Nurse Plants, Mycorrhizae, and Plant Establishment in a Disturbed Area of the Sonoran Desert

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Abstract

Arbuscular-mycorrhizal (AM) fungi stabilize the soil and enhance plant growth by alleviating nutrient and drought stress. Their contributions to agriculture are well known, but their role in desert ecosystems has received less attention. The AM status of perennial plants in disturbed and undisturbed plots were investigated in the Sonoran Desert near La Paz, Baja California Sur, Mexico to determine if AM fungi contribute to resource-island stability and plant establishment. All perennial plants (46 species) in the study plots were AM, but root colonization varied widely (<10 to >70%). Roots of plants that established in greatest numbers in plant-free zones (colonizers) of disturbed areas were highly AM. Plants with trace (<10%) root colonization (cacti of the tribe Pachycereae: *Pachycereus pringlei*, *Machaerocereus gummosus*, and *Lemaireocereus thurberi*; and *Agave datilyo*) established preferentially in association with nurse trees. The pachycereid cacti grew under *Prosopis articulata* and *A. datilyo* under *Olneya tesota* canopies. Of the nine species of trees and arborescent shrubs in the area, the mature (>20 yr) nurse-legumes *P. articulata* and *O. tesota* supported the largest number of under-story plants. Younger plants had only occasional associates. AM propagule densities in plant-free areas were lower than under plant canopies (40 vs. 280 propagules/kg soil). Occurrence of soil mounds (islands) under plants owing to soil deposition was related to the nature of the canopies and to the AM status of the roots. Island soils were enmeshed with AM-fungal hyphae, especially in the upper layer (approximately 10 cm). Seedlings of *P. pringlei*, growing in a screenhouse for six months in soil collected under *P. articulata*, had a biomass ten times greater than plants growing in bare-area soil. The results are consistent with the proposition that AM fungi contributed to the plant-soil system of our study area by: (1) helping to stabilize windborne soil that settles under dense plant canopies; (2) enhancing the establishment of colonizer plants in bare soils of disturbed areas; and (3) influencing plant associations through differences in the mycotrophic status of the associates.

Introduction

Natural plant communities are being inexorably converted to disturbed ones (Warren et al. 1996), calling for an ever-increasing understanding of the mechanisms that operate in natural ecosystems so that disturbed ones may be managed to restore and stabilize the environment (Grover & Musick 1990; Agnew & Warren 1996). Some factors that contribute to the fragility of arid ecosystems, such as limiting water, nutrient, and temperature conditions (Vinton & Burke 1995; Nobel 1996) are well known. Others, like soil microbes (Herrera et al. 1993; Francis & Read 1995; Herman et al. 1995), are little known, although their role in soil formation, plant establishment, and plant-community structure has been recognized (Callaway 1995).

Some plants modify the impact of adverse environmental conditions by changing their habitats (Gurney & Lawton 1996). This process of habitat engineering (Jones et al. 1997) may also facilitate the establishment of other plants (nurslings), whose survival often depends on the availability of an associate (Pugnaire & Haase 1996). A well-known nurse plant-nursling association is that between leguminous trees and desert succulents (Nobel 1988; Arriaga et al. 1993). Important nurse effects are the attenuation of temperature extremes (Valiente-Banuet & Ezcurra 1991) and nutrient accumulation (Callaway 1995), but adequate levels of soil water content are probably the decisive factor in seedling establishment (Jordan & Nobel 1981). Because the nurse plant affects water-holding capacity by modifying soil structure in its root zone (Joffre & Rambal

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1993), drought stress and soil structure are closely linked (Noy-Meir 1973).

Specifically, some perennial plants create within the reach of their roots and branches "resource islands" (Halvorson et al. 1994), mounds that originate from the deposition and subsequent stabilization of windborne soil particles under plant canopies (Armbrust & Bilbro 1997). These fine-textured soils become habitats for entire communities of organisms. Such "island" soils have a greater impact on their biota than is implied by the term "fertility island" with its emphasis on nutrients (Garner & Steinberger 1989). This impact is based on soil characteristics such as low bulk density, high water-holding capacity, better aeration and finer texture, and a stable aggregate structure in addition to higher nutrient levels than in the surrounding areas: conditions that favor active communities of soil organisms (Burns & Davies 1986).

Among soil microbes, arbuscular-mycorrhizal (AM) fungi stand out in harsh and limiting environments because of their role in stress alleviation (Sylvia & Williams 1992). Their hyphae permeate large volumes of soil (Camel et al. 1991), interconnect the root systems of adjacent plants facilitating an exchange of nutrients between them (Allen & Allen 1990; Bethlenfalvay et al. 1996), and contribute to plant growth and to soil structure because of their intimate association with the living cells within both root and soil (Bethlenfalvay & Schüepp 1994; Degens et al. 1996; Schreiner et al. 1997; Wright & Upadhyaya 1998). AM fungi are therefore recognized as an essential component of plant-soil systems of deserts (Bethlenfalvay et al. 1984; Allen 1991; Cui & Nobel 1992; Requena et al. 1996).

The purpose of this study was to elucidate some of the relationships between plants, AM fungi, and soils which may be helpful in the revegetation of disturbed areas, especially with plants of shallow root systems, such as pachycereid cacti. Specifically, we aimed to determine whether: (1) island formation was related to the AM status of nurse plants; (2) nurse plants were needed for the establishment of pachycereid cacti and *Agave datilyo*; and (3) the AM status of nurse-plant dependent seedlings differed from that of independent early colonizers of bare areas.

Materials and Methods

Study Area

The study area is located 16 km northeast of La Paz, Baja California Sur, Mexico, at 24°1N, 110°2W, where Sonoran desert scrub and sarcocaulescent scrub intergrade (León de la Luz et al. 1998). Geomorphologically, the area is an alluvial coastal plain formed by the deposition of granitic alluvium derived from erosion of the Sierra de la Laguna mountains (Maya & Guzmán 1998). The climate is arid with annual mean precipitation of 180 mm, mainly in late summer. Mean temperatures vary from the coldest (January, 18°C) to the warmest month (August, 30°C), but include large day-night variations. A phenological study of the floristic composition of the wider area, characterized as a transition between xerophilic matorral and dry tropical forest, showed plant diversity to be relatively modest at 136 angiosperm species (León de la Luz et al. 1996).

