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Assessment of VA mycorrhizal inoculum potential in relation to the establishment of cactus seedlings under mesquite nurse-trees in the Sonoran Desert

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Abstract

A commonly observed preferential association was quantified between mature native mesquite (*Prosopis articulata*) trees and the seedlings of six cactus species (*Pachycereus pringlei*, *Opuntia cholla*, *Lophocereus schottii*, *Machaerocereus gummosus*, *Lemaireocereus thurberi*, *Mammilaria* sp.) in a previously-disturbed area of the Sonoran Desert of Baja California, Mexico. We hypothesized that, in addition to more favorable edaphic factors, the inoculum potential of beneficial vesicular–arbuscular mycorrhizal (VAM) fungi was higher, and therefore, more favorable for cactus seedling establishment under the mesquite tree canopy (UC) compared to adjacent barren areas (BAs) away from the trees. In the greenhouse inoculum potential assays, VAM fungi were detected in onion (*Allium cepa*) trap plants from all soil samples regardless of collection site, but cardon cactus (*P. pringlei*) trap seedlings formed no VAM even after 6.5 months. Test soils were further used to preinoculate new onion seedlings transplanted into pots, to serve as nurse plants to inoculate adjacent cardon seedlings by vegetative transfer. After 15 months, cardon seedlings did develop slight VAM colonization, confined exclusively to the outermost cortical layers. Examination of test soils for spores or root fragments revealed very few to none, and spore production on onion trap plant roots was also sparse even though colonization was high. Analysis of UC and BA soils revealed that the water holding capacity, nutrient content, cation exchange capacity, total carbon, and total nitrogen contents of the UC soils were all higher than those of the BA soils. Since the VAM inoculum density in this study was not different between sites under and away from the mesquite tree canopy, we concluded that VAM inoculum density is not the primary factor for the establishment of cactus seedlings and that edaphic factors probably play a more important role. Our results suggest, however, that VAM inoculum potential in these hot desert soils, although relatively low, is probably maintained in the upper layers by means of hyphal fragments rather than spores.

Keywords: Desert revegetation; Inoculum potential; Soil disturbance; Sonoran desert; Vesicular–arbuscular mycorrhizae; VAM fungi

1. Introduction

Areas of the Sonoran Desert near agricultural and urban centers in Baja California are increasingly being cleared to create space for new, but usually marginal and economically unsuccessful, agriculture (Anonymous, 1994). Soon thereafter, cultivated lands are

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being abandoned for reasons of low soil fertility, water shortage, or increased soil salinity. This abandonment creates barren landscapes subject to severe soil erosion, causing airborne dust when strong winds prevail (Bashan et al., 1992). The dust pollution is probably indirectly responsible for the high frequency of human respiratory diseases (Strannegaard and Strannegaard, 1990; Servin and Tejas, 1991; Ortega-Rubio et al., 1998). Therefore, revegetation by any means is essential, and reforestation has been made an official priority of contemporary Mexico.

Some of the plants responsible for holding the undisturbed desert topsoil in place are various large cactus species having immense subsurface root systems (Nobel, 1996). Unfortunately, these plants are difficult to transplant and establish in barren areas (BAs) under arid conditions, for reasons yet unknown, and their survival rates are low. Numerous revegetated areas of cactus in the city of La Paz, BCS, Mexico, have failed to persist during the last decade.

In the surrounding desert areas of Baja California Sur, Mexico, it is common to find young cacti growing under the canopy of large, isolated mesquite (*Prosopis articulata* L.) trees (Fig. 1A and B). Although some cacti may grow under other tree species, bushes, or in open areas, mesquite trees serve as the major nurse plant for several common species of cactus, including cardon (*Pachycereus pringlei* (Watson) Britton and Rose) (Franco and Nobel, 1989). In contrast, the barren soil areas immediately adjacent to a tree typically have no young cacti and rarely any perennial vegetation (Fig. 1C). Though the annual rainfall is less than 200 mm, the short rainy season from July through September does support a 'carpet' of annuals on these BAs (Fig. 1D).

