arid regions worldwide (none were from arid regions in South America), 89% were found to be mycorrhizal, and members of 84% of the families surveyed formed exclusively AM fungal associations (Dhillion and Zak 1993). However, only 69% of the species sampled (a total of 338) were mycorrhizal, largely due to the predominance of typically nonmycorrhizal species of the Chenopodiaceae (Dhillion and Zak 1993). Allsopp and Stock (1993) also showed that only 62% (a total of 332 species examined) of the flora of Cape Floristic Region of South Africa formed AM. They attributed the low mycorrhizal rep-

Table 1 Characteristics (mean \pm SD) of soil samples removed from the surface hardpan layer in Lagunillas (n=21) (adapted from Gutiérrez et al. 1992), and from under the canopy of *Atriplex* spp. plants at Canela Alta (n=3), Trapiche (n=3), Canto del

resentation to the dominant nonmycorrhizal families of the region, the Proteaceae and Restionaceae.

Rainfall is extremely variable in the environment studied and frequently the plants must be able to recover from one or more years of drought (Armesto and Vidiella 1993). Plants exist as seeds, rhizomes, tubers or bulbs awaiting adequate moisture conditions. The presence of arbuscules, active sites of exchange between host and fungus, suggest functional relationships between the symbionts. Mycorrhizal associations can provide a substantial advantage to plants by adding to the volume of soil exploitable by the root system for water and inorganic nutrients. In arid regions, plant groups which are typically nonmycorrhizal may sustain AM, e.g. members of Amarantheceae long classified as clearly nonmycorrhizal in most systems were found to be highly mycorrhizal in semi-arid regions of India (Neeraj et al. 1991).

Mycorrhizal fungal species

Spore richness was low (6 species, Table 2). The common AM spore types were *Glomus* sp.1, *Glomus* sp.2 and *Glomus aggregatum*, in order of decreasing abundance. Spores of at least one species were found in the root-zone soil of each plant which was mycorrhizal, except in the root-zone soil of *Helenium aromaticum* and *Homalocaropus bowlesioides* (Table 2).

Viable mycorrhizal fungi persist within roots of perennial hosts over the dormant season, but annuals may depend more on propagules in soil for new colonization each growing season. In arid and semi-arid regions experiencing extreme drought and a prolonged number of dry months between precipitation periods, it is likely

Agua (n=3), Obispito (n=3), and Copiapó (n=3). Soils associated with *Acacia caven* (n=5) shrubs were collected at Tangue, Las Cardas, Tololo and Chapilca, all sites located within a 50-km radius of Lagunillas

Site	рН	Electrical conductivity (mmho/cm)	Organic matter (%)	N	P	K	Ca	Mg
				(ppm)				
Lagunillas								
	6.78	0.7	1.0	14.0	19.5	213	791	86
Atriplex spp.								
	Canela Alta	l ^a						
	7.3	1.0	1.2	9.0	12.0	324		
	Trapiche ^b							
	7.9	4.1	1.0	6.0	9.0	229		
	Canto del A	Agua ^c						
	8.1	2.8	0.7	7.0	19.0	293		
	Obispito ^c							
	8.0	1.5	0.4	1.0	3.0	79		
	Copiapó							
	7.9	0.9	1.0	5.0	11.0	172.		
Acacia caven								
	7.3	0.6	0.8	14.0	33.0	237		

^a Within 50 km of Los Choros

^b Within 50 km of Rodillo

[°] Within 50 km of Copiapó

Table 2 Collection sites, habit, species geographic distribution of and arbuscular mycorrhizal (AM) status of plant species (% root length colonized by AM fungi) and AM fungal species collected from the fog-free Pacific coastal desert of Chile. When known, the photosynthetic system ($CAM\ C_3$, C_4) and conservation status (E endangered, R rare) is provided (CONAF 1989; Arroyo et al. 1990. AM colonization is given as fungal arbuscules (A), vesicles (V) and spores (S) present in roots; for $Acacia\ caven\ arbuscules$ and vesicles were present in roots but percent colonization was not obtained. The AM species isolated from root-zone soil were 1 $Glomus\ aggregatum,\ 2\ Glomus\ sp.1,\ 3\ Glomus\ sp.2,\ 4\ Glomus\ sp.3,\ 5\ Gigaspora\ albida,\ 6\ Scutellospora\ sp.\ (+\ intact\ spores\ present\ but\ not\ identified,\ -\ spores\ absent). <math>Amphitropical$

(sensu Raven 1963) occurring primarily in warm deserts of North and South America, but also present in the American tropical regions; *Andean* genera mostly restricted to the tropical and/or temperate Andes of South America; *Cosmopolitan* species of genera distributed in several continents both in temperate and tropical regions, *Endemic* genera confined to the Pacific coastal desert of Chile and Peru; *Tropical America* genera primarily distributed in the lowland tropics of Central and South America; *Mediterranean* genera distributed in the Mediterranean regions, North America, South Africa, Canary Islands, Australia, Arabia, and Chile. The nomenclature of all species follows Marticorena and Quezada (1985) except for that of the Nolanaceae, which follows Mesa 1981)

