

Arbuscular mycorrhiza, carbon content and soil aggregation in Sonoran Desert plants

Micorriza arbuscular, contenido de carbono y agregación del suelo en plantas del Desierto Sonorense Micorriza arbuscular, conteúdo em carbono e agregação do solo em plantas do Deserto Sonorense

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ABSTRACT

Desert trees and shrubs play a relevant role in stabilizing the deserts ecosystems, and mycorrhizal association is very important for its adaptation and survival in arid and semi-arid areas. The influence of mycorrhizic fungi on the formation of water stable aggregates through glomalin and on soil carbon content has been studied. We sampled the rhizosphere of representative trees (*Olneya tesota, Prosopis juliflora*, and *Parkinsonia microphylla*), and shrubs (*Jatropha cuneata* and *Larrea tridentata*) of the Sonoran Desert for four seasons in order to evaluate the mycorrhizal status, carbon and glomalin accumulation, and their relationship with water stable aggregates. Results showed that mycorrhizal colonization, with variations depending on the season. The accumulation of carbon in the soil profile has significant differences between plants and ranged from 1.1 to 1.75% for *Larrea* and *Prosopis*, respectively. The water stable aggregates were significantly different between plants and ranged between 24% and 42%. Glomalin correlation with carbon content and water stable aggregates shows the role of mycorrhizal fungi on soil quality, highlighting influence on carbon content in rhizosphere.

RESUMEN

Los árboles y arbustos del desierto juegan un papel relevante en la estabilización de los ecosistemas desérticos y la asociación micorrízica es muy importante para su adaptación y supervivencia en zonas áridas y semiáridas. Varios autores han estudiado la influencia de los hongos micorrízicos sobre la formación de agregados estables en agua a través de la glomalina y sobre el contenido de carbono. La rizosfera de árboles (Olneya tesota, Prosopis juliflora y Parkinsonia micorphylla) y arbustos (Jatropha cuneata y Larrea tridentata) representativos del Desierto Sonorense se muestreó durante las cuatro estaciones del año con el fin de evaluar el estado de micorrización, la acumulación de carbono y glomalina, y su relación con los agregados estables en agua. Los resultados mostraron que la asociación micorrízica está presente durante todo el año en las plantas de esas especies de zonas semiáridas, con valores de 1,2% a 57% de colonización micorrízica, con variación entre las estaciones. La acumulación de carbono en el suelo varía significativamente de 1,1% a 1,75% para Larrea y Prosopis, respectivamente, mientras que los agregados estables en agua fueron también significativamente diferentes entre plantas, con valores de 24% y 42% para esas especies. El contenido de glomalina se correlacionó con el porcentaje de agregados estables en agua y el contenido de glomalina se correlacionó con el porcentaje de agregados estables en agua y el contenido de carbono, lo que pone de manifiesto el papel de los hongos micorrízicos en la calidad del suelo, destacando su influencia en el contenido de carbono de la rizosfera.

AUTHORS

Armenta Calderón A. D.¹

Moreno-Salazar S. F.²

Furrazola Gómez E.³

Ochoa-Meza A.^{@,2} andres.ochoa@ unison.mx

@ Corresponding Author

¹Universidad Estatal de Sonora. Ley Federal del Trabajo y Perimetral s/n. Hermosillo, Sonora, México.

²Departamento de Agricultura y Ganadería. Universidad de Sonora. Carr. a Bahía Kino km 21. Hermosillo, Sonora, México.

³Instituto de Ecología y Sistemática. Carretera Varona 11835 e/Oriente y Lindero, La Habana 19. 11900, Calabazar, Boyeros, La Habana, Cuba.



RESUMO

Arvores e arbustos do deserto desempenham um papel fundamental na estabilização dos ecossistemas dos desertos e a associação dessas plantas com micorrizas é muito importante para a sua adaptação e sobrevivência em áreas áridas e semi-áridas. Tem sido estudada a influência dos fungos micorrízicos na formação de agregados estáveis em água através da glomalina e do conteúdo em carbono no solo. Foram colhidas, durante as quatro estações do ano, amostras da rizosfera de árvores (Olneya tesota, Prosopis juliflora e Parkinsonia microphylla) e arbustos (Jatropha cuneata e Larrea tridentata) representativas do Deserto Sonorense com o objetivo de avaliar o estado de micorrização, a acumulação de carbono e glomalina e a sua relação com os agregados estáveis em água. Os resultados mostraram que a associação micorrízica está presente durante todo o ano nas plantas estudadas, com valores de 1,2 a 57% de colonização micorrízica, com variações entre as estações do ano. A acumulação de carbono no perfil do solo apresentava diferenças significativas entre plantas e variava entre 1,1 e 1,75% para a Larrea e Prosopis, respetivamente. Os agregados estáveis em água eram significativamente diferentes entre plantas e variavam entre 24 e 42%. O conteúdo em glomalina correlacionou-se com o de carbono e com a percentagem de agregados estáveis em água o que evidencia o papel dos fungos micorrízicos na qualidade do solo, destacando-se a sua influência no conteúdo em carbono na rizosfera.