Observations of enhanced seedling survival under the canopies of nurse plants in arid lands have been well documented (Callaway, 1995). The prevailing hypotheses to explain this phenomenon suggest that the primary factors provided by nurse-trees are increased shading (Valiente-Banuet and Ezcurra, 1991), increased soil moisture content (Franco and Nobel, 1989; Callaway, 1995), and increased fertility (Garner and Steinberger, 1989). However, the supplemental role of microorganisms such as mycorrhizae or other bacteria in these unique microecosytems (high litter layer, a nitrogen-fixing tree, large deposit of dust) has received little specific attention. The plant-growth-promoting bacterium, *Azospirillum brasilense*, enhanced the initial growth of cardon cactus seedlings in a similarly disturbed site (Puente and Bashan, 1993). Fluxes and cycling of C, N, and other nutrients between the ecosystem's biotic components (plant and microorganisms) and its geochemical matrix are fundamental characteristics that control ecosystem functioning (Barea, 1991; Miller and Jastrow, 1994). These factors may lead to high concentrations of cactus seedlings under single trees far away from others, assuming uniform distribution of seeds by birds under the canopy of all woody vegetation.

In addition to differences in edaphic factors, one of the biotic factors contributing to such improved establishment might be that mycorrhizal fungal inoculum potentials are higher under the canopy of these trees than in adjacent open areas. These fungi are known to benefit plant establishment and growth under stressful conditions, and thus, could aid cactus seedling establishment.

Many desert plants are known to be mycorrhizal (Rose, 1981; Bethlenfalvay et al., 1984; Pond et al., 1984; Bloss, 1985; Bloss and Walker, 1987; Cui and Nobel, 1992), including columnar cacti (Rose, 1981), although no studies have determined the relative dependence on mycorrhizae. We sought to evaluate whether vesicular–arbuscular mycorrhizae (VAM) fungi have a role in the primary establishment of cactus species under mesquite trees.

In this study, we sought to (i) measure VAM inoculum potential under the canopy of mesquite tree versus nearby BAs in a previously disturbed site, (ii) assess the potential contribution of VAM fungal inoculum to the establishment of young cardon cactus under the canopy of mesquite trees, and (iii) measure the comparative chemical and physical characteristics of soil under and away from the mesquite tree canopy at this specific site.

2. Materials and methods

2.1. Site location for sampling

The study site was a once-disturbed area in the rural residential neighborhood of El Comitan, 17 km northwest of La Paz, Baja California Sur, Mexico (24°10′N;

