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ARBUSCULAR MYCORRHIZAL FUNGI ASSOCIATED WITH COASTAL VEGETATION IN CHUBURNA, YUCATAN, MEXICO

[HONGOS MICORRIZÓGENOS ARBUSCULARES ASOCIADOS A LA VEGETACIÓN COSTERA EN CHUBURNÁ, YUCATÁN, MÉXICO]

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SUMMARY

Plant species that successfully establish in environments of recent formation, such as barrier islands, exhibit life history traits that allow them to efficiently capture nutrients and water, such ability may be largely due to interactions these plants establish with mutualistic arbuscular mycorrhizal fungi (AMF). The goal of this work was to characterize plant community present at two sites, a barrier island and a coastal dune system; the influence of marine proximity against the lagoon proximity and to relate aspects of these plant communities to soil fertility and AMF presence in roots y la rhizosphere. The study was conducted at “La Carbonera” in Chuburná, Yucatan, Mexico. At each site we established transects, where we placed three 5 x 5-m plots. Within each plot we surveyed vegetation (recording present species and plant cover), collected root samples to assess AMF colonization, and collected soil samples for nutrient analyses and quantification of AMF spores in rhizosphere. We found a total of 36 plant species from 28 families, with herbaceous life form being the most common. All plant species recorded were colonized by AMF. Nonetheless, AMF spores were scarce in soil, which may be due to immediate AMF root colonization of host plants trigger by low phosphorus and nitrogen availability in soil. Our results suggest that the AMF propagules may colonize the roots since the first stages of plant establishment on sand dunes.

Keywords: Barrier island; plant composition; coastal dune; arbuscular mycorrhizal fungi; propagules; succession.

RESUMEN

Las especies vegetales que se establecen de forma exitosa en ambientes de reciente formación, como los sistemas dunares y las islas de barrera, presentan características de historia de vida que les permiten aumentar la eficiencia en la incorporación de nutrimentos y agua, como puede ser la capacidad de establecer asociaciones mutualistas como la micorriza arbuscular. Con el fin de conocer la estructura de la vegetación en una isla de barrera y en un sistema de dunas costeras, la influencia de la vecindad marina contra la lagunar, y relacionar estos aspectos con la fertilidad y la presencia de hongos micorrizógenos arbusculares (HMA) en las raíces y la rizósfera. Este estudio se llevó a cabo en “La Carbonera”, Chuburná, Yucatán, México. Se trazó una línea longitudinal sobre la isla de barrera iniciando en el punto de acumulación de sedimento y cada 50 m se colocaron tres cuados de 5x5 m, uno pegado al mar, otro en la parte media y el último aledaño a la laguna. En la duna costera se tiró una línea iniciando en la línea de mar y concluyendo en el borde del matorral de duna y cada 5m se colocó un cuado de 5x5 m. Para cada especie vegetal dentro del cuadro, se estimó su cobertura, se colectaron sus raíces y se verificó la presencia de HMA. En cada cuadro se colectó 1 kg de suelo rizosférico para separar, cuantificar e identificar las esporas de HMA. Se encontraron 36 especies vegetales pertenecientes a 28 familias, siendo más abundante la forma de vida herbácea. Todas las especies analizadas presentaron HMA en sus raíces. Sin embargo, no se encontraron esporas de HMA en el suelo rizosférico, lo que podría significar una rápida germinación y colonización de las raíces de plantas hospederas debido a una baja disponibilidad de fósforo y nitrógeno en suelo. Nuestros resultados sugieren que los propágulos de los AMF colonizan de manera rápida de las raíces desde las primeras fases de establecimiento de las plantas en las dunas costeras.

Palabras clave: Isla de barrera; composición vegetal; duna costera; hongos micorrizógenos arbusculares; propágulos, sucesión.

INTRODUCTION

In coastal habitats, plant succession begins with pioneer species arrival. They can tolerate extreme conditions such as: low water availability, being burried due to sand movement, and high levels of soil salinity and temperature (Moreno-Casasola, 1982, 1988; Moreno-Casasola and Castillo, 1992; Martínez *et al.*, 1997). One potential strategy to cope with such conditions and ensure successful establishment in these habitats is via interactions with arbuscular mycorrhizal fungi (AMF). These fungi develop mutualistic associations with plants and provide them with benefits such as higher resistance to water stress (Azcón-Aguilar y Barea, 1996; Augé, 2001), plant nutrient status improvement, and ability to colonize. In doing so, AMF facilitate plant succession, increase plant community diversity (Sanders *et al.*, 1996; van der Heijden *et al.*, 1998), and promote more suitable physical, chemical, and structural soil properties for plant growth (Requena *et al.*, 2001).

Research on AMF in Mexican coastal systems is scarce. Sigüenza *et al*. (1996) conducted a study in Baja California which showed that AMF spore abundance changed as a function of water availability. In addition, Corkidi and Rincón (1997a) reported that 97% of the known plant species found in coastal dunes in Veracruz had AMF colonization and inoculation likelihood increased with stability in soil conditions. In addition, Corkidi and Rincón (1997b) also emphasize the importance of mycorrhizal colonization for biomass production of plant species in coastal dune systems. In Yucatan, a previous study reported colonization by AMF in roots of several pioneer species in coastal dune vegetation (Carrillo *et al*., 2004; Guadarrama *et al*. 2012), and Ramos-Zapata *et al*. (2011) reported that AMF propagule availability is mainly determined by seasonality than by the degree of dune physical stability.