The study centered on disturbed (3) and undisturbed (1) plots, delimited in size (160 × 80 m, 1.3 ha) by dirt roads and a desert wash (Fig. 1). The undisturbed plot contained native, old-growth vegetation, whereas all three disturbed plots had been cleared for urban development in the mid 1970s, with some of the larger trees and cacti left in place for their esthetic value. Soil disturbance by bulldozing was shallow (5–20 cm) and did not remove the topsoil. Many small channels traverse the area, carrying ephemeral flow during the occasional cloudbursts of the rainy season. One of the disturbed plots (plot 3) was cleared a second time 15 years before this study, but was in all other respects comparable to the other two disturbed plots. Vegetation was permitted to recover on all disturbed plots, as the development did not take place.
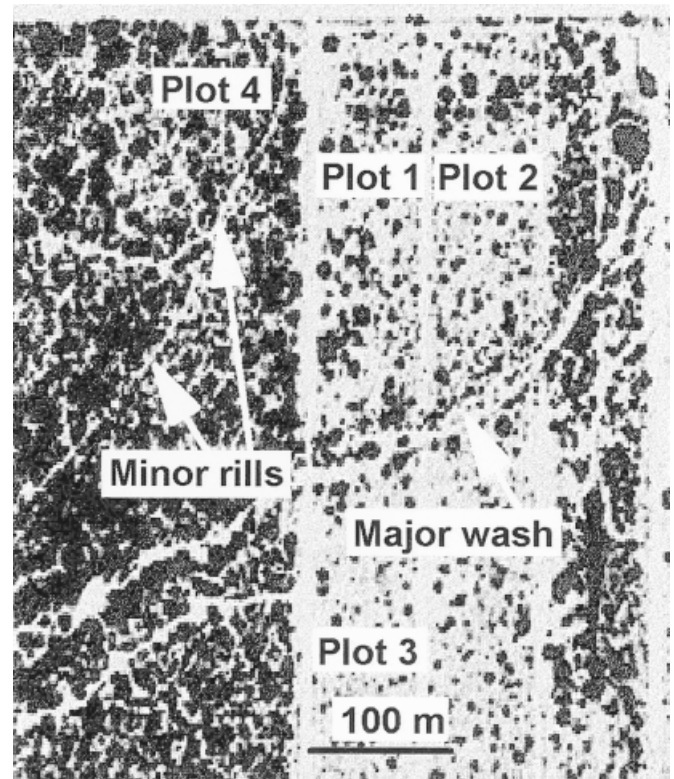

Figure 1. Aerial photograph of the study site. Black dots indicate vegetation. Disturbed plots 1 and 2 were partially cleared in the mid-1970s. Disturbed plot 3 was partially cleared for a second time in the mid-1980s. Plot 4 is part of a larger undisturbed area that contains native, old-growth vegetation.

Plant Description and Count

We counted all perennial plants taller than 0.5 m to gain an overview of the vegetation patterns and differences in the disturbed and undisturbed plots. In describing plant canopies, we emphasized characteristics that affect the deposition of windborne soil particles around plants (Armbrust & Bilbro 1997). Canopy traits at the base were classified as either "closed" (decumbent or drooping branches) or "open" (no branches near the ground), whereas those at the top were classified as "dense" (limited or no visibility through the canopy) or "loose" (good visibility).

The sparse vegetation in the disturbed plots permitted counting of plants in 16 segments, 10 m wide. Owing to the dense plant cover of the undisturbed plot, smaller areas were sampled. Because *Prosopis articulata* (mesquite), a dominant plant, did not support below-canopy nurslings until it reached a certain size (a trunk diameter of approximately 20 cm), we used this number as a convenient mark to differentiate between "young" (<20 cm) or "mature" (>20 cm) plants. Young mesquites in the disturbed plots represented regrowth that has occurred since the disturbance and were generally 20–25 years old. Arborescent cacti, such as *Pachycereus pringlei, Lophocereus schottii, Machaerocereus gummosus, Lemaireocereus thurberi* of the tribe Pachycereae (Bravo-Hollis 1978) have growth rates around 2.5 cm/yr during the first decades (Roberts 1989). Pachycereids up to 0.5 m tall (20–25 years) therefore approximated populations established since the disturbance, permitting us to use 0.5 m as the cut-off between young and mature cacti.

Mycorrhiza Determination

Mycorrhizal samples were collected in November and February 1997, 2 and 5 months after an unusually wet rainy season. For the determination of plant AM status, fine roots were excavated from surface soil (5–30 cm) and followed to the stem of the plant of origin before excising. Six root samples of each species from randomly selected plants within plots were cleared in KOH (5%, w/v, 30 minutes, 90°C), washed with water, acidified (0.01 *N* HCl, 1 hr), and stained with trypan blue (0.05%) in lacto-glycerol (glycerol:lactic acid:water, 1:1:1; 15 minutes; 90°C). After de-staining with lacto-glycerol, root colonization was estimated by the grid-line intersect method (Giovanetti & Mosse 1980). When the roots were too thick or opaque to identify colonization at the intersects, they were dissected longitudinally to expose the AM root mycelium (Fig. 2B). The numbers of AM and nonAM cortical segments were then determined to calculate the percentage of AM root colonization.

To determine the abundance of AM-fungal propagules among different microenvironments (Allen & Allen
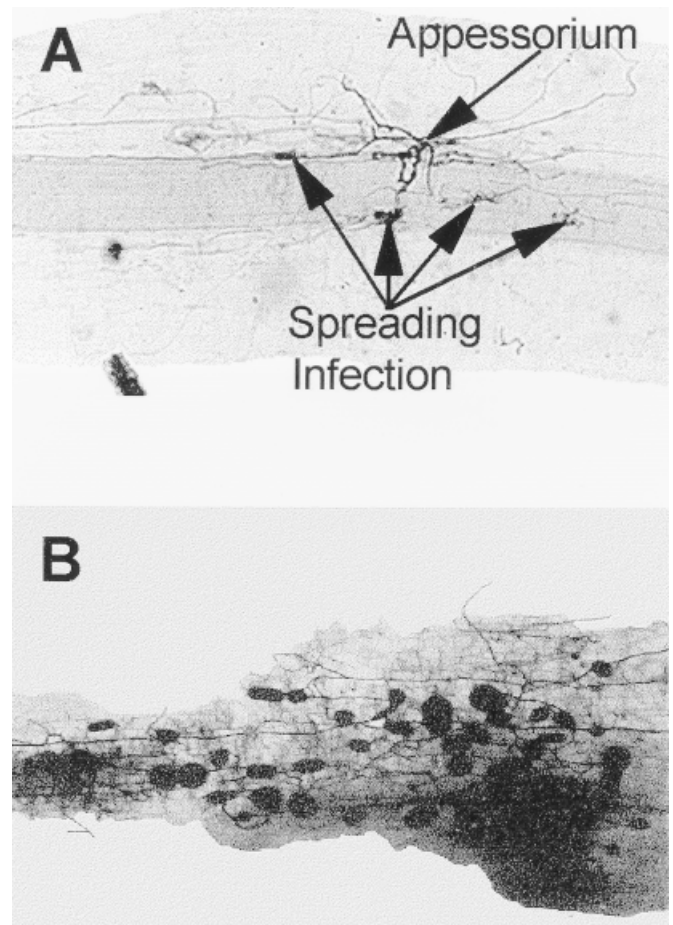

Figure 2. Intraradical structures of arbuscular mycorrhizal fungi: A. The first stage of root colonization by an AM fungus: an infection unit with spreading root colonization. B. Vesicles and spore-like structures between root cells.