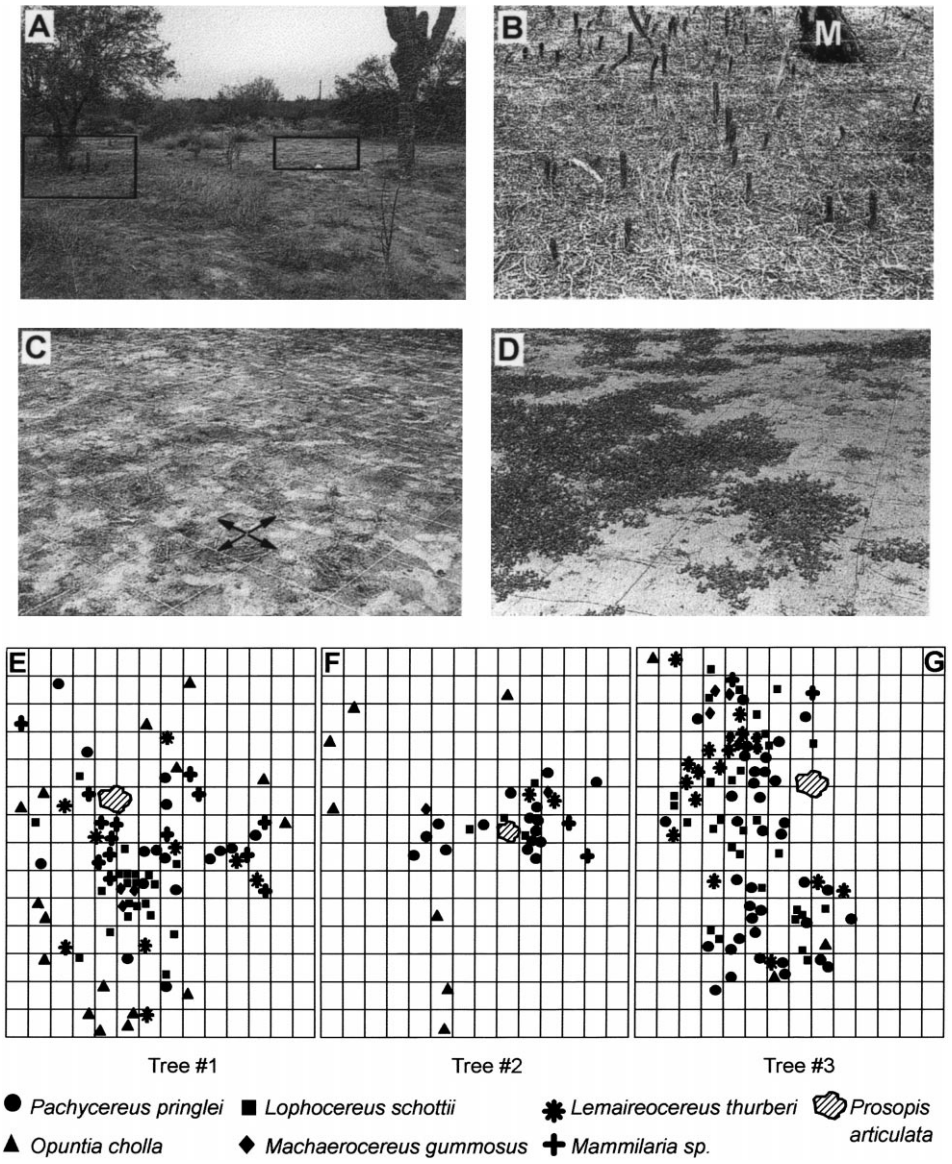

Fig. 1. (A) General view of one study site (plot #3) showing the mesquite nurse-tree (left) and the barren area nearby (right). Boxed areas in (A) are magnified in (B) and (C), showing areas under the canopy and the barren area, respectively, during the dry season. Arrows and white squares on the ground (B) and (C) mark the sampling grids (M: mesquite trunk). (D) The annual weeds which cover the barren area during the short rainy season. (E)–(G) show the spatial distribution patterns of the six cactus species under each mesquite tree, representing the actual grid layout in (B) and (C).

110°20′W). The area was partially cleared in 1973 for a proposed residential development, but then was abandoned, and has since remained undisturbed, leaving few mature mesquite trees and large cardon cacti (*P. pringlei*) (Fig. 1A). The distances between the individual remaining trees were in general >20 m. Most of the area is barren all year round except for the short summer rainy season when many species of annuals

grow. During this experiment, the most common annual providing a carpet-like covering was *Trianthema portulacastrum* L. (Fig. 1D). Three typical mature mesquite trees harboring many young cacti under their canopy were chosen as major sampling site-plots (Fig. 1A). All trees were in an area of about 1 km^2. The selection criteria, apart from being representative of the nurse-tree phenomenon, were (a) that the trees were not close to the main dirt road (to avoid foot and vehicle traffic), (b) that the canopy structure was high enough to allow working underneath, and (c) that a large BA was adjacent to each tree (Fig. 1B), but in no case further away than 5 m.

For each sampling area (14 m × 14 m), a grid of squares (45 cm × 45 cm, total of 196 squares) was marked, using mason's string, on the ground beneath each canopy (Fig. 1B), and an identical 196-square grid was marked in the adjacent BA (Fig. 1C).

2.2. Sampling procedures

Soil samples from sites under the tree canopy (UC) were taken from squares (i) without cactus seedlings (A), (ii) containing one cactus species (B), and (iii) containing more than one cactus species (C). Three replicate squares of each cactus-species type (A, B, C) were randomly selected within each tree-plot. Approximately, 300 g of soil were collected at each selected cactus-species site to a 10 cm depth, placed in plastic bags and transferred promptly to refrigerated storage (8+2°C). Samples from sites in the adjacent BAs were taken similarly (three replicate squares per tree-plot). All samples were obtained during the dry season (April 1996) when only remnants of senescent annuals could be found. Soil samples designated for soil analyses also were taken, stored at room temperature (average 30°C) for 4 days, and shipped within 3 days to the USDA-ARS Horticultural Crops Research Laboratory (HCRL), Corvallis, OR, USA. There they were stored at 5°C for 10 days until they were analyzed.

2.3. Soil analyses of site samples

Extractable nutrient levels of selected soil sites were determined by the Central Analytical Services Laboratory at the Oregon State University. Extractable phosphorus was analyzed by the sodium bicarbonate method (Olsen and Dean, 1965). Extractable cation bases were determined with atomic absorption spectrophotometry (AAS) after extraction with ammonium acetate. Total C and total N were directly analyzed on solid soil samples without acid digestion by using a Leco CNS-2000 MacroAnalyzer. Other extractable components of Fe, Mn, Cu, Zn were determined with AAS after DTPA extraction (Lindsay and Norvell, 1978). Moisture retention values of these very sites were also obtained through field capacity (−33 kPa) and permanent wilting point (−1500 kPa) measurements (Klute, 1986) in the laboratory.