Coastal areas of the state of Yucatan are affected by hurricanes which drive changes in the availability of nutrients and substrate, as well as modify the structure of the vegetation (Rivera-Arriaga *et al*., 2004). Depending on their intensity, hurricanes may destroy entire plant communities (González-Loera and Moreno-Casasola, 1982). In 1988, hurricane Gilbert caused changes in coastal lagoon system structure of "La Carbonera" in Chuburna, Yucatan. Fourteen years later, hurricane Isidore affected the same area, destroying the littoral zone. As a result of impacts of these two hurricanes, a connection now exists between the lagoon system and the ocean. In addition, due to sediment accumulation, a barrier island has been formed and has been swiftly colonized by plant species belonging to coastal dune vegetation of this region. Barrier islands develop by continuous nutrient deposition from the ocean, and are characterized by loss and gain of land depending on tide movement. Vegetation is also influenced by the ocean because salinity affects plant species both mechanically and physiologically. Plant species established close to shoreline tend to weight less (Reys and Acosta, 2003). Plant community succession in coastal dunes and barrier islands is a dynamic process where AMF may play a relevant role; however, regardless this importance, information on plant-AMF interactions in coastal habitats is scarce. Accordingly, the main goals of this study were: *i)* to describe plant community structure and composition present at a barrier island located in a coastal lagoon system of "La Carbonera" in Chuburna, Yucatan (Mexico), as well as in an adjacent coastal dune site; *ii)* to determine AMF presence in roots of plants located at both sites, *iii)* to identify AMF species present at both sites through quantification and identification of spores found in rhizosphere.

MATERIAL AND METHODS

Study area.

This work was conducted in a lagoon system called "La Carbonera", located between Chuburna and Sisal towns, in Yucatan, Mexico (21°13' 94" N, 89°53' 69" W y 21°14' 4" N, 89°53' 42" W) (Figure 1). This system was formed in 1988 by marine water movement over the littoral zone caused by hurricane Gilbert, as well as by an increase in water volume in marsh due to the high amount of rainfall caused by this hurricane. Subsequently, in 2002 hurricane Isidore caused a physical modification in the lagoon system that brought as a consequence littoral strip interruption, and the creation of a water channel and a barrier island. This latter is being actively colonized by plant species as substrate builds up. Adjacent to the island, and in direct contact with the ocean, a group of small coastal dunes can be found. Coastal sand dunes at "La Carbonera" are found adjacent to the barrier island, and are mainly composed of calcareous material (61-94% carbonate) (Moreno-Casasola and Castillo, 1992; Castillo and Moreno-

Casasola, 1998). Vegetation associated with these dunes shows a high affinity to that present in Central America, South America and the Antilles. Overall, coastal sand dunes in Mexico are composed of up to 271 species, 7% of which are endemic, and represent the second place in endemism at the national level (Durán *et al*., 2011; Espejel, 1984, 1987; Carnevali *et al*., 2010). Coastal sand dune vegetation can be divided into three zones: a) one area adjacent to the beach which is established on unstable dunes and is characterized by the presence of herbs and small shrubs, b) an area with pioneer plant species, and c) an area with more stable and nutrient-rich substrate, characterized by plant species that are less tolerant to environmental changes, and it is dominated by shrubs and trees which vary in height depending on the aridness of the area (Chan *et al*., 2002; Durán *et al*., 2011; Torres *et al*., 2010).

The lagoon system also has islands of vegetation known as “Petenes” which are associated to a freshwater spring that allows the development of perennial forest (we can find species such as *Ficus* sp., *Jacquinia auranthiaca*, and *Sabal yapa*). Finally, mangrove islands can also be observed at sites where small amounts of substrate have been deposited. The lagoon system is surrounded by coastal dune vegetation and mangroves, being *Avicennnia germinans* the dominant mangrove species (Obs. Per.).