1990), areas were compared beneath (1) mature mesquite, or (2) *Olneya tesota* (ironwood), because these plants harbored the greatest number and diversity of under-story plants among potential nurse plants in the plots, (3) areas beneath young mesquite plants, because none of these supported more than an occasional nursling, and (4) areas free of plants (bare areas). From these four categories, five plants were selected at random within one of the disturbed plots (plot 1, Appendix 1), and five soil cores (1.2 L each, 5–35 cm depth) were taken from the twenty sites at evenly spaced distances from the trunks out to the edge of the canopy. The samples were used to establish trap cultures for AM fungi, to make spore counts, and to perform an AM propagule-density bioassay.

AM Spore Count, AM Culture, AM Propagule Density, and Cactus Response Assays

Spore numbers were determined by wet-sieving (45, 75, 100, and 200-μm sieve openings), decanting, and su-

crose-gradient centrifugation (Brundrett et al. 1994) of the soil samples. Trap cultures were established for the propagation of AM fungi on sorghum (*Sorghum halepense* cv. Pampa Verde), and the cultures were grown for 12 weeks in a screenhouse at light intensities approximately one-half of full sunlight (900 mole/m² sec). The plants were senescent at harvest. Upon excising the stems, the rooted soil clumps were air-dried for 2 weeks before being broken down for spore counts. Stems were separated into vegetative and reproductive structures, dried (70°C), and weighed.

Soil AM propagule densities were determined by the infection-unit (IU) method (Franson & Bethlenfalvay 1989), growing sorghum in the soils collected from the 20 sites (two samples per site in 80-mL tapered growth tubes). We measured root and shoot dry weight, root length (Giovanetti & Mosse 1980), and the number of IU in the entire root system, sampled roots and IU daily from day 10 on, and assayed at 14 days when the root tips reached the bottom of the tube and discrete IUs (Fig. 2A) began to coalesce.

Pre-germinated seeds of *P. pringlei* were planted in pots (six replicates) in soils from young or mature mesquite, mature ironwood and bare areas, and harvested after 6 months to determine growth responses to the different soils by cacti, and to compare these responses to those of sorghum. Soil characteristics (water content, pH, and texture) were determined by standard methods (Klute 1986). Root contents of the original soil were determined by retrieving coarse roots through sieving and fine root fragments through adherence to electrostatically charged sheets of plastic. The roots were weighed, and root length and percent AM colonization were determined by the grid-line intersect method (Giovanetti & Mosse 1980). Plant fresh mass and soil traits were evaluated by analysis of variance and orthogonal contrasts.

Bacterium numbers were determined as a measure of the soil microbiota other than AM fungi. Colony-forming units (cfu) of total culturable bacteria were counted on nonspecific soil-extract agar according to Wollum (1982).

Island Formation, AM Soil Mycelia, and Plant-Canopy Structure

The fine-textured island soil that surrounded plants was inspected for the presence of AM soil hyphae visually (Fig. 3). A relationship between soil accumulation and the AM status of the roots and the nature of the plant canopy was derived from comparisons of canopy and mycorrhiza (fungus-root) characteristics.

Associations and the Distribution of Nurslings

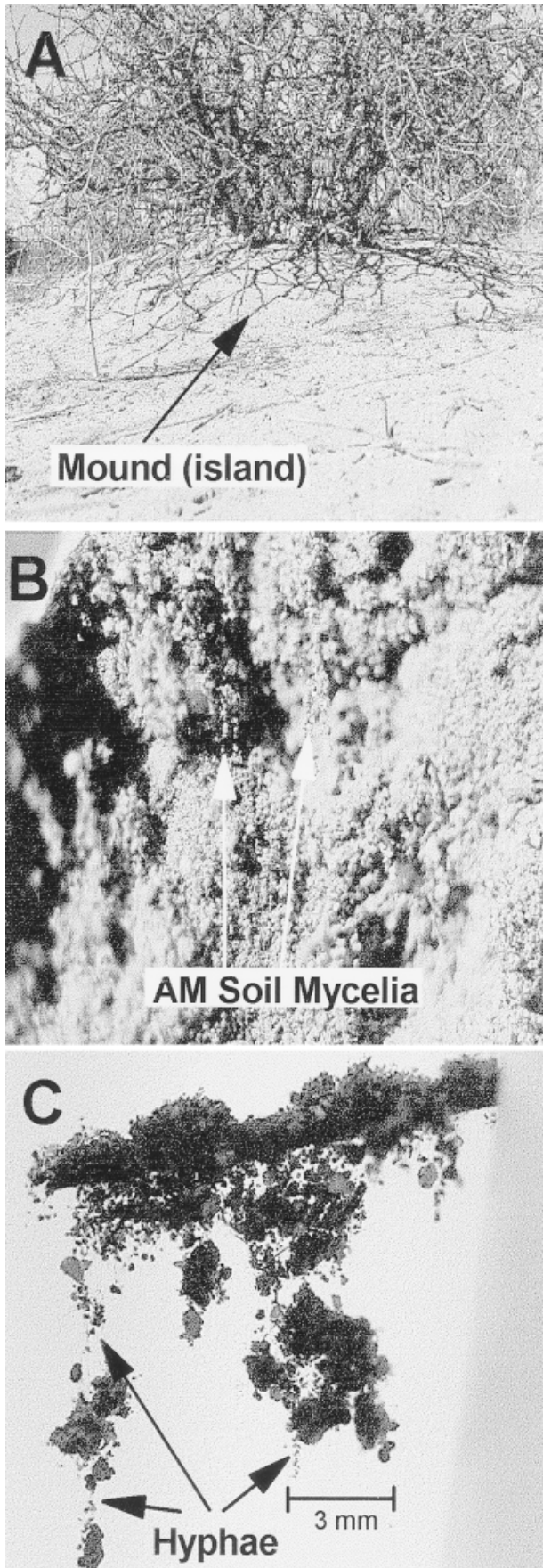To illustrate in detail the effects of age, species, and presence of nurse plants on the distribution of nurslings, all nurslings associated with the five individual plants (mature mesquite, mature ironwood, and young mesquite) and five bare areas were counted. These were the sites within plot 1 from which soil samples for mycorrhiza determinations had also been taken.