2.4. Light intensity, air and soil temperature measurements at the field site

Light intensity measurements were taken during three consecutive days, 16–18 August 1995 (rainy season, all trees with foliage) at 11:30–12:30 hours. Data were collected at 15–22 different squares at the three UC and BA sites using a quantum photometer (Li-Cor, Model LI-185A, Lincoln, NE). Air and soil surface temperatures (s.s.t.) were also measured at UC and BA sites using a conventional laboratory thermometer.

2.5. Greenhouse studies

To determine the VAM fungal inoculum potential of soils from the various sites, a greenhouse study was established at USDA-ARS-HCRL in Corvallis, OR. Soils sampled from each site were serially diluted with a base of steam-pasteurized (60°C; 30 min) loam:sand (1:1, v:v) in a two-fold dilution series to 2^{-2} of the original soil. There were three replicates for each dilution, and three replicates for non-diluted samples.

Cardon cactus and bunching onion (*Allium cepa* L. var. White Lisbon) were used as trap plants for VAM fungi. Onions are well known to be responsive to the presence of any viable VAM fungal propagules in soil with low nutrient content, and thus, were chosen as the primary bioassay host. Onion seeds were purchased locally near Corvallis, OR. Though the mycorrhizal status of young cardon seedlings had not been established at the time of sampling, Bethlenfalvay (personal communication) has since determined that they form weak VAM associations in the experimental site.

Cardon fruits were collected from the wild in Baja California and the seeds removed (Puente and Bashan, 1993).

Soil dilutions were mixed manually in plastic bags and poured into white plastic columnar 'Super Cell' container-tubes (Ray Leach^{TM} Cone-tainers, Stuewe & Sons, Corvallis, OR). Cactus seedlings were grown in 60 ml tubes and onions were grown in 160 ml tubes. Each tube was filled to 85% capacity with a soil dilution mix, lightly tapped to settle soil evenly, then directly sown with either two cardon cactus or three onion seeds. The seeds were then covered with a final layer of a loam:sand mix (5–10 ml) and misted with tap water to moisten the soil. In addition, 12 tubes per assay host were filled with steam-pasteurized loam:sand for control checks for contamination.

Upon seedling establishment, plants were thinned to one per tube for the duration of the experiment. Plants were grown in the greenhouse at 28–32°C with a photoperiod of 16 h:8 h (light:dark), and under an average illumination of 450 μmol/cm^2/s supplied by high-pressure multivapor lamps. Plants were watered according to need, typically twice a week during the cardon's development, and three times a week for onions.

2.6. Experimental design and statistical analysis

The greenhouse study for MPN determination of VAM fungal propagules represented a factorial experiment (3×4) consisting of three major mesquite tree sampling plots, three cactus-species-type sites (A, B, C) UC, plus a BA site. Mesquite tree-plots were categorized as a main factor because of the variability in physiochemical and biological effects that may have evolved from the initial disturbance of this area. The UC cactus-species-type sites (A, B, C) and the BA sites were randomly sampled (replicated) three times within each tree-plot, yielding 36 experimental samples. Each of these samples was replicated three times at each MPN dilution for each bioassay host, yielding a total of 216 samples per host. Plants in the study were arranged in a randomized complete block design on a greenhouse bench.

MPN values and biomass data were subjected to statistical analyses of variance for significant effects at $p \leq 0.05$ (Wilkinson, 1990). Untransformed data demonstrated best fit to the model, and were analyzed as real data.

2.7. VAM fungal inoculum potential and growth measurements

Cardon seedlings were grown for 6.5 months (the time needed for adequate lateral root development) and onion plants for 11 weeks, after which time they were harvested for determination of VAM colonization to assess inoculum potential. After having been removed from its tube, each onion was severed at the base of the bulb to separate shoot from root. Each cactus was severed at the point where the main root adjoins the base of the shoot. Biomass measurements were also taken on oven-dried (65°C for 2–3 days) shoots. Roots were washed free of soil and evaluated for VAM colonization by clearing and staining, using a modified Phillips and Hayman (1970) technique, replacing lacto-phenol with lacto-glycerin.