1. Introduction

Deserts in North America are represented by the Great Basin, Mojave, Chihuahuan, and Sonoran Deserts. From these four deserts, the Sonoran Desert has the largest number of life forms and communities (Shreve and Wiggins 1964). Desert shrubs and trees play a major role in stabilizing the fragile desert ecosystems in arid regions. In many deserts, trees are considered as keystone species as they support the life of many other faunal and floral species (Munzbergova and Ward 2002). The beneficial effects of desert trees and shrubs under their canopies include the reduction in the extremes of environmental temperatures (Chandregowda et al. 2018) by deposition of fine textured soil particles of low bulk density, then increasing water-holding capacity, stable aggregate structure and high nutrient levels that becomes a habitat that supports communities of soil organisms (Aguilera et al. 1999), this is known as resource islands.

The most ubiquitous resource limiting production in deserts is the lack of water, but other resources as mineral nutrients may also be limiting, especially during periods when water is abundant. Other abiotic factors also have important impacts on desert plants and their function, like the typically low but both spatially and temporally heterogeneous nutrient availability. On the other hand, the influence of soil microorganisms is poorly understood (Carrillo-García et al. 1999), despite its strong influence on soil formation and the establishment and survival of plant and community structure (van der Heijden and Sanders 2002). Because of their widespread distribution, broad host range and abundant members of the soil biota, arbuscular mycorrhizal fungi (AMF) are considered an important biotic factor in the terrestrial ecosystems. AMF stand out from all the soil microorganisms as an essential component of the plant-soil systems in the desert. Despite the importance of AM fungi associated with the root system of plants, the distribution and activity of AM fungi in desert ecosystems are poorly known (Bashan and De-Bashan 2010).

KEYWORDS

Leguminales, symbiosis, Bradford reactive soil protein, water stable aggregates.

PALABRAS CLAVE

Leguminales, simbiosis, proteína del suelo reactiva a Bradford, agregados estables en agua.

PALAVRAS-CHAVE

Leguminosas, simbiose, proteína do solo reativa de Bradford, agregados estáveis em água.

The advantage of mycorrhization for plants is mainly in the improvement of phosphate absorption from mineral and organic phosphorus sources in the soil. In basic soils, mycorrhizae can prevent iron chlorosis and manganese deficiency symptoms. AMF act as an "antistress factor" for higher plants, which creates a positive effect, particularly in sites with low water and mineral nutrient availability (Smith and Read 2008; Blume et al. 2016). Mycorrhizal association enhances soil quality through the release of a glycoprotein called glomalin, which acts as glue with hydrophobic properties (Driver et al. 2005; Shuab et al. 2017) and enhances the formation of stable macro-aggregates and thus provides with a greater resistance of the soil to wind and water erosion (Bedini et al. 2009; Leifheit et al. 2014).

Soil structure is important for facilitating water infiltration, biogeochemical cycling processes, resistance against erosional loss, and soil carbon storage. The process of soil aggregation is complex. In this process, numerous organisms and binding agents are involved (Rillig et al. 2015). Several studies have been carried out to correlate AMF presence and soil structure. Wright and Upadhyaya (1998) and Bedini et al. (2009) reported positive correlations between the content of glomalin and stability of soil aggregates. In soils with high concentration of glomalin, it has been reported that the C content in the protein structure may correspond to 5% of the total soil organic carbon (Rillig et al. 2001), meanwhile Emran et al. (2012) reported that in soils with a better aggregate stability (attributable to glomalin) favorable conditions for protection of carbon are created. The aim of this paper is to gain insights into arbuscular mycorrhizal fungi, water stable aggregates, carbon content and their interactions on rhizosphere of representative plant species of the Sonoran Desert.