To provide a measure of the capacity of plants to act as nurses, the percentages of nurse plants associated with each nursling species were calculated. To do so, nurse-dependent young plants (*A. datilyo* and the pachycereid cacti, *L. schottii, P. pringlei, M. gummosus,* and *L. thurberi*) were counted within and outside the canopies of all potential nurse plants. Similarly, the percentage of nurslings associated with larger plants was calculated as a measure of the dependence of selected nurslings on their nurse plants. We present the data plot-by-plot to provide comparisons for consistency among like plots (plots 1, 2, and 3, disturbed) and for the difference between the disturbed plots and the undisturbed plot.

Analysis of Disturbance and Nurse-Association Effects

The distribution of two groups of plants was analyzed by the *G*-test of independence (Sokahl & Rohlf 1981) to determine whether the occurrence of these plants on disturbed and undisturbed land was significantly influenced by disturbance. The two groups of plants were: (1) plants that established preferentially with a nurse plant ("nurse-dependent"; *A. datylio, L. schottii, P. pringlei, M. gummosus,* and *L. thurberi*); and (2) plants that established in greatest numbers in bare areas ("colonizers"; *Caesalpinia pannosa, Jatropha cinerea, Jatropha cuneata,* and *Opuntia cholla*). To distinguish between disturbance effects alone or disturbance effects modified by the presence of a nurse plant (mesquite), two analyses were used: one based on total plot areas (3.9 ha, three disturbed plots combined; 1.3 ha, one undisturbed plot), and the other on the areas under the canopies of mature mesquite trees in disturbed or undisturbed plots. The null hypothesis of the analysis postulated that plant distributions were not affected by disturbance or by the presence of nurse plants. According to this hypothesis, the expected numbers of plants in each type of area were proportional to the sizes of the areas (disturbed:undisturbed, 3:1). When the numbers of plants actually observed deviated significantly from those expected according to area-size proportionality, their distribution indicated disturbance effects, nurse-plant effects, or a combination of both.

The distribution of *A. datylio, L. schottii, P. pringlei, M. gummosus,* and *L. thurberi* was also analyzed by the *G*-test to compare the occurrence of these nurse-dependent plants as a function of their association with one of two nurse plants (mesquite or ironwood) in disturbed and undisturbed plots. Sub-canopy areas of three disturbed plots were not combined; the plots were evaluated indi-

Figure 3. The stabilization of windborne soil. A. The mound under the drought-deciduous canopy of *Jatropha cuneata*. Shrub canopy is globose in shape (diameter 1.2 m). B. Soil layer at the mound surface permeated by AM hyphae. Figure height is 1 cm. C. soil particles and sand grains adhering to AM hyphae obtained from surface soil at a depth of 5 cm.

vidually to test for the consistency of nursling distribution among similar plots. Distributional comparisons of interest were the observed versus the expected number of nurslings: (1) in association with mesquite or without mesquite, and (2) in association with mesquite or with ironwood.

Results

Mycorrhizal Status of Plants and of Resource Islands

The study area contained 46 species of perennial plants in 23 families (Appendix 1), representing approximately one-third of the flora of the larger area (León de la Luz et al. 1996). The roots of all plants were colonized by AM fungi, but colonization levels varied widely among species (Appendix 1). Plants of the Euphorbiaceae and Fabaceae were highly AM, whereas root colonization of the cacti varied. Of the cacti of special interest in soil stabilization, the columnar species of the tribe Pachycereae, *P. pringlei, M. gummosus*, and *L. thurberi*, showed only traces of AM root colonization, whereas *L. schottii* had highly colonized roots.

Approximately half of the species (22) formed mounds of soil within the reach of their canopies (Appendix 1, Fig. 3A), whereas some others (5) were facultative island formers. Soils of resource islands were permeated by AM-fungal mycelia (Fig. 3B) and qualitative observations showed that they had finer texture than those of the surrounding bare-area soils. The top 10 cm of island soils tended to be root free. Soil particles adhered firmly to the AM hyphae that permeated this layer even after disturbance (Fig. 3C), confirming observations by others (Degens et al. 1996, Tisdall et al. 1997, Wright & Upadhyaya 1998).

Island formation depended on both the nature of the canopy and the AM status of the roots (Appendix 1). The majority of the plants that did form islands had dense canopies closed at the base. Those that did not, had loose canopies open at the base, whereas facultative island formers had a combination of open-dense or open-loose canopies (Fig. 4). Plants with loose canopies that were also closed at the base were not observed. About 80% of the island-forming plants with closed-dense canopies had roots that were well-colonized (>40%) by AM fungi. On the other hand, plants that did not form islands and had open-loose canopies, had predominantly
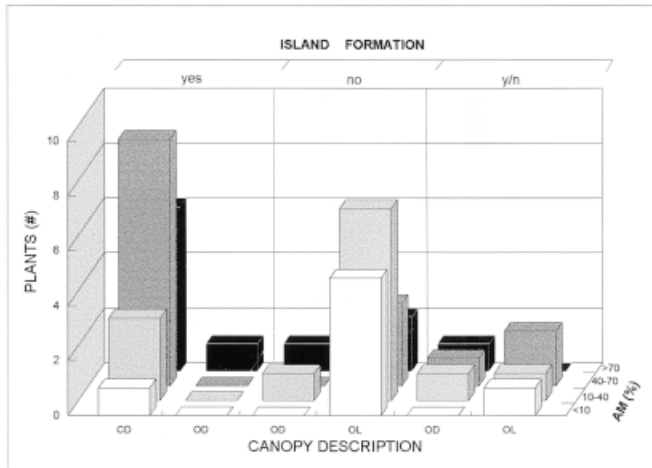
Figure 4. The relationship of island formation with canopy type and arbuscular-mycorrhizal (AM) root colonization. Canopy: CD, closed-dense; OD, open-dense; OL, open-loose. Island formation: always, yes; never, no; sometimes, y/n. AM: percentage of root length colonized.

(70%) poorly colonized roots (Fig. 4). These relationships indicated a strong association between AM fungi and resource islands. Most shrubs with closed-dense canopies did not support under-story plants, even though they formed island-mounds. Of the trees, mature mesquite and ironwood had the most diverse communities of associated plants (Table 1).