Both cardon and onions were evaluated for mycorrhiza formation and inoculum potential using the most probable number (MPN) technique (Porter, 1979; Woomer, 1994). Each cleared and stained root system was examined microscopically and scored for the presence or absence of VAM colonization. The presence of any VAM-fungal hyphal penetration points, vesicles, arbuscules, or internal hyphae was considered a positive result. MPN values were then derived using appropriate tables for dilution levels (Woomer, 1994).

2.8. VAM fungal isolation and identification

Residual soil removed from harvested onion roots was saved for examining VAM fungal spore populations and diversity. Replicates from each treatment were pooled, and 100 g subsamples were wet-sieved and decanted through a series of 38–250 μm mesh sieves (Gerdemann and Nicolson, 1963). The sediment rinsed off sieves was examined with a stereo dissecting microscope.

To increase spore populations for eventual identification and quantification, onion pot cultures were started from part of the undiluted soils from each tree-plot×cactus-site-type treatment. Pot cultures were maintained in the greenhouse for one 8-month cycle before evaluation for spore production.

2.9. Onion 'nurse plant' study

Soil remaining from the inoculum potential experiment was used to establish a 'nurse plant' greenhouse study to examine the possibility that cardon could become mycorrhizal via hyphal connections from the neighboring colonized plants. Onion seedlings were grown in 80 ml plastic columnar tubes. When onions exhibited signs of being mycorrhizal (approximately 4 weeks), they were carefully removed from the tubes and planted in the center of 15 cm round plastic pots (one plant per pot) filled with a pasteurized loam–sand mix. After settling and moistening the soil, cardon seeds were sown in shallow holes placed in four compass directions, approximately 3 cm away from the centered onion plant. Three replicate pots of each plot×species-type treatment were planted. As each bunching onion matured and senesced, it was removed and a new plant reseeded directly in the middle to replace it. This cycle was repeated three times over 15 months. After 15 months, one cardon was then carefully removed from each pot, its root system washed, cleared, and stained for evaluating the extent of mycorrhizal colonization. If one replicate plant from a pot was not colonized, another plant was removed and examined.

3. Results

3.1. VAM inoculum potential measured by onion trap plants

After 4 weeks of growth, onion plants began to exhibit visual symptoms of mycorrhization (i.e. distinct growth increases) in several site treatments in the undiluted soils, with increasing numbers of plants becoming mycorrhizal as the study progressed. All onions grown in undiluted soils and most in the first dilution level (2^{-1}) became mycorrhizal by the end of the study.

ANOVA tests indicated no significant effects ($p \leq 0.05$) on MPN values by any main factor alone (mesquite tree-plot or cactus-type site) or any interactions. Orthogonal contrasts of MPN values obtained from UC versus BA sites indicated that the inoculum density in the BAs away from the mesquite trees was comparable to the density levels under the canopy (Fig. 2).

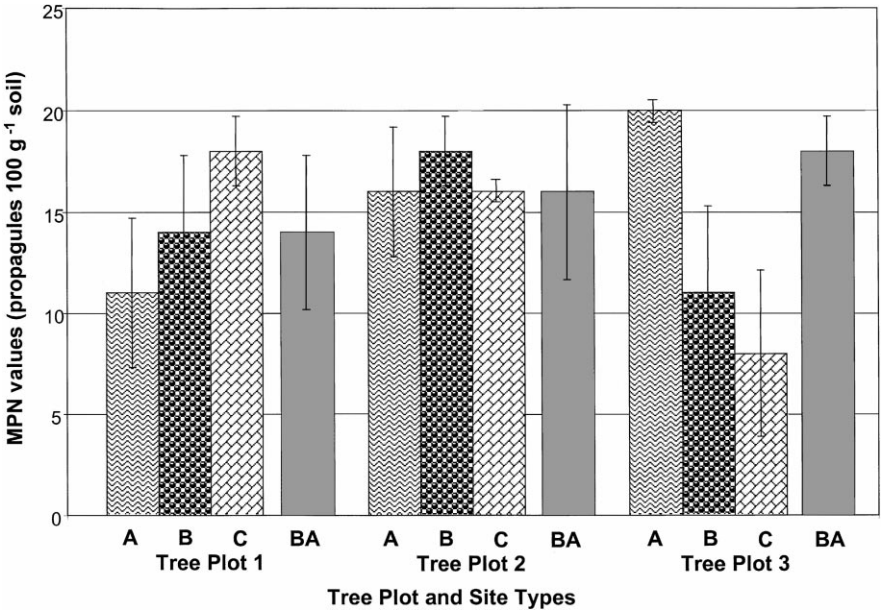

Fig. 2. Most probable number values obtained from a mesquite nurse-tree study site in the Sonoran Desert. Three mesquite tree-plots with three site types for cactus species growing under canopy (UC): (A) no cactus present; (B) one species present; (C) more than one species present); BA: barren area outside canopy.