2. Materials and Methods

2.1. Site selection and soil sample

The study area is located at the Costa de Hermosillo, Mexico (29°00'57" N, 111°12'25" W). The vegetation is sarcocaul scrub; the soil is an Eutric Lithosol, typically shallow, with sandy texture and low organic matter content (INEGI 2005). The yearly average rainfall is 125 mm, with summer rainfall regime and minimal rainfall in winter, and an annual average temperature of 24 °C with an intra-annual variability from 1 to 42 °C (Shreve and Wiggins 1964; INEGI 2005).

Soil sampling was done four times a year, in the last third of each season. The sampled vegetation consisted of three adult individuals of each of the following species, Jatropha cuneata Wiggins & Rollins, Larrea tridentata (DC.) Coville, Parkinsonia microphylla Torr., Olneya tesota A. Gray, and Prosopis juliflora (Sw.) DC. The canopy area was divided into guadrants and a quadrant was sampled in each season. One and a half kg of rhizospheric soil plus roots (from 0.01 to 0.20 m depth) were collected from each selected plant. The sample was taken between 0.1 m from the base of the trunk, to half the radius of the plant cover (Figure 1). A total of 15 samples were taken on each season, for a grand total of 60 samples. Soil samples were air-dried and sieved through 2 mm mesh before analysis. When soil surface had ephemeral grasses or herbs, their roots were individually removed in order to avoid mycorrhizal determinations on roots other than those of the selected trees and shrubs.

2.2. Physical and chemical soil analysis

Soil analysis included texture, cation exchange capacity (CEC), electrical conductivity of saturated soil-paste extract (EC-e), pH, organic matter, phosphorus (P) and iron (Fe) content, according to the methods of Pansu and Gautheyrou (2006).



Figure 1. Scheme of the sampling site in each plant.

2.3. Mycorrhizal assessment

Mycorrhizal root colonization (MRC) and extraradical mycelium (ERM) were determined by triplicate for each sample. The methods proposed by Gerdemann and Nicolson (1963), Phillips and Hayman (1970) and Giovannetti and Mosse (1980) as modified by Herrera-Peraza et al. (2004) were performed. The ERM was estimated by using two soil fractions after wet sieving (Herrera-Peraza et al. 2004).

2.4. Soil organic carbon (SOC) and Bradfordreactive soil protein (BRSP) content

SOC was determined by calcination in muffle, according to the method described by Aysha et al. (2015). Glomalin content was measured as BRSP (Rillig 2004), following the Wright and Upadhyaya (1998) method, and using the Bradford assay (Sigma-Aldrich, Inc.) with bovine albumin serum as a standard.

2.5. Aggregate stability (Water Stable Aggregates, WSA)

The percentages of dry soil aggregates and WSA were calculated. Gravel was not present as a lithic phase. Soil was separated according to aggregate size, $\emptyset > 0.5$, > 0.25 and > 0.063 mm. WSA was determined manually by dipping the sieve in water for 5 min according to the Nichols and Toro (2011) method, which includes a correction by sand content.

2.6. Statistical analysis

The ANOVA for each variable was performed using the statistical package NCSS 2000 software (NCSS Statistical Software, Kaysville, UT, USA). When mean differences were present, the Tukey-Kramer multiple comparison test was used (0.05%). Mycorrhizal variables were transformed to get normal distributions as follows: a) mycorrhizal root colonization (MRC) was Arcsine transformed and b) extra-radical mycelium (ERM) was Log transformed. The Pearson correlation coefficient (r) was used to determine the relationship between variables.

3. Results

3.1. Physical and chemical soil properties

All samples have a sandy loam texture. Soil analysis shows typical attributes of arid soils such as low CEC and low organic matter content; EC-e values were lower than 1 dS m⁻¹,

meaning salinity is not a problem in these soils. Phosphorous (P) contents are different between species, ranging from 15 to 51 ppm in *Larrea* and *Prosopis* soils respectively. pH values are slightly acid for *Jatropha* and *Prosopis*, neutral for *Larrea* and basic for *Parkinsonia* and *Olneya* soils. *Prosopis* soils have the highest iron content. All parameters were not statistically different among seasons but only among studied plants (Table 1).