Family and species (number of plants sampled)	Collection site	Habit	Distribution	Colonization (mean %)	AM species
Aizoaceae					
Mesembryanthemum cristallinum	(2)Lagunillas	Annual, CAM	Mediterranean	32 (A)	1–6
Amaryllidaceae					
Hippeastrum bagnoldii (3)	Carrizal Bajo	Geophyte,	Andean	62 (A)	2, 3
Hippeastrum bagnoldi (3)	Lagunillas	Geophyte,	Andean	40 (A, V)	1-6
Leontochir ovallei (2)	Carrizal Bajo	Geophyte, E	Endemic	36 (A, V)	2, 3, 6
Rhodophiala sp. (1)	Carrizal Bajo	Geophyte, R?	Andean	25 (V)	2, 3, 6
Asteraceae				2.1	
Chaetanthera linearis (2)	Lagunillas	Annual	Andean	24	2, 3
Chaetanthera sp. (1)	Carrizal Bajo	Annual	Andean	15	2, 4 2, 3
Encelia canescens (5)	Lagunillas	Shrub, C ₃	Amphitropical	42 (A, V)	2, 3
Helenium aromaticum (4)	Rodillo	Annual	Ainphitropical	0	_
Helenium aromaticum (5)	Carrizal Bajo	Annual	Amphitropical	23	_
Helenium aromaticum (2)	Lagunillas	Annual	Amphitropical	15 (A)	2, 3 2, 3, 5
Perityle emoryi (10)	Rodillo	Chamaephyte	Amphitropical	47 (A, V)	2, 3, 5
Boraginaceae					
Cryptantha glomerata (2)	Lagunillas	Annual	Cosmopolitan	18	2 3, 6
Tiquilia litoralis (1)	Rodillo	Hemicryptophyte	Amphitropical	19 (V)	3, 6
Chenopodiaceae					
Atriplex coquimbensis (3)	Trapiche ^a	Shrub, C ₄	Endemic	0.7	+
Atriplex deserticola (3)	Canto del Agua ^b	Shrub, C ₄	Endemic	3.4	+
Atriplex madariagae (3)	Copiapó	Shrub, C ₄	Endemic	1.6	+
Atriplex madariagae (3)	Obispito ^c	Shrub, C ₄	Endemic	0	_
Atriplex repanada (3)	Canela Altad	Shrub, C ₄	Endemic	5.1 (A, V)	+
Gramineae					
Schismus arabicus (4)	Lagunillas	Annual	Cosmopolitan	6	2
Iridaceae			-		
Sisyrinchium graminifolium (2)	Carrizal Bajo	Geophyte, R	Tropical America	37 (A, V)	3
Fabaceae (Leguminosae)	•	1 2	•	, , ,	
Acacia caven (3)	Tanque ^d	Shrub, C_4	Endemic	(A, V)	+
Acacia caven (3)	Las Ĉardas ^d	Shrub, C ₄	Endemic	(A, V)	+ + + 3 2
Acacia caven (3)	Tololo ^d	Shrub, C4	Endemic	(A, V)	+
Acacia caven (3)	Chapilca ^d	Shrub, C₄	Endemic	(A, V)	+
Adesmia filifolia (2)	Carrizal Bajo	Annual, C ₃	Andean	46 (A, V)	3
Adesmia tenella (2)	Carrizal Bajo	Annual, C_3	Andean	25 `	2
Liliaceae	- ······ , ·	, 3			
Camassia biflora (8)	Rodillo	Geophyte	Amphitropical	43 (A, V)	3, 4, 6
Malvaceae		1 3	1 1	` ' '	
Cristaria glaucophylla (2)	Los Choros	Shrub	Endemic	43 (A, V)	5, 6
Nolanaceae				` ' '	•
Nolana paradoxa (1)	Lagunillas	Annual	Endemic	24 (A)	1
Onagraceae (1)	2480	£ 20077 -7771		(*)	
Camissonia dentata (2)	Lagunillas	Annual	Amphitropical	20	1, 2
Oenothera sp.1 (5)	Lagunillas	Annual	Amphitropical	15 (A)	2, 3
Oenothera sp.2 (2)	Rodillo	Annual	Amphitropical	0	<u>_</u>
Oenothera sp.3 (3)	Carrizal Bajo	Annual	Amphitropical	6	2
Oenothera sp. 4 (8)	Los Choros	Annual	Amphitropical	15 (A, V)	5, 6
Plantaginaceae	200 010100			(-) -/	, =
Plantago hispidula (3)	Lagunillas	Annual	Cosmopolitan	34 (A, V)	2,3,4,5
Portulacaceae	2454111140	- **********	2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	()	, , , , , , ,
Calandrinia grandiflora (4)	Rodillo	Annual, CAM	Andean	8	2
Calandrinia sp. (5)	Rodillo	Annual, CAM	Andean	Ö	_
Philippiamra celosioides (2)	Rodillo	Annual, CAM	Endemic	32 (A)	2, 3
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Table 2 (continued)