Onion biomass data (not shown) did not demonstrate any growth responses that might have reflected any differences in MPN values for VAM fungal inoculum with different sites.

Throughout the study, cardon cacti remained non-mycorrhizal, thereby precluding any MPN assessment for this host.

3.2. Isolation of VAM fungal endophytes

Examination of plot soil (used in onion trap cultures) sieved for VAM fungal propagules indicated negligible spore populations in at least 25 randomly selected samples, regardless of the tree or the cactus species-site, although external hyphal fragments were abundant. Random sampling of initial field-collected soils also revealed few or no spores, as well as no hyphal fragments. Although not an unexpected finding, this precluded identifying any fungi. Further pot culture with onions for 6 months again yielded a paucity of spores for evaluation, despite high root colonization.

Debate as to when cardon cacti might become mycorrhizal or if they could become mycorrhizal via hyphal connections from neighboring colonized plants prompted the further trial using onions as nurse plants. Based on random sampling at different times, no cactus seedlings were found to be mycorrhizal before 10 months, but many had become so by the next sampling at 15 months, at which time the onion and cardon roots had grown together. There was no correlation between sampling site under the tree and VAM colonization.

The nature of root colonization in cardon was noticeably different from that observed for most other endomycorrhizal hosts. Any VAM fungal structures found were confined exclusively to the outermost cortical layers (one to two cell layers deep), which easily sloughed away from the remaining cortex and endodermis. There was no evidence of fungal penetration or activity below this layer. Vesicles or arbuscules were rarely seen. The more abundant internal hyphae and chlamydospores of an unidentified *Glomus* sp. appeared to be located intercellularly. External hyphae were few, existing only along the root surface and connecting chlamydospores formed in the cortex layer.

Preliminary observations of the spore populations in the pot cultures indicated a nominal increase in their quantities, but it was enough to assess some species composition. Two *Glomus* spp. and one *Gigaspora* sp. were detected, but they remained unidentified. All spores were sized in the 38–75 μm range. The *Glomus* spp. appeared to be common at most of the sites, independent of any canopy, cactus-species-type, or plot location, whereas the *Gigaspora* sp. was found in two samples, only in the UC soils. The difficulty in increasing spore populations from native soils with low or non-sporulating endophyte populations is not uncommon, and may require multiple, successive trap-culture cycles to detect species diversity (Stutz and Morton, 1996).

3.3. Chemical and physical properties of collection site soils

Analysis of chemical and physical properties of the UC and BA soils revealed that nutrients generally were higher and water-holding capacity was greater in the former than in the latter (Tables 1 and 2). The only measured elements that were not noticeably greater were Ca, Fe, and Cu. Total C was 2.2 times greater, total N and Mn were 3.5 times greater, and plant-available P was 2.3 times greater in the UC than in the BA soils.

3.4. Light intensity and soil surface temperature under and outside the canopy of mesquite trees

Light intensity differed under the canopy of each mesquite tree depending on its canopy structure. Average values measured under the canopy were 865 $\mu mol/cm^2/s$, while intensity values in the adjacent bare areas averaged 1775 $\mu mol/cm^2/s$.

Soil surface temperature varied according to the time of day and the air temperature. Representative measurements during the dry season showed that, when air temperature at 09:00 hours was 30°C, the average s.s.t. was 39°C in the shade and 42°C in the sun. At 13:00 hours, when air temperature was 35°C, the average s.s.t.'s in the shaded and unshaded areas were 46 and 54°C, respectively.