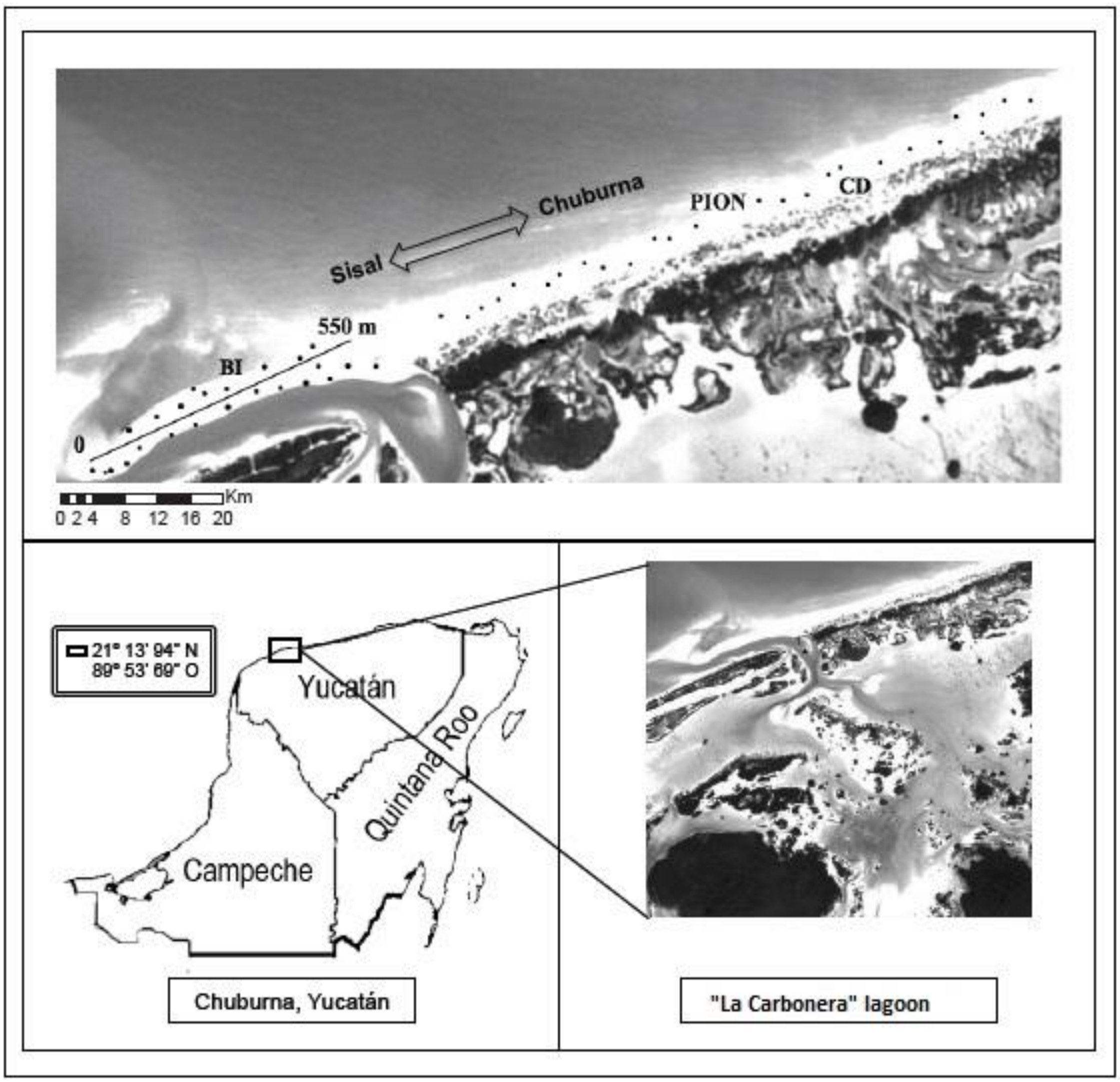

Figure 1. Coastal lagoon image located at La Carbonera, in Yucatan, Mexico. BI: barrier island. PION: area of pioneers species and CD: area of shrubs species, in coastal dunes.

Climate is warm-dry, corresponding to subtype BS_1 (h')w (Duch, 1988). The mean annual temperature is 26 ºC, the mean total annual rainfall is 600 mm, and evaporation is 1,682 mm annually. Climate at the study site is characterized by three seasons: dry season, summer rains, and winter rains. Winter rain season is characterized by presence of cold winds from north and it is commonly known as "nortes" (windy season). Dry season spans from March to May, total precipitation is up to 20 mm and maximum temperatures reach 43ºC. The rainy summer season spans from June to October, mean total precipitation is120 mm. Finally, rainy winter season takes place from November to February, and it is characterized by polar winds accompanied by a low atmospheric pressure, low temperatures and precipitation (mean values are 23.8 ºC and 25 mm, respectively) (PRONATURA, 1996; CONAGUA, 2006).

Soils at "La Carbonera" were formed by shell deposits from the Quaternary, mainly from the Holocene, and consist of deep sandy substrates, white to yellow in color, and classified as calcareous regosols according to FAO/UNESCO classification (Duch, 1988). Substrate from the barrier island was alkaline (pH= 8.7±1.7) with a low percent of nitrogen (N= 0.06±1.7%) and phosphrous (P= 0.31±1.7%). Soil from coastal dune site showed a similar pH (8.8±0.03), and low nitrogen (N= 0.065±0.005%) and phosphorus (P= 0.68±0.01%) content (Table 1). pH was quantified based on soil:deionized water relation (1:10 p/v) and a potentiometer (Corning®). Total nitrogen was determined through acid digestion following micro-Kjeldahl method and determined colorimetrically (Technicon, 1977). Inorganic phosphorus was extracted with sodium bicarbonate (pH 8.5) and quantified with ascorbic acid molybdate (Murphy and Riley, 1962).

Table 1. Soil characteristics at three points (0, 250 and 500 m) along a barrier island and an adjacent coastal dune habitat (pioneers and shrubs) located more inland.

Site	Distance	pH	N (%)	P (%)
Barrier Island	*0 m*	9.03	0.08	0.66
	250 m	8.76	0.06	0.12
	550 m	8.8	0.06	0.14
Coastal dune	Pioneers	8.85	0.06	0.67
	Shrubs	8.91	0.07	0.69

Study design and field sampling.

We conducted a vegetation survey and characterized soil conditions and AMF presence in the barrier island and coastal dunes at "La Carbonera", Chuburna, Yucatan during February 2010.

Barrier island.