**Plant Establishment, Mycorrhizal Status, and
Soil Characteristics**

Four species established the largest numbers of young plants since the clearing of the disturbed areas (Appendix 1): *C. pannosa, J. cinerea, J. cuneata,* and *O. cholla.* These colonizer species were intensely mycorrhizal and predominantly nurse-free. Nurse-associated plants, on the other hand, like *A. datylio, L. schottii, P. pringlei, M. gummosus,* and *L. thurberi,* had sparsely (<10%) AM roots. *P. pringlei* predominated under mesquite and *A. datylio* under ironwood (Table 1). Some other species, like the cacti *L. schottii* and *Mammillaria dioica,* the exotic grass *Cenchrus ciliaris,* and the ever-present pioneer, *J. cinerea,* also proliferated under mesquite, but not under ironwood. Neither young mesquite (Table 1) nor young ironwood (data not shown) supported more than an occasional nursling. Nurslings of different species apparently required different soils, and desirable soil traits were apparently engineered by some nurse plants (especially mesquite), but not by others.

The sandy-clay-loam (Gee & Bauder 1986) island soil of mature mesquite abutted the loamy sand of the bare area surrounding it, and had significantly greater water content (44%) and lower (neutral) pH than the latter (Ta-

ble 2). The loamy-sand soil under ironwood was not significantly different from bare-area soil, whereas the sandy-loam young-mesquite soil was intermediate between bare-area and mature-mesquite soils, identifying it as a phase in the soil improvement process engineered by mesquite. Soils under mesquite apparently acquired characteristics in texture and structure that permitted the formation of greater root mass and length, better soil penetration, and more intensive AM colonization than in the other soils (Table 2). Probably because of enhanced C input into the soil by mycorrhizae (fungus-roots), soil bacteria were more numerous in island than in bare-area soils (Table 2). Of the soil traits measured, bacteria numbers were correlated ($r = 0.994$, $p = 0.006$) only with AM root colonization.

Mesquite-Cactus-Agave Associations

The percentage of mature mesquite trees associated with young *P. pringlei* was many times larger than that of other trees in both disturbed and undisturbed plots (Table 3), an observation that generally held also for the associations of the other three pachycereid cacti. The percentage of mesquite plants associated with *P. pringlei* was lower ($p = 0.070$) in the undisturbed than in the disturbed plots, indicating that it was more dependent on mesquite under disturbance. In comparison, fewer mesquite trees associated with *A. datylio* than most other large plants. Of the five nurslings with sparsely AM roots (*A. datylio, L. schottii, P. pringlei, M. gummosus,* and *L. thurberi*), more associated with mesquite than with any of the other potential nurse plants (Table 4).

Comparisons of observed versus expected numbers of plants in disturbed and undisturbed plots showed significantly more early colonizers in the disturbed area and fewer in the undisturbed area than were expected based on a random distribution independent of disturbance (Table 5). Conversely, the numbers of nurse-dependent plants were smaller (or statistically the same) than expected in the disturbed areas and were larger than expected (or statistically the same) in the undisturbed one. These findings indicate that disturbance favored the establishment of colonizer plants and inhibited that of the nurse-dependent ones. Under mesquite, however, the observed numbers of both colonizer and nurse-dependent plants were significantly greater in the disturbed area and smaller in the undisturbed area, than numbers expected owing to chance alone. We interpret this "mesquite effect" as follows. The effects of the mature-mesquite resource island within a disturbed area are distinct from those of surrounding areas and their benefits are shared by all seedlings. Under the mostly overlapping canopies of the large plants in undisturbed areas (Fig. 5C), on the other hand, conditions favorable for plant establishment (shading and soil quality) are less patchy and more continuous throughout than

Table 1. Nursling flora under individual mesquite and ironwood trees in a disturbed area (plot 1).*

Family	Species	Mature Mesquite 1	2	3	4	5	Young Mesquite 1	2	3	4	5	Mature Ironwood 1	2	3	4	5
Acanthaceae	*C. californica*	1	—	—	—	1	—	—	—	—	—	1	2	—	—	—
	R. peninsularis	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Agavaceae	*A. datylio*	4	—	2	3	33	1	—	—	1	—	60	27	48	55	3
Anacardiaceae	*C. edulis*	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—
Burseraceae	*B. hindsiana*	—	1	—	—	—	—	—	—	—	—	1	—	—	—	1
	B. microphylla	—	—	—	—	—	—	—	—	—	—	2	—	2	—	1
Capparidaceae	*A. emarginata*	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Cactaceae	*L. thurberi*	4	—	9	3	—	—	—	—	—	—	—	—	—	—	—
	L. schottii	15	2	19	1	2	—	—	—	—	—	—	—	—	—	—
	M. gummosus	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
	M. dioica	2	1	12	13	3	—	—	—	1	—	—	—	—	—	—
	P. pringlei	28	11	15	14	11	—	—	—	—	—	1	—	—	—	—
	O. cholla	—	—	24	5	7	1	—	—	—	—	—	1	—	—	1
Celastraceae	*M. phyllantoides*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Compositae	*E. diffusa*	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Chenopodiaceae	*A. barclayana*	35	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cucurbitaceae	*I. sonorae*	—	2	1	4	3	—	—	—	—	—	—	—	—	—	—
Graminae	*Cenchrus ciliaris*	30	19	6	4	6	—	—	—	—	—	16	—	—	—	—
Euphorbiaceae	*J. cinerea*	33	11	27	18	15	—	1	—	—	—	11	9	7	—	—
	J. cuneata	5	—	—	2	1	—	—	—	—	—	—	1	—	—	—
	P. macrocarpus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
	D. lanceolata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Fabaceae	*C. pannosa*	—	—	—	—	—	—	—	—	—	—	—	—	3	—	1
Krameriaceae	*K. paucifolia*	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—
Malvaceae	*A. californicum*	—	—	—	—	1	—	—	—	—	—	—	1	—	—
Phytolaccaceae	*S. halimifolia*	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Rhamnaceae	*C. globosa*	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—
	Z. obtusifolia	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—
Simaroubaceae	*C. peninsularis*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Solanaceae	*L. fremontii*	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
	S. hindsianum	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—
Zygophyllaceae	*L. tridentata*	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—

*Five trees of each type were sampled. Bare areas are not shown, as they did not contain any nurslings.

in disturbed areas, approximating those of the resource island. Relative to the large concentration of associated plants found under mesquite in disturbed areas (Table 1), the concentration of nurslings under mesquite in the undisturbed area may, therefore, decline. Since the roots of adjacent large plants intermingle in the undisturbed area, plants share the most limiting resource, water, to a greater

extent than in the disturbed one. This more uniform resource availability may contribute to a more even distribution of the seedlings over the undisturbed area.