3.5. Evaluation of cactus populations under the canopy of mesquite trees

Every cactus seedling growing in the UC sites in this study was counted, located, and identified in 1995. A

Table 1
Chemical properties of soils from mesquite nurse-tree study site in Baja California, Mexico, comparing nutrient values from under canopy sites with barren areas outside canopy

Plot/site-type[a]	pH	P (mg/kg)	K (mg/kg)	Ca (cmol (p^+)/kg)	Mg (cmol (p^+)/kg)	Na (cmol (p^+)/kg)	CEC (cmol (p^+)/kg)[b]	EC (S/m)[b]	Fe (mg/kg)	Mn (mg/kg)	Cu (mg/kg)	Zn (mg/kg)	TC (g/kg)[b]	TN (g/kg)[b]	TIC (g/kg)[b]
1/UC	6.4	27	653	3.8	1.7	1.1	7.4	0.29	9.5	19.4	0.8	0.3	0.6	0.05	0.01
1/BA	6.6	18	507	2.7	1.5	0.6	5.4	0.21	18.4	6.4	1.0	0.4	0.3	0.02	0.01
2/UC	8.1	24	995	10.5	2.3	0.3	11.6	0.13	3.5	11.4	1.0	0.4	1.0	0.08	0.06
2/BA	8.9	8	745	11.2	1.9	0.3	11.2	0.01	2.2	3.1	0.7	0.2	0.4	0.02	0.05
3/UC	7.5	33	1279	9.6	2.6	0.3	13.0	0.18	6.7	15.0	0.6	0.5	1.2	0.09	0.04
3/BA	8.9	10	605	9.6	1.7	0.2	9.2	0.08	2.0	3.7	0.8	0.3	0.4	0.02	0.06
Means															
UC	7.3	28	976	8.0	2.2	0.6	10.7	0.20	6.6	15.3	0.8	0.4	0.9	0.07	0.4
BA	8.1	12	619	7.8	1.7	0.4	8.6	0.10	7.5	4.4	0.8	0.3	0.4	0.02	0.4
% Change[c]	–	133	58	3	29	56	24	100	15	248	0	33	125	250	0

[a] Mesquite tree under canopy (UC) plots (1–3) with averaged data from cactus species sites within each plot (as indicated in Fig. 1A–C); BA: barren area outside canopy.
[b] CEC: cation exchange capacity; EC: soluble salts; TC: total carbon; TN: total nitrogen; TIC: total inorganic carbon.
[c] Indicates percent change in nutrient content (increase or decrease) between UC and BA site averages.

Table 2
Moisture-holding capacities of soils from mesquite nurse-tree study site Baja California, Mexico, comparing values from under canopy sites with barren areas outside canopy

Plot/site-type	Soil water content (%)		Plant-available water (%)[a]
	−33 kPa	−1500 kPa	
1/UC[b]	13.38	6.56	6.82
1/BA	10.24	4.85	5.39
2/UC	15.72	7.33	8.39
2/BA	13.84	7.17	6.67
3/UC	14.69	8.39	6.30
3/BA	12.66	16.97	5.69
Means			
UC	14.60	7.43	7.17
BA	12.25	6.33	5.92
% Change[c]	19	17	21

[a] Values derived as the difference between soil water contents at field capacity (−33 kPa) and permanent wilting point (−1500 kPa).
[b] Under canopy (UC) plots (1–3) with averaged data from cactus-species sites (A)–(C) within each plot; BA: barren area outside canopy.
[c] Indicates percent change in moisture content between UC and BA site averages.

schematic diagram of spatial distribution of each plant species relative to the mesquite trunk is given in Fig. 1 E–G. A total of 236 young cactus plants were growing under the canopy of three mesquites, from 30 to 96 cacti per tree. All the six common cactus species growing in the El Comitan area were represented under the mesquite trees in 1995. Cardon (*P. pringlei*, 23 plants per mesquite) and garambullo (*Lophocereus schottii*, 18 plants per mesquite) had the highest populations, and pitahaya agria (*Machaerocereus gummosus*, four plants per mesquite) had the lowest. 3 years later, the cactus population had decreased to 216 plants, but all the plant species were still present. The empty areas under the canopy remained barren and no new cacti grew during that period.

4. Discussion

VAM fungal inoculum potential has a major influence on mycorrhizal effectiveness (Limonard and Smits, 1985) and on early root infection (Menge et al., 1985). The VAM inoculum potential may be low in disturbed soils (Parke et al., 1984; Fischer et al., 1994). In contrast, mycorrhization is high where land is covered with mycorrhizal plants (Benjamin et al., 1989). The VAM fungal inoculum potential in previously-disturbed desert areas is, however, unknown.