We established a 550 m central transect at the barrier island starting from the distal extreme of the barrier island, where substrate accumulation begins, up to coastal dune vegetation begins. Along the transect, every 50 m we established 10 transversal line starting from lagoon border up to marine zone one, based on which three zones were differentiated at each point: lagoon = L, center= C, and marine = M. Within each zone, we placed one 5 x 5-m plot where all plant species present and their cover were recorded; cover was measured following Braun-Blanquet (1964) dominance scale. We established three plots in the transversal line (total 33 plots), and within each plot, we also collected fine roots (< 2 mm in diameter) from specimens of all plant species, as well as a 1-kg soil sample (total of 33 soil samples).

Coastal dune site.

We established two 100 m transects separated by 50 m. Each transect extended from the tide line up to coastal shrub vegetation limit (ca. 100 m total length), including both coastal dune zones: pioneers and shrubs. Every 5 m along each transect we placed 5 x 5-m plots, (20 plots in each transect), and followed previously described protocol for surveying vegetation, as well as root and soil sampling. A total of 12 1-kg soil samples were collected (six per transect). All soil samples were placed in black bags and stored at 10°C for subsequent laboratory work.

Laboratory analyses

The presence of AMF in fine roots was determined for each of the sampled plant species. Fine root samples were processed and dyed following Phillips and Hayman procedure (1970), modified by Hernández-Cuevas *et al*. (2008). We obtained root segments from each fine root sample, and mounted on slides with polyvinil-lactoglicerol alcohol (PVLG). Slides were examined under the microscope for AMF structure presence (hyphae, arbuscules, vesicles, and coils).

We quantified AMF spore abundance and identified them taxonomically. Soil samples were weighed, and from each sample we used 100 g to separate, quantify, isolate and identify AMF spores following Gerdemann and Nicolson procedure (1963), modified by Hernández-Cuevas *et al*. (2008). Subsequently, spores were placed on slides with PVLG, covered and pressed to break spore walls and identify them taxonomically based on morphology. Observations were conducted with an optical microscope (at 40X and 100X). Spore identification was based on the International Culture Collection of Arbuscular and Vesicular-Arbuscular Endomycorrhizal Fungi at http://www.invam.caf.wvu.edu/Myc_Info/Taxonomy/species September 2010).

Calculations and statistical analyses.

We used Shannon-Wienner index to calculate plant species diversity for each site, as well as the Jaccard´s similarity index to assess degree of similarity in plant species composition between sites (Mueller-Dombois and Ellenberg, 1974; Magurran, 1988). To detect statistical differences in diversity and similarity between the different zones of the barrier island, we performed a combined randomization test based on pairs of samples, using 10,000 repetitions (Solow, 1993)**.** We calculated dispersion index (*DI*) for abundances based on variance (S^2) and sample mean ratio, in order to explain spatial distribution of organisms (random if *DI*=1, uniform if *DI*<1, or aggregated if *DI*>1) (Samo-Lumbreras *et al*., 2008). We also conducted an exploratory ordination analysis of the different study zones based on plant cover and soil variables using a Detrended Correspondence Analysis (DCA) in PC-ORD 5.1 (McCune and Mefford, 2006). Total plant cover values for the barrier island and the two coastal dune zones (pioneers and shrubs) were compared with a non-parametric analysis of variance (ANOVA), and pairwise mean differences were assessed with the Student-Newman-Keuls test (Zar, 1999).

RESULTS

Vegetation

A total of 37 plant species, belonging to 27 families, were identified in both, barrier island and coastal dune sites. Of these, 18 species were herbs, three were creeping, two were climbers, 11 were shrubs, and three were trees (Table 2, Figure 2). Particularly, at barrier island, we recorded 13 plant species belonging to 11 families, most of which were herbs (seven species), followed by three shrub, two creeping, and one tree species (Figure 2). Following our classification in three zones (L, C, and M), inside barrier island, we recorded 10 species in L and C, and eight species in the marine influence zone (M). Three species were exclusively at barrier island (*Amaranthus greggi*, *Sesuvium portulacastrum* and *Suaeda linearis*).

Coastal dune site had a total of 34 species, belonging to 26 families. Of these, 17 species were present in pioneer zone, 13 of them were herbs, five shrubs, three were crawlers, and three were climbers, while in shrub zone we recorded 20 species, 10 shrubs, 13 herbs, three trees, two climbers, and one creeping (Figure 2). 11 species were found in both pioneer and shrub zones. And a total of nine species (25% of total) had a wide distribution, as they were present both in barrier island and coastal dunes (Table 2).

Plant cover at the barrier island was lower than 5%, and differences among zones were not significant (C = 0.6%, L = 0.09%, and M = 0.09%). In contrast, the coastal dune had an average plant cover of 25%, and the zone of pioneers had a lower cover (17%) than the shrub zone (34%). The ANOVA showed significant differences in percent cover values between barrier island and two coastal dune zones (H=142.6, df=2, P <0.001), pairwise differences were statistically different only between barrier island and coastal dune, but not between the two coastal dune zones.