Plot-by-plot comparisons of the observed versus expected numbers of plants under mesquite, relative to those in the total plot area, showed a consistently greater concentration of plants observed under mesquite and

Table 2. Growth of *Pachycereus pringlei* in soils from islands formed by mature and young *Prosopis articulata* (mesquite), mature *Olneya tesota* (ironwood), and from bare areas free of plants.*

Soil	*P. pringlei* Fresh Mass** (g)	Soil Characteristics Water (%)	pH	Texture (%) clay	silt	sand	Roots (g/kg)	(m/kg)	AM (%)	Bacteria (10^5 cfu/g)
Bare area	0.9a	2.2a	7.8c	7.7a	8.0a	84.3c	0.41a	9.7a	13a	3.1a
Ironwood (I)	3.4b	2.5ab	8.3d	6.9a	7.8a	85.3c	0.90b	25.8b	46b	5.2ab
Young mesquite (Ym)	4.3b	2.9b	7.3b	12.1b	14.8b	73.1b	0.87b	38.8b	71d	7.3b
Mature mesquite (Mm)	10.4c	3.9c	7.0a	22.5c	14.4b	63.1a	1.92c	87.0c	57c	6.5b
ANOVA (*p*-values)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.178

*Numbers denote the means of six replicates and are significantly different ($p \leq 0.05$, orthogonal contrasts) when followed by different letters.
**Fresh mass data are average values of shoot mass divided by the number of surviving plants (10 plants/pot; 6 replicates).

Table 3. Percentage of nurse plants associated with pachycereid cacti and *Agave datylio.*

Nursling	Bursera hindsiana	Bursera microcarpa	Cyrtocarpa edulis	Fouquieria digueti	Jatropha cinerea	Olneya tesota	Pachycereusp ringlei	Prosopis articulata	Zyziphus obtusifolia
Plot 1									
Agave datylio	100	67	100	50	8	63	43	44	—
Lemaireocereus thurberi	—	—	—	—	—	—	—	19	—
Lophocereus schottii	—	—	—	—	3	—	—	38	—
Machaerocereus gummosus	100	22	—	20	—	12	5	12	—
Pachycereus pringlei	—	—	—	—	—	—	—	96	—
Plot 2									
A. datylio	100	50	60	100	13	86	29	71	83
L. thurberi	—	—	—	—	—	—	—	—	—
L. schottii	—	—	—	—	—	—	—	14	—
M. gummosus	—	—	—	—	—	—	—	14	—
P. pringlei	—	—	—	—	13	14	—	85	—
Plot 3									
A. datylio	—	22	33	—	11	100	10	33	—
L. thurberi	—	—	—	—	—	—	—	17	—
L. schottii	—	—	—	—	—	—	—	42	—
M. gummosus	—	—	—	8	—	33	—	17	11
P. pringlei	—	11	—	8	—	33	3	92	11
Plot 4[a]									
L. thurberi	—	—	5	—	—	—	—	—	—
L. schottii	—	—	5	—	1	14	—	—	4
P. pringlei	—	—	5	4	10	14	—	68	7

[a]Numbers for *A. datylio* and *M. gummosus* could not be obtained due to overlapping nurse-plant canopies and cloning (*M. gummosus*).

smaller numbers of plants without mesquite, regardless of disturbance (Appendix 2). This same pattern of establishment was observed for the cacti in comparisons of plant numbers under mesquite versus those under ironwood in plots 1 and 2, but not in plot 3, which was disturbed for a second time 10 years later. In plot 4 (undisturbed), only *P. pringlei* numbers showed a significant mesquite effect. The numbers of *A. datylio* associated with ironwood were generally higher than those associated with mesquite, regardless of disturbance.

Table 4. Percentage of nurslings (< 50 cm tall) associated with mature nurse plants.

Mature Nurse Plant	Plot 1					Plot 2					Plot 3					Plot 4[b]		
	Ad	Lt	Ls	Mg	Pp	Ad	Lt	Ls	Mg	Pp	Ad	Lt	Ls	Mg	Pp	Lt	Ls	Pp
No nurse plant	12	—	—	—	1	9	—	—	—	—	9	—	—	—	—	20	—	4
Bursera hindsiana	3	—	—	20	1	7	—	—	—	—	—	—	—	—	—	20	4	2
Bursera microphylla	12	—	—	13	—	25	—	—	—	5	15	—	—	—	2	—	—	—
Cyrtocarpa edulis	—	—	—	—	—	3	—	—	—	—	—	—	—	10	—	—	—	—
Fouquieria digueti	16	—	—	13	1	2	—	—	—	—	—	—	—	10	2	—	—	1
Jatropha cinerea	6	—	—	—	—	2	—	—	—	5	7	—	—	—	—	—	4	14
Larrea tridentata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Maytenus phyllantoides	—	—	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	—
Lysiloma candida	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	2
Olneya tesota (ironwood)	24	—	7	—	1	18	—	—	—	5	29	—	11	10	—	—	4	1
Opuntia cholla	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Pachycereus pringlei	14	—	—	—	—	5	—	—	—	5	9	—	—	—	2	—	—	—
Prosopis articulata (mesquite)	13	100	93	54	95	23	—	100	100	85	31	100	89	70	92	40	80	70
Zyziphus obtusifolia	—	—	—	—	1	1	—	—	—	—	—	—	—	—	2	—	4	1

[a]Ad, *Agave datylio*; Lt, *Lemaireocereus thurberi*; Ls, *Lophocereus schottii*; Mg, *Machaerocereus gummosus*; Pp, *Pachycereus pringlei.*
[b]*A. datylio* and *M. gummosus* are not shown, as association could not be distinguished due to overlapping canopies or cloning.

Table 5. Observed and expected numbers of nurse-dependent or colonizer plants in disturbed and undisturbed plots based on total-area or mesquite-area comparisons.*

Plant[a]	Total Area[b]					Area Under Mesquite[c]				
	Disturbed		Undisturbed			Disturbed		Undisturbed		
	Obs.	Exp.	Obs.	Exp.	p-value	Obs.	Exp.	Obs.	Exp.	p-value
Nurse-dependent										
Agave datylio	1,522	1,932	1,054	644	<0.001	304	224	496	576	<0.001
Lophocereus schottii	79	75	22	26	0.450	72	25	19	66	<0.001
Pachycereus pringlei	211	272	152	91	<0.001	197	84	104	217	<0.001
Machaerocereus gummosus	29	26	6	9	0.268	32	10	2	24	<0.001
Colonizer										
Jatropha cinerea	1,224	1,029	149	344	<0.001	431	129	33	362	<0.001
Jatropha cuneata	368	333	76	111	<0.001	56	21	21	56	<0.001
Caesalpinia pannosa	255	210	25	70	<0.001	0	0	0	0	<0.001
Opuntia cholla	565	516	124	172	<0.001	152	55	43	140	<0.001

*Differences between observed and expected numbers were evaluated by the *G*-test of independence.
[a]Root colonization by AM fungi of nurse-dependent plants was light (<10%), that of colonizers was heavy (>70%).
[b]The total area of the three disturbed sites was 3.9 ha; that of the undisturbed site was 1.3 ha.
[c]The area under all mature mesquite trees of the three disturbed sites was 0.15 ha; that in the undisturbed site was 0.39 ha.