Table 1. Chemical properties of rhizospheric soil on selected plants of the Sonoran Desert

Plant species *	рН	EC-e (dS m ⁻¹ at 25 ºC)	CEC (cmol ₍₊₎ kg⁻¹)	Organic matter (%)	Phosphorous (ppm)	lron (ppm)
Prosopis juliflora	5.9 a	0.29 a	9.7 a	1.0 b	51 d	8.8 c
Jatropha cuneata	6.4 a	0.66 b	7.0 a	0.6 ab	32 bc	3.7 b
Parkinsonia microphylla	7.6 b	0.43 ab	11.7 ab	0.5 ab	19 ab	0.9 a
Olneya tesota	7.6 b	0.61 b	16.1 b	1.0 b	33 c	1.1 a
Larrea tridentata	7.2 b	0.38 ab	10.0 ab	0.4 a	15 a	0.7 a
Significance (P = 0.05)	*	*	*	*	*	*

*Means are values from 12 replicates. Data with same letter in a column are statistically equal.

3.2. AMF-Plant interactions

The mycorrhizal root colonization (MRC) varied in all species between seasons, but no statistical significances were found (Table 2). All species show their lowest values of MRC in spring (*Parkinsonia, Larrea* and *Olneya*) or summer (*Jatropha* and *Prosopis*). It is noticeable that Olneya and Larrea despite their low values when compared with *Jatropha* or *Parkinsonia*, show the highest change of MRC on a year cycle, with values 19 and 11 times higher when compared with its lower value of MRC.

Extra radical mycelium (ERM) values in winter were the lowest in all species. Statistical differences were found between seasons for ERM in *Jatropha*, *Olneya* and *Larrea*, but not in *Parkinsonia* and *Prosopis* (Table 2). The highest increases on ERM were shown by *Larrea* and *Jatropha* with 28 and 25 times respectively, while *Prosopis*, *Parkinsonia* and *Olneya* showed ERM increases of 10, 11 and 15 times respectively.

3.3. Soil Organic Carbon (SOC) and Bradford Reactive Soil Protein (BRSP) content

No statistical differences were found in the total SOC between seasons, with 1.4% as an average annual value. However, significant differences between species were found: *Prosopis* soil showed the highest value (1.76% SOC), while *Larrea* and *Parkinsonia* had the lowest values (1.1 and 1.13% SOC), respectively (Figure 2).

BRSP showed an increase from winter to fall, from 486 to 1201 mg/kg of soil (Figure 2). The BRSP content in *Prosopis* decreased from winter to summer and almost doubled during fall. It is noteworthy that among the analyzed species, *P. juliflora* had the highest value of BRSP, particularly during fall (Figure 2).

Variable	Season	Species				
		Jatropha cuneata	Parkinsonia microphylla	Olneya tesota	Prosopis juliflora	Larrea tridentata
ERM (mg/dm ³)	Winter	2.2 a	2.8 a	2.7 a	2.8 a	1.7 a
	Spring	18.0 ab	21.4 a	37.0 ab	23.1 a	22.0 ab
	Summer	50.6 bc	32.3 a	41.4 b	26.3 a	48.3 b
	Autumn	55.8 c	20.9 a	24.6 ab	29.4 a	22.2 ab
Significance	(P = 0.05)	*	n.s	*	n.s	*
MRC (%)	Winter	25.3	54.4	4.8	19.3	4.1
	Spring	31.9	24.6	1.2	17.6	1.6
	Summer	14.0	57.1	8.9	4.6	18.0
	Autumn	44.9	52.5	22.7	16.0	4.9
Significance	(P = 0.05)	n.s	n.s	n.s	n.s	n.s

Table 2. Seasonal variation on mycorrhizal root colonization (MRC) and extra-radical mycelium (ERM) on five representative species of Sonoran Desert

*Means are values from 12 replicates. Data with same letter in a column are statistically equal.



Figure 2. Contents of soil organic carbon (SOC) and Bradford Reactive Soil Protein (BRSP) in the rhizosphere of five representative species of Sonoran Desert. Bars are mean values and the same letter indicates no statistical differences (P = 0.05).

3.4. Water stable aggregates

For analyzed samples, over 80% of soil was retained in any of the three diameter (\emptyset) classes of aggregates (2-0.5, 0.5 to 0.25 and 0.25-0.063 mm). However, less than 10%

corresponded to water stable aggregates in the highest diameter (2-0.5 mm), while in Ø sizes smaller than 0.25 mm, water stable aggregates were between 10 and 20% for *Olneya*, *Jatropha* and *Prosopis* and less than 10% in *Larrea* and *Parkinsonia* (Figure 3).