The barrier island zones had similar plant diversity values based on the de Shannon-Wienner index: H=1.9 (L), H=2.1 (C) and H=1.9 (M). Based on the Solow test (1993), we found no statistical differences in diversity between these zones (P=0.05). The plant community established at the coastal dune site had a greater diversity compared with that from the barrier island. Within the coastal dune site, the zone of pioneers showed a lower diversity (H=2.709) compared to the shrub zone (H= 3.043). The Solow´s test showed statistically significant differences among all the sites (P<0.05), with the shrub zone being the most diverse compared to the zone of pioneers or the barrier island (Figure 3).

Table 2. List of plant species present at a coastal dune site (P=pioneers, S=shrub vegetation) and a barrier island (L=lagoon, C=center, M=marine) and arbuscular mycorrhizal fungi (AMF): presence (+) o absence (-). Names assigned after Carnevali *et al*. (2010).

Family	**Species**	**Growth habit**	**Coastal dune**		**Barrier island**			**AMF**
			P	S	L	C	M	
Agavaceae	*Agave angustifolia* Haw.	Herb		x				+
Acanthaceae	*Bravaisia tubiflora* Hemsl.	Herb		x				+
Aizoaceae	*Sesuvium portulacastrum (*L.) L.	Herb			x		x	+
Amaranthaceae	*Amaranthus greggii* S.Watson	Herb			x	x	x	+
	Amaranthus spinosus L.	Herb						+
	Gomphrena dispersa Standl.	Herb	x	x				+
	Salicornia bigelovii Torr.	Herb			x			+
	Suaeda linearis (Elliott) Moq.	Herb		x	x	x	x	+
			x					
Anacardiaceae	*Metopium brownei* Urb.	Tree		x				+
Asteraceae	*Ambrosia hispida* Pursh	Creeping	x	x				+
	Bidens pilosa L.	Herb	x	x				+
Bataceae	*Batis maritima* L.	Herb	x					+
Brassicaceae	*Cakile lanceolata* O.E.Schulz	Herb	x		x	x	x	+
Cactaceae	*Acanthocereus pentagonus* (L.) Britton & Rose	Herb		x				+
Boraginaceae	*Tournefortia gnaphalodes* R.Br.	Shrub	x			x	x	+
Combretaceae	*Conocarpus erectus* L.	Tree		x	x	x		+
Convolvulaceae	*Ipomoea pes-caprae* (L.) R. Br.	Herb, creeping	x			x		+
Cyperaceae	*Cyperus sp.*	Herb	x					+
Euphorbiaceae	*Croton punctatus* Jacq.	Shrub	x	x				+
	Euphorbia buxifolia Lam	Herb	x		x	x	x	+
Fabaceae	*Canavalea rosea* (Sw.) DC.	Herb, creeping	x		x			+
	Pithecellobium keyense Britton in Britton & Rose	Tree or shrub		x				+
Goodenaceae	*Scaevola plumieri* (L.) Vahl.	Shrub	x	x	x	x		+
Lauraceae	*Cassytha filiformis* L.	Climber	x	x				+
Malvaceae	*Gossypium hirsutum* L.	Shrub		x				+
	Malvaviscus sp.	Shrub		x				+
	Waltheria americana L.	Herb						+
			x					
Passifloraceae	*Passiflora foetida* L.	Climber	x	x				+
Poaceae	*Cenchrus echinatus* L.	Herb	x	x		x	x	+
	Distichlis spicata (L.) Greene var. *spicata*	Herb	x	x				+
Portulacaceae	*Portulaca oleracea* L.	Herb	x					+
Polygonaceae	*Coccoloba uvifera* (L.) L.	Herb		x				+
Primulaceae	*Jacquinia aurantica* Aiton	Shrub		x				+
Rubiaceae	*Ernodea littoralis* Sw.	Shrub	x	x				+
Sapotaceae	*Bumelia retusa* L.	Shrub		x				+
Simarubaceae	*Suriana maritima* L.	Shrub	x	x	x	x	x	+
Solanaceae	*Lycium carolinianum* Walter.	Shrub		x				+
	Zone total number of species		21	23	10	10	8	
	Site total number of species		34		13			

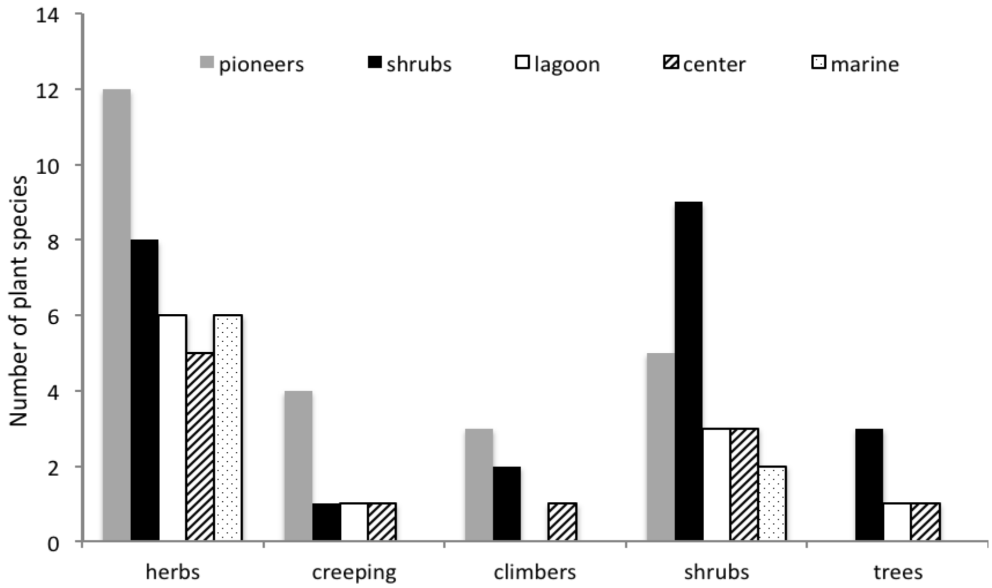

Figure 2. Growth habits of plant species present in pioneer and shrub zones at a costal dune site, as well as in three different zones (lagoon, center, and marine area) at a barrier island at "La Carbonera", Chuburna, Yucatan, Mexico.