Nurse-Plant Soils Test-Plant Growth, and AM-Fungal Propagules

We had little success in isolating spores from soil collected from mature mesquite, young mesquite, mature ironwood, and bare area sites, perhaps because spores were smaller than the openings of the finest-mesh (45 μm) sieve used. Counts of spores larger than 45 μm were extremely low (zero at most sites), confirming similar results obtained by Rose (1981). However, many spore-like AM-fungal structures were found in approximately 25% of the root fragments examined (Fig. 2B). The trap-culture of AM spores in the four different soils produced only one extraradical spore type in all cultures. These small (<75 m), hyaline spores were subtended by straight, septate hyphae, and were supported by a copious proliferation of mycelium. They may have been juvenile forms of different morphotypes (Morton 1988). A determination of total AM propagules (viable hyphal and root fragments) by the IU method, however, showed similar levels of propagule density in the three sub-canopy soils, and a significantly lower AM presence in the bare-area soils (Table 6).

Sorghum plants grown in mature-mesquite soil (2 weeks, IU method) had significantly greater shoot and root dry masses, and root length than those grown in the other soils. Plants grown in the other three soils did not differ, but the root/shoot ratio of plants grown in bare-area soil was greater than that of the other plants, indicating a greater resource allocation to roots that is common in poor soils. The best growth of sorghum in the mature-mesquite soil (Table 6) persisted at 12 weeks in another assay undertaken for the production of AM spores in trap cultures (Brundrett et al. 1994). Here, given more time to develop, plants in young-mesquite soil significantly outgrew those planted in ironwood and bare-area soils. Similarly, at 6 months after planting, growth of *P. pringlei* was best in mature-mesquite and poorest in bare-area soils (Table 2).

Discussion

Two models are available that help in understanding the dynamics of AM associations during recovery from disturbance (Allen & Allen 1992). One postulates that early-colonizing plants do not need AM fungi but cannot successfully compete with later seral AM plants that succeed them after AM-fungi invade the site. A second model considers the ability of plants dispersed in patches to attract inoculum, and assumes that early colonists are facultatively symbiotic and are able to form AM associations whenever AM propagules become available. Both models share the view that early AM associations not only enhance the colonizer plants, but also provide inoculum for later seral stages of vegetation.

The intensive AM colonization of the roots of our colonizer plants fits these models, as many of these perennial colonizers establish immediately after disturbance without being preceded by annuals. The presence of low but measurable levels of AM propagules that either survive disturbance or are supported by the wide-ranging roots of survivor plants probably accelerates this process. Colonizers that invaded bare areas in largest numbers in the study area (Appendix 1) did not, therefore, need to wait for the chance dispersal of AM fungi: it was not coincidental that the most frequent colonists were solitary plants with highly AM roots. The AM condition apparently permitted them to occupy the newly available open space, optimizing the uptake of water and nutrients.
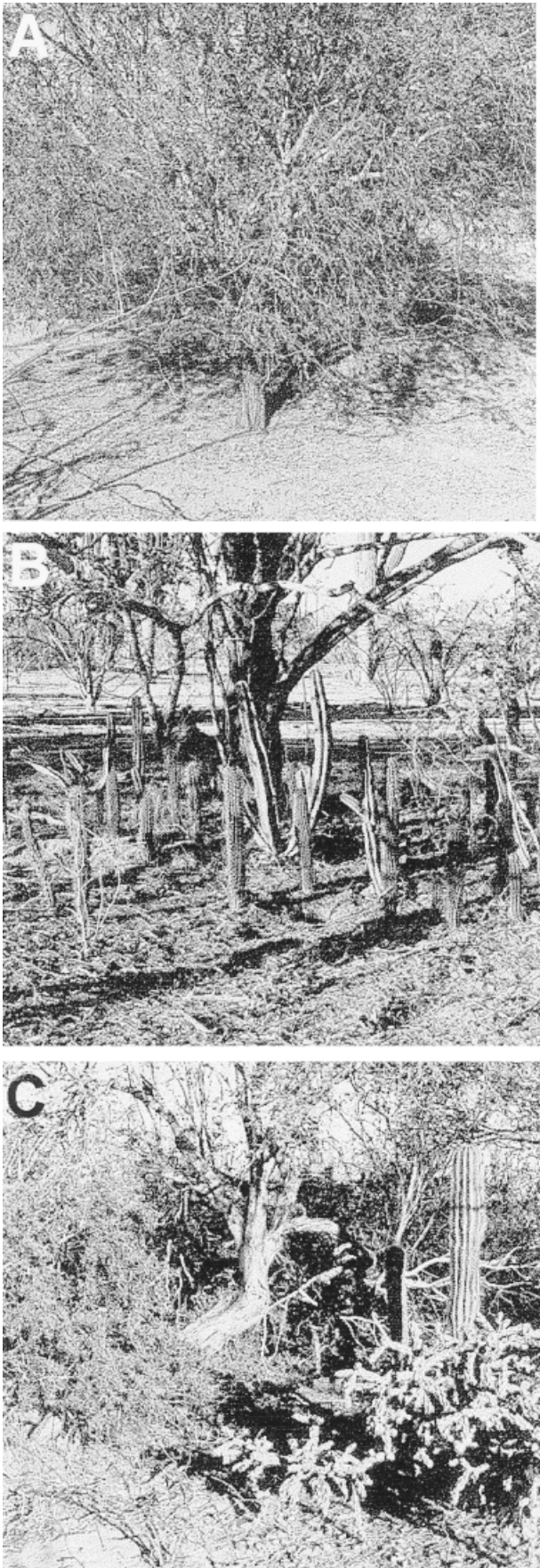
Plants with only trace AM root colonization, on the other hand, like the climax plants *P. pringlei* and *M. gummosus*, that may become AM only after a long (>1 year) lag phase (R. G. Linderman, personal communication, 1998), are more difficult to fit to the model. As nurse-dependent seedlings in the study area, they may be an exception to the classical view held for nearly a century (Stahl 1900) that early successional habitats are colonized predominantly by nonmycotrophic plants (Miller 1987), and that plants are necessarily mycorrhizal (obligately mycotrophic) in late seral stages (Gemma & Koske 1992; Cordiki & Rincón 1997).