Figure 3. Cumulative percent of water stable aggregates in Ø classes > 0.5, > 0.25 mm and > 63 µm. Values are means of 12 replications.

The highest values of WSA were found in *Prosopis*, during spring, summer and fall, whereas lowest WSA values were found in *L. tridentata*. Highest values of total soil aggregation (30-46%) were also found in *O. tesota* and *J. cuneata* in summer and fall seasons.

3.5. Correlation analysis

Table 3 shows the correlation matrix between some variables analyzed. SOC has a positive correlation with BRSP and WSA (P < 0.001), while the correlation with ERM is negative and less significant. BRSP has a significant correlation with WSA at all sizes while ERM is significantly correlated with the bigger WSA, and the correlation with smaller WSA (\emptyset > 63µm) is less significant.

Table 3. Correlation analysis for extraradical mycelium (ERM), Bradford Reactive Soil Protein (BRSP) content, Water Stable Aggregates (WSA) and soil organic carbon (SOC) in the rhizosphere of five representative species of Sonoran Desert

Variables	SOC	BRSP	WSA (> 0.5 mm)	WSA (> 0.25 mm)	WSA (> 63 μm)
BRSP	0.784 P = 0.0001	-	-	-	-
WSA > 0.5 mm	0.373 P = 0.0030	0.487 P = 0.0001	-	-	_
WSA > 0.25 mm	0.361 P = 0.0050	0.538 P = 0.0001	0.879 P = 0.0001	-	-
WSA > 63 µm	0.556 P = 0.0001	0.554 P = 0.0001	0.498 P = 0.0001	0.543 P = 0.0001	-
ERM	-0.033 P = 0.8000	0.155 P = 0.2370	0.449 P = 0.0001	0.511 P = 0.0001	0.209 P = 0.1090

4. Discussion

4.1. Soil analyses

Both physical and chemical characteristics of soil do not show statistical differences among seasons but only among plants. Ochoa-Meza et al. (2009) and Hernández-Zamudio et al. (2018) also found no temporal variation in soil properties when they analyzed *Agave angustifolia* and *Larrea tridentata* rhizospheres respectively, both representative species of arid soils. Low content of organic matter is characteristic of arid or semiarid soils but reflects the low net productivity of the ecosystem and low return rate caused by scarce water availability despite litter accumulation on the resource island promoted by plants canopy (Herrera-Peraza et al. 2004).

Agricultural soils in the region have pH values near neutral and basic (Pacheco, pers. comm.). Prosopis as a phreatophyte has capacities for obtain underground water and modify its rhizospheric conditions (Archer et al. 2017; Wilcox et al. 2017). It has been stated that some plants acidify their rhizosphere in order to make some nutrients soluble (Azcón-Bieto and Talón 2008), this is true for P and Fe content in our case, rhizosphere of Prosopis has the lowest pH value and the highest P and Fe contents. Phosphorous is recognized as the main element involved in the development of mycorrhizal colonization (Smith and Read 2008), but other conditions as hydric stress and low nutrients availability influence the mycorrhizal association too. Iron content is relevant on glomalin production (Rillig et al. 2003), and Prosopis rhizosphere have the highest content of BRSP (Figure 1).

4.2. AMF-Plant interactions

In arid and semiarid regions, mycorrhizal symbiosis is essential for the establishment and survival of plants, especially by low availability of water and nutrients (Blume et al. 2016). Redistribution of soil nutrients and their location under shrubs as fertility islands can maintain ecological processes that are of high relevance for restoration efforts (Bashan and De-Bashan 2010; Alday et al. 2014; Allington and Valone

2014). MRC values reported here for all plant species were not greater than 60%. This result disagrees with that of Carrillo-García et al. (1999) who reported values higher than 70% in *J. cuneata*, *O. tesota, Prosopis articulata* and *L. tridentata*. This difference can be due to the nature of the mycorrhizal symbiosis, the identity of the HMA symbionts and their adaptation to the rhizospheric conditions (Verma et al. 2008). *Parkinsonia praecox* (= *Cercidium praecox*) in Baja California Sur (Mexico) shows moderately high colonization rates, between 40 and 70%, which is consistent with the values reported here for *P. microphylla* that only showed values lower than 30% in the spring.