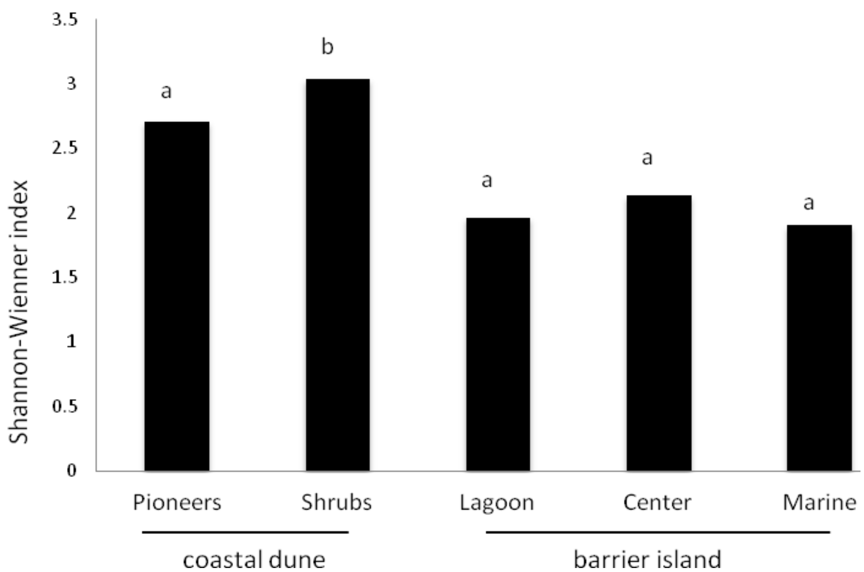

Figure 3. Shannon-Wiener index of plant community at a coastal dune site (n=40) and a barrier island (n=33) at "La Carbonera", Chuburna, Yucatan, Mexico. Different letters indicate significant differences ($p<0.05$).

The vegetation of the barrier island varied depending on proximity to the ocean. The Jaccard similarity index showed differences between the species established at the M and L zones (38% similarity), while the central one (C) shared a greater number of species with both the M and L zones (50 and 54% similarity, respectively). With regards to the vegetation at the coastal dune site, the barrier island showed a greater similarity with the zone of pioneers (36%) than with the shrub zone (16%). The pioneer and shrub zones from the coastal dune site had a similarity lower than 30%.

With respect to the spatial distribution of species, the vegetation established at the barrier island showed a clumped distribution, both close to the ocean as well as in the lagoon. A similar clumped pattern was observed also in the zone of pioneers of the coastal dune site. In contrast, the shrub zone showed a random distribution (Table 3).

Arbuscular mycorrhizal fungi (AMF)

The roots of all plant species found at the barrier island and coastal dune site exhibited colonization by AMF. The fungal structures with the highest frequency were hyphae. Nonetheless, substrate from the barrier island showed no evidence of AMF spore presence, while spore abundance was extremely low at the coastal dune site, with only two spore and two species being identified: *Glomus geosporum* and *Scutellospora gregaria*.

Soil-vegetation relationship

The DCA analysis (Figure 4) showed that the first axis explained 0.83 of the variance, representing the gradient of zones within the barrier island. This gradient spanned from the zone where the substrate accumulates (left area of the figure), to the zone with more stable substrate (right area of the figure) and a greater number of herb species are found (which are characteristic of pioneer zones and dominated the vegetation of the barrier island). Associated with the embrionary coastal dunes, we found a group of herb and shrub species that characterize coastal dune systems (Amaranthus greggii, A. spinosus, Suaeda linearis, Sesuvium portulacastrum, Portulaca oleraceae y Cakile lanceolata, these species are showed separate by a curve line at the left of figure), while at the other extreme we found a group of species which are dominant in coastal shrub vegetation (*Distichlis spicata, Bidens pilosa, Conocarpus erectus, Pithecellobium keyenses, Gossypium hirsutum, Bumelia retusa, Gomphrena dispersa, Agave angustifolia, Lycium carolinianum, Coccoloba aurantica, Metopium brownie, Bravaisia tubiflora*, *Acanthocereus pentagonus* y *Malvaviscus* sp.). This gradient is explained to a similar extent by the percent of N and P in the soil towards the central zone of the shrub vegetation. The second axis explained 0.42 of the variance, from pioneer species of coastal dune sites to shrub species, with pH and N spanning from low to high values along this axis.