Family and species (number of plants sampled)	Collection site	Habit	Distribution	Colonization (mean %)	AM species
Rubiaceae Cruckshanksia sp. (2)	Carrizal Bajo	Hemicryptophyte, CAM	Endemic	21 (A, V)	2, 3, 5
Santalaceae Quinchamalium excresens (1)	Carrizal Bajo	Annual	Andean	0	_
Solanaceae Schizanthus candidus (2)	Carrizal Bajo	Annual, C ₃ , R	Endemic	14 (A, V)	3
Tecophilaeaceae Zephyra elegans (2)	Carrizal Bajo	Geophyte	Endemic	46 (A, V, S)	3, 5
Zephyra elegans (2) Umbelliferae	Los Choros	Geophyte	Endemic	35 (A, V)	2, 6
Eryngium coquimbanum (1) Homalocarpus bowlesioides (3)	Lagunillas Los Choros	Annual, C_3 Annual, C_3 R?	Cosmopolitan Endemic	0 5	_

a Within 50 km of Los Choros

that fungal spores serve as important perennating propagules. However, the importance of different inoculum types varies considerably in different communities (Gemma et al. 1989; Friese and Allen 1991; Friese and Allen 1993; Dhillion and Anderson 1993).

Spores found were of three genera, representative species of which are described below:

Glomus aggregatum Schenck and Smith

Chlamydospores globose to subglobose, rarely cylindrical, diameter of globose spores 65–80 μ m, while subglobose 60–96 \times 57–74 μ m, light yellow to light tan, spore wall 2 μ m thick, outer light yellow 1.20 μ m thick, inner yellow-tan, 0.80 μ m, membranous, subtending hyphae curved, 4 μ m diameter, pore open, spore contents extending into subtending hyphae.

Glomus sp. 1

Spores globose, light yellow, 165 μ m mean diameter, wall 17.50–20.50 μ m thick, double-layered, outer spore wall slightly wrinkled, straight subtending hyphae. *Glomus* sp. 2

Spores globose, golden-brown, 135 μm mean diameter, wall 17.25 μm thick, double-layered, outer spore wall

wrinkled, straight subtending hyphae. *Glomus* sp. 3

Spores globose, dark brown (yellowish hue), 180 μ m mean diameter, wall 15.00 μ m thick, double-layered, outer spore wall ridged, straight subtending hyphae.

Gigaspora albida Schenck and Smith

Spores globose to subglobose, light yellow, diameter 225–232 μm when globose and when subglobose 225 \times 242.5 μm , bulbous attachment 45 \times 33 μm , wall 3.85 μm thick, laminated, inner wall yellow-brown, 1.6 μm thick.

Scutellospora sp.

Spores globose to subglobose, golden-yellow to yellow-brown, 160–245 μm diameter, wall 10 μm thick, three-layered, subtending hyphae 22.5 μm at base, swelling up to 37.5 μm and then tapering to 7.5 μm , 57.5 μm long, two to three septa present, subtending hyphal wall 2.5 μm thick.

Given the high occurrence of mycorrhizal associations in the Chilean arid regions, and the potential benefits of the mycorrhizal symbiosis on plant establishment and survival and on soil structure, it is imperative that their study be incorporated into restoration and rehabilitation practices (Allen 1989; Dhillion and Zak 1993). The importance of studying plant-mycorrhizal associations is further heightened by the fact that these obligate fungal symbionts are adversely affected by soil disturbances and processes associated with desertification (Allen 1989; Allen 1991; Dhillion and Zak 1993). Thus it is possible that the loss of endemic plant species may be in part related to the loss of indigenous beneficial AM symbionts or vice versa. Because the mycorrhizal status of certain families and genera is varied, it is important to evaluate mycorrhizas in terms of soil characteristics, and the mycorrhizal status of the dominant species, and thus the inoculum, prevailing in any particular habitat (Allsopp and Stock 1993; Dhillion and Zak 1993; Dhillion and Friese 1994). Specifically, largescale studies should attempt to include investigations on (1) the relationship of endemic plants (especially rare or endangered species) and mycorrhizal fungi, (2) AM fungal propagules and their precise role and mode of survival in this region, and (3) the impact of disturbance (and desertification) on AM fungi and the soil environment.

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^b Within 50 km of Rodillo

^c Within 50 km of Copiapó

^d Within 50 km of Lagunillas

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