In L. tridentata MRC is low for most of the year except in summer; this may be due by development of new rootlets susceptible to mycorrhizal colonization during the rainy season, meanwhile in the dry seasons the roots became thick and less susceptible to have mycorrhizal colonization. The seasonal behavior of the mycorrhizal association and the MRC values in Larrea, are like those registered by Apple et al. (2005) in the Mojave Desert, but they are different from Hernández-Zamudio et al. (2018) and Collier et al. (2003) results in Chihuahuan Desert, which report MRC as high as 83.2% and 77% respectively. These differences could be attributable to rainfall amounts, where the Mojave and Sonoran Deserts do not receive more of 200 mm per year, while the Chihuahuan Desert receives 300 mm as an annual average (Abd El-Gahni et al. 2017).

Few studies about the mycorrhizal status of *Prosopis* in wild conditions have been performed; among them, Verma et al. (2008) reported a MRC of 49-89% in *P. cineraria* in arid areas at India. In this paper, *P. juliflora* plants showed MRC not greater than 25% during the year, probably due to the soil conditions of the site and adaptability of AMF to soils where these individuals stand.

AMF are recognized as key elements of soil fertility, absorbing water and soil mineral nutrients by ERM, and delivering them to host plant roots (Smith and Read 2008). Average ERM values are between 21 and 160 mg L^{-1} of soil (Giovannetti and Avio 2002) but in the studied plants values are lower in winter, and

increase up on summer and fall, The highest ERM values are those of *Jatropha* and *Prosopis* on summer which agree with the conclusions of Pepe et al. (2018) and Janoušková et al. (2011) who stated the relevance of ERM for functional traits to prompt establishment of mycorrhizal symbioses and thus to maintain soil biological fertility and mycorrhizal inoculum potential.

4.3. SOC and BRSP content

Soil organic carbon (SOC) is the amount of carbon present in the organic matter of the soil. The balance between the carbon input by the forest and microorganism determines the soil carbon pool (Kumar et al. 2016). Seasonal variation of the BRSP content in Prosopis decreases from winter to summer and it is almost doubled during the fall (Figure 1). It is noteworthy that P. juliflora had the highest value of BRSP, particularly during the fall. These increases could be attributable to the plant root system and its ability to develop mycorrhizal rootlets, which favors a greater density of fungal structures capable of releasing proteinaceous material to the environment, as stated by Bird et al. (2002) for P. articulate.

The values of BRSP increases from winter to fall, and its values are consistent for desert areas where the content of this substance is less than 2 mg/g soil (Halvorson and González 2006). Low concentrations of BRSP, according to Bird et al. (2002) may be due to low organic matter content and its low rate of decomposition. However, an increasing tendency can be observed in drought seasons (fall and spring), when previously produced mycelium and spores die and release the protein (Driver et al. 2005).

4.4. Water stable aggregates

Soil structure is essential to maintenance and support of plants and animals that inhabit it. Several studies correlate positively the AMF with soil aggregation, with it being well known that ERM has the capacity to entangle soil particles to form macro-aggregates, besides being the source for the glomalin release, allowing a stable binding of particles and therefore better soil structure (Gianinazzi et al. 2010). Bird et al. (2002) reported high levels of WSA in the fractions above 250 μ m at different depths of *Prosopis rhizosphere*, which varied from 65 to 80% during the summer, attributed mainly to the organic matter accumulation. In this sense, all plants in this study, showed the highest percentages of soil stable aggregation during the fall, which matches with the highest content of BRSP, possibly due to its release to soil by the hyphae and spores as stated by Driver et al. (2005).

4.5. Correlation analysis

The significant correlation values between BRSP and content of SOC and with all fractions of WSA, remarks that AMF could promote macroaggregates formation (> 0.25 mm) in which, according to Nichols and Toro (2011) organic matter is encapsulated, protecting it from decay. The correlation values between BRSP and ERM are consistent with those reported by Bedini et al. (2009) who cannot establish a significant correlation between these two variables.

5. Conclusions

Mycorrhizal association on Sonoran Desert plants varies during the year, showing seasonality related to temperature and soil moisture conditions. Our data shows the role of BRSP on soil quality promotion by increasing water stable aggregates at all levels. The rhizosphere conditions of Prosopis and Olneya favor a higher carbon content, while Jatropha promotes a higher ERM. It can be declared that for these reasons the three species have the highest values of WSA of the studied species. The results highlight the need to better understand the biochemical and microbiological characteristics of soil in desert plants to help us make the best decisions about the management of natural resources.

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