DISCUSSION

Vegetation

Barrier island and coastal dune system studied at "La Carbonera" exhibited a species-rich plant community. Indeed, up to 37 species were recorded at both sites, similar value reported for conserved dune vegetation at Sisal (Guadarrama *et al.*, 2012). This reported richness is a higher value relative to that reported by Torres *et al*. (2010) for nearby coastal shrub vegetation at Sisal (25 species) and Chuburna (26 species); moreover, the present study shares only two species with previously cited work, *Metopium brownei* and *Pithecellobium keyense*. Likewise, Ramos-Zapata *et al*. (2011) conducted a study at the coastal dunes near Sisal town and reported five dominant species of embryonic, mobile and stabilized coastal dunes. Of these, three correspond to dominant pioneer species of coastal dune habitats of the region (*Scaevola plumieri*, *Cenchrus echinatus* and *Ambrosia hispida*) reported in the present work, as well as one dominant species of coastal shrub vegetation (*Suriana marítima*) which was also recorded at La Carbonera. Based on these findings, we conclude that species richness levels observed for coastal vegetation in La Carbonera are on the same range or higher compared to other coastal systems. Differences in species richness may respond to environmental heterogeneity across sites which promotes high number of species and structural diversity in these ecosystems.

Table 3. Spatial distribution of plants based on Pearson's variation index (DI) for a coastal dune site and a barrier island at "La Carbonera", Chuburna, Yucatan, Mexico.

	Coastal dune		Barrier island		
	Pioneers	Shrubs	Lagoon	Center	Marine
Mean	2	0.9	2.6	1.8	1.5
Variance	7.5	0.7	8.9	2.5	3.3
DI	3.8	0.8	3.4	1.4	2.1
Type of distribution	clumped	random	clumped	clumped	Clumped

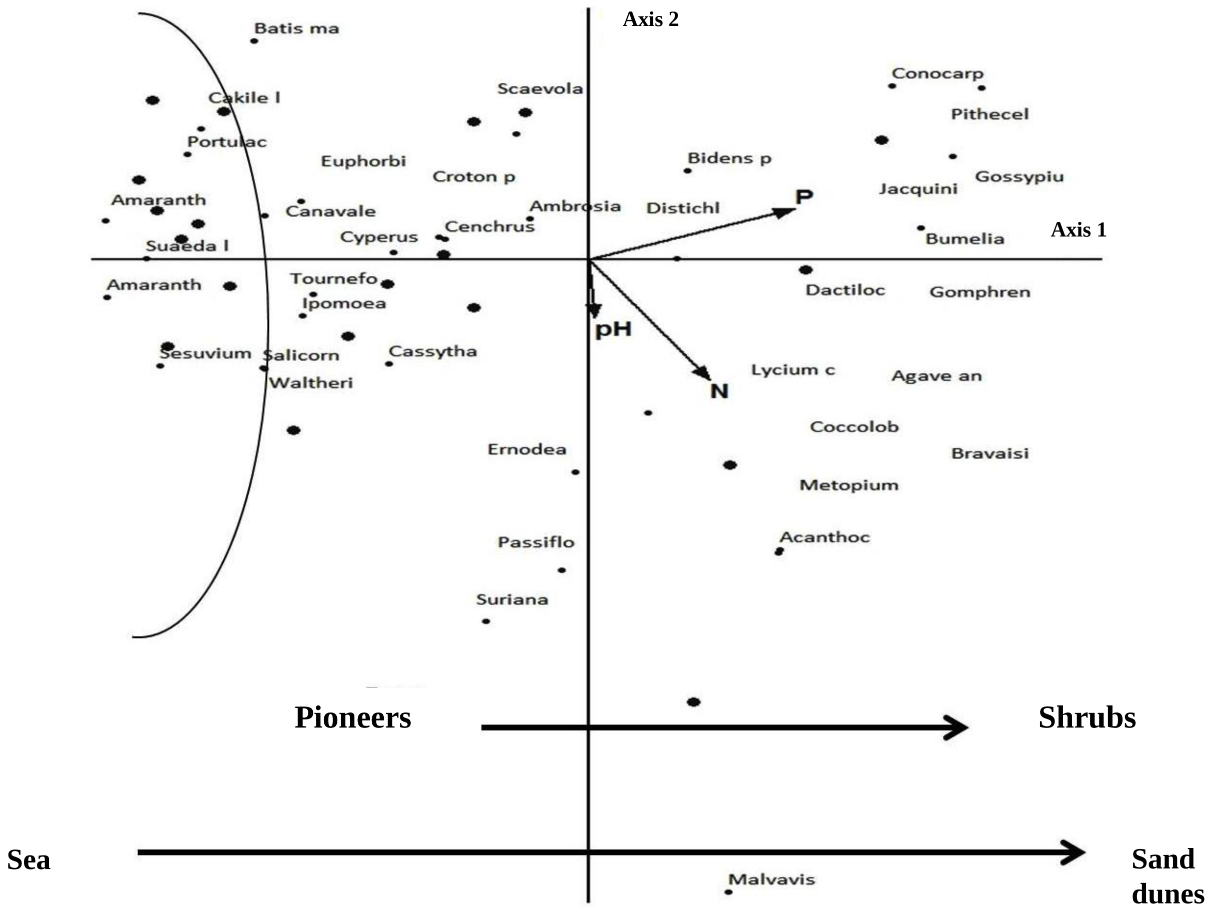

Figure 4. Detrended correspondence analysis (DCA) of plant cover and soil variables on barrier island and the two coastal dune zones (pioneers and shrubs). (Complete plant names are listed on Table 2, the figure only show the first letters of the name)