Our study revealed that the VAM fungal inoculum potential, measured by onion trap plants, is similar but low under the mesquite canopy and in the BA lacking perennial plants at the time of year the soils were sampled. The source of VAM fungi in the BA and under the canopy could be the annuals which ‘carpet’ the area for a short time each year following seasonal rains. The mycorrhizal status of these annuals was not determined in this study and has not been documented elsewhere. Since we found very few spores or identifiable root fragments in our soil samples that we now know contained VAM fungal propagules, and observed abundant external hyphal fragments in the pot-cultured soils, we suggest that the latter are the effective inoculum units in these soils. Tommerup and Abbott (1981) found hyphal fragments to be viable propagules existing in senescent plant roots remaining in soil sun-dried to −500 kPa and stored for 6 months. Under the mesquite tree canopy, the source of VAM fungal inoculum might be hyphae from roots of annuals or from perennials whose roots can cover the entire subsurface (Nobel, 1996). Still another source could be inoculum propagules carried with dust from adjacent areas.

Although it seems that VAM fungal inoculum potential is not the major factor affecting establishment of cacti in a barren, disturbed area, it might have a role in cactus growth under the tree. Once a cactus seedling establishes under the tree and acquires enough water to survive the first dry season, it will carry over to the next growth stage where VAM fungi may contribute to its further growth and survival. This may be more important for other cactus species that more readily form VAM than cardon, which appears from our study to be minimally mycorrhizal.

Commonly, VAM fungal inoculum potential and inoculum density are considered to be the same. However, this might not be necessarily so in the case of cacti. In the BAs, the fungal inoculum propagules are most likely resistant hyphae; under the tree, they could be spores or vegetative mycelia from colonized perennial roots. Therefore, in the short rainy season (about 2 months), it would take time for the resistant hyphae

to form an active mycelial network that might infect a young cactus seedling root that takes several months to develop. However, when cactus seeds germinate under the canopy, the seedling roots, when adequately developed, could encounter an active VAM fungal mycelial network maintained by a mesquite tree. Therefore, although our results indicate that the inoculum propagule densities under the tree and in the BA are similar, the inoculum potential under the tree might be greater.

As suggested by Stutz and Morton (1996), the low levels of sporulation reported in other desert soil surveys (Rose, 1981; Pond et al., 1984; Cui and Nobel, 1992), as well as their own detection of many non-sporulating VAM fungal species, indicate that lack of sporulation is a common if not predominant phenomenon in some arid regions. This makes it initially difficult to evaluate species diversity in any particular study. In our study, the low spore numbers found even after successive cultures on trap plants would also suggest the presence of some low- or non-sporulating species, and that any root colonization of indigenous plants in the surveyed sites is largely contingent on active fungal hyphae in the soil, possibly forming 'bridges' between the root networks of different plants (Allen and Allen, 1990).

Chemical and physical analyses from these sites (Tables 1 and 2) indicate substantial differences in composition between the UC and BA sites. Major and minor elements, organic C, and water holding capacity were all greater under the canopy, confirming previous reports (Franco and Nobel, 1989; Garner and Steinberger, 1989). It seems probable that these differences are enough to account for differences in cactus seedling survival for the first season. Given more nutrients, cooler soil temperatures, and more available water longer into the dry season, seedlings could remain alive and become mycorrhizal during the second season.

Given that soil nutrients and moisture are greater in the UC than in the BA sites, one would expect that microbial populations (bacteria, actinomycetes, and fungi) would be higher in the former than in the latter. Although we did not measure such populations in this study, a parallel study by Carrillo et al. (personal communication) did find that to be the case. Greater microbial populations under the older mesquite trees could provide support for young cactus seedlings through various means, including nutrient acquisition and nitrogen fixation by the mesquite tree, as well as from the production of plant growth regulators or stimulants.

In summary, in this disturbed area of the Sonoran Desert, VAM fungal inoculum potential appears not to be the main factor in the establishment of cacti under mesquite trees, and may play a secondary role to other environmental factors. The results presented here support the idea that the accumulation of nutrients and organic matter, and increased water retention of the soils under mesquite trees of sufficient age, can account for the differences in survival of cactus seedlings under the canopy compared to adjacent open areas where only short-lived annuals can grow. Cactus seedlings in the BAs may develop their roots too slowly before drought sets in and before they can be colonized by any viable VAM fungi that might aid in their survival. However, the fact that there is inoculum, probably in the form of resistant hyphae, both under the canopy as well as in the open areas away from the canopy, is a finding that may characterize desert ecosystems. Confirmation of that idea would require further observation and experimentation.

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