Barrier island of La Carbonera started forming 24 years ago, and its greatest length during a given year is 600 m. It has small sand ridges above sea level. We found 5% of plant cover, in contrast to other barrier island in Argentina that reached 70% of plant cover (Cortizo and Islas, 2007). Nonetheless, two characteristics of the studied barrier island must be emphasized: first, that it is of more recent formation relative to that studied by Cortizo and Islas (24 years), and that the studied island may represent a more dynamic system due to a greater degree the accumulation and loss of substrate resulting from the effect of tides (obs. per.). The barrier island shared 10 plant species with adjacent coastal dune site (77%), suggesting similar environmental characteristics in both zones. Coastal dune system present at La Carbonera is constituted by a narrow strip of land (Chan *et al*., 2002), that exhibited a plant cover that was three times greater than that observed at the barrier island. In addition, this site showed a gradient of increasing plant cover from the shore to the coastal shrub vegetation. These coastal shrub sites thus act as sites for plant recruitment and represent propagule sources which facilitate and drive plant community succession (Morrison and Yarranton, 1974).

Arbuscular mycorrhizal fungi

Mycorrhizae were present in roots of all plant species sampled, including *Cakile lanceolata* (Brassicaceae) and *Sesuvium portulacastrum* (Aizoaceae) both previously reported as non-mycorrhizal (Allen, 1991; Koske and Gemma, 1990; Annapura *et al.*, 1996). This suggests that strong nutrient limitation present in soils of coastal systems in Yucatan may lead to plant species depending to a greater extent on mutualistic interactions with AMF in order to increase nutrient uptake. Mycorrhizae presence in roots of pioneer plants of barrier island suggests that plant species in recently formed habitats are likely to associate with AMF to increase their establishment and survival probability, however the studies in this environments are scarce. Since all plants species analyzed showed mycorrhizae colonization, our results are agree with previous studies conducted in tropical coastal dune systems, where plant species have been shown to establish associations with AMF, in Hawaii (Koske *et al*., 1992) and Paraganuá, Venezuela (Alarcón and Cuenca, 2005), Veracruz, México (Corkidi and Rincón 1997a, 1997b) and Yucatán, México (Ramos-Zapata et al. 2011, Guadarrama et al. 2012). It is thought that AMF colonization increase with dune stability degree (Nicolson, 1960; Corkidi and Rincón, 1997a), however in a recent study by Ramos-Zapata *et al*. (2011) it was reported that AMF colonization levels did not differ among coastal dune zones (embryonic, mobile and stabilized dunes) in a coastal dune site in Yucatan, Mexico.

Although all the plant species sampled exhibited associations with AMF, we detected very low levels of spore abundance in the rhizosphere. In fact, only two morphospecies were identified, both at the coastal dune site (*Glomus geosporum* and *Scutellospora gregari*); no AMF spores were found in soil samples from the barrier island. A previous study by Analia *et al.* (2001) reported that AMF spore number in soil increased with stability degree at a coastal dune site in Santa Catarina, Brazil. In addition, Ramos-Zapata *et al*. (2011) reported from one to five spores per 50 g of soil in embryonic dunes in Yucatan, Mexico. Up to 19 spores per 50 g of dry soil were observed more inland at a coastal shrub vegetation site. The authors concluded that AMF spore density responded more strongly to factors driving seasonality in abundance, than to the degree of dune stability. In this sense, it should be noted that the barrier island studied in the present work likely does not maintain spore abundances for long periods of time, given tide changes and strong winds that reduce spore density in the soil. Further research will be devoted to quantifying other types of AMF propagules present in soils of this system, which may represent the main sources for root colonization of the plant species studied.

Soils at "La Carbonera" are alkaline, and only minimal variations in physical and chemicals properties were observed between sites. Previous studies have shown that soil parameters such as pH and nutrient availability influence mycorrhizal activity inside the roots (Nelsen *et al*. (1981). In response to stress in coastal environments, plant species may readily establish associations with AMF. This explains the ubiquity of AMF root colonization, as well as the possibility of extra-radical mycelia formation to increase nutrient uptake surface (while spore production remains low). Thus, main AMF propagules sources are hyphae which grow from the roots of perennial plants, while spores are present at low densities but are highly infective.

CONCLUSIONS

Barrier island and coastal sand dunes under study are influenced both by ocean, and lagoon environments. While its vegetation cover and composition is strongly affected by plant community present in the adjacent habitat. These biotic and abiotic factors determine nutrient availability in the island, as well as the response of plant species to environmental stress, both of which may be favoring AMF root colonization. Nonetheless, soil samples from the barrier island lacked AMF spores, suggesting that the few spores arriving at this site germinate and immediately establish an association with plant species. Likewise, this spore lack may suggest that AMF dispersal primarily occurs through movement of hyphae in soil, entailing a low energetic cost due to reduced spore production.

Nonetheless, the mechanisms of AMF dispersal are not well understood, especially during early succession in coastal environments. Future research on AMF dispersal will generate information which serves as a tool to understand plant community succession, as well as plant-AMF interactions and their relationship with soil fertility in barrier islands and coastal dune ecosystems.

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