Since the improvement of stress tolerance by AM fungi is important for plant establishment and survival in marginal habitats (Barea & Jeffries 1995), the apparent lack of dependence of pachycereid cacti and of *A. datylio* on their fungal symbionts is problematic. Two explanations may be offered for this apparent anomaly. One is the special root structures that agaves and cacti form in response to wetting. These "rain roots" increase the uptake of water and nutrients (Nobel 1988, 1996), a function that in most plants is enhanced by AM fungi (Bethlenfalvay et al. 1988). When cacti, such as *Opuntia*, form both rain roots (Dubrovsky et al. 1998) and AM associations (Appendix 1), the duplication of uptake functions may confer special advantages. When the stem segments of *Opuntia* root during its establishment phase, the AM mycelium present in the soil rapidly integrates the plant into the existing plant community by establishing hyphal connections with other roots (Read et al. 1985). Once established, uptake functions may shift to the rain roots during subsequent rain episodes of the growth phase. Such special adaptations are little known but could contribute to the success of some species as colonizers of arid lands.

The second explanation rests on the influence of the nurse plant on the island-microcosm soil: our observations confirm findings of others that both the identity of the nurse plant (Barth & Klemmedson 1982) and the time it needs to sufficiently improve the soil (Archer et al. 1988) influence the establishment of nurslings. The recruitment of nurslings, of course, depends also on the plants' diverse propagule-dispersion vectors (Hubbell 1979) and, in addition to soil development under tree canopies (Virginia 1986), on the amelioration of temperature extremes through shading by nurse plants (Valiente-Banuet & Ezcurra 1991; Valiente-Banuet et al. 1991). The differences observed in the growth of *P. pringlei* under uniform conditions but in different soils (Table 2), and in

Figure 5. A. Young (<20 years) *Prosopis articulata* (mesquite) tree showing a lack of understory plants. B. Mature (>20 years) mesquite with subcanopy cactus nurslings in a disturbed area. C. Aspect of the old-growth vegetation in the undisturbed plot.

Table 6. Plant and arbuscular-mycorrhizal (AM) propagule-density bioassay by the infection-unit (IU) method (2-wk old plants).*

Treatment-Soils [a]	2-Wk Old Plants					12-Wk Old Plant Shoots	
	Shoot Dry Mass (g)	Root Dry Mass (g)	Root Ln (m)	Root/shoot Ratio	IU (#/100 g soil)	Vegetative Dry Mass (g)	Reproductive Dry Mass (g)
Bare area	0.54[a]	0.92[a]	6.45[a]	1.57[b]	4[a]	1.72[a]	0.07[a]
Ironwood	0.69[a]	0.86[a]	6.80[a]	1.26[a]	29[b]	1.98[a]	0.19[a]
Young mesquite	0.78[a]	0.93[a]	8.01[ab]	1.25[ab]	24[b]	5.54[b]	1.61[b]
Mature mesquite	1.35[b]	1.52[b]	9.77[b]	1.13[a]	31[b]	8.46[c]	2.04[b]
ANOVA (p-values)	<0.001	<0.001	0.008	0.015	0.009	<0.001	<0.001

*Twelve-week old plants were grown for AM trap cultures.
[a]Sorghum was grown in soils obtained from sites under mesquite or ironwood canopies or from areas free of vegetation (bare areas).

different soils and subjected to different shading and soil temperature regimes (Carrillo-Garcia et al. 2000) demonstrate the importance of the soil factor.

Changes in the soil habitat are not engineered by the plant alone. The establishment of an AM-hyphal network for inter-plant nutrient exchange, soil-to-plant transfer of mineral nutrients, and plant-to-soil transfer of organic compounds (Allen & Allen 1992; Bethlenfalvay & Schüepp 1994) not only enhances plant development, but also results in soil-building interactions between the biotic and abiotic components of the soil (Belsky et al. 1989). The dense mats of AM mycelia that enmesh the soil particles of resource islands (Fig. 3) may be a key to an aggregating and stabilizing process (Miller & Jastrow 1992; Wright & Upadhyaya 1998), counteracting erosion by increased soil deposition (Coppinger et al. 1991) and influencing erosion-driven changes in soil-surface layers that may ultimately alter the composition of the vegetation (Valiente-Banuet et al. 1995).

In contradiction to our observations, however, one often finds plants with sparsely AM roots, like *P. pringlei*, in undisturbed areas covered by old-growth vegetation on the Baja California Peninsula, that apparently grow unaided by an associated nurse plant. The mechanism of that phenomenon is not clear to us, but in the disturbed observation area described here, mesquite functioned as a keystone species (Mills et al. 1993), in that its absence may have resulted in a loss of the pachycereid cacti.

Conclusions

Arbuscular mycorrhizal (AM) fungi influence the development and stability of the plant-soil system as colonists of both root and soil. In arid ecosystems characterized by a patchy distribution of individual plants or of plant microhabitats centered on nurse plants, an early integration of mycotrophic seedlings into the community through a pre-established common AM mycelium may increase their survival rate, whereas nonmycotrophic plants would benefit from the improved growth conditions provided by the resource islands formed by nurse plants. The profusion of AM mycelia in the top layers of resource-island soils suggests a function for AM fungi beyond that of nutrient uptake. Proliferating in a favored, shaded microenvironment, they apparently contribute to the binding of windborne soil particles that settle under plant canopies. Thus, they form a link in an autocatalytic cycle of plant-soil interrelationships: the fungi improve plant growth through enhanced nutrient uptake, the more vigorous plant intercepts more windborne soil, this soil is bound by the mycorrhiza into a growing mound, and the mound provides more nutrients to the plant and a growth substrate for the fungus, thus, closing the cycle.

In our study area, plants differed in their ability to form resource islands, and among all potential nurse plants, mesquite was the most effective. Although nurslings took advantage of the availability of resource islands regardless of their AM status, plants with sparsely AM roots depended on mesquite more in disturbed than in undisturbed areas, whereas plants with intensely AM roots were colonists of areas bare of plants. Further work is needed to integrate the role of AM fungi with the plant-soil system in deserts.

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Appendix 1. Plant description, mycorrhizal status, and island formation at the Sonoran Desert study area.

Family	Species	H[a]	AM[b]	If[c]	Canopy at base	Canopy at top	Plants per Plot[d] 1D	2D	3D	4U
Acanthaceae	*Carlowrightia californica*	S	++	+	open	loose	2	6	0	5
	Ruellia peninsularis	S	++	−	closed	dense	8	23	11	175
Agavaceae	*Agave datylio*	acaS	+	−	open	open	630	756	134	1054
Anacardiaceae	*Cyrtocarpa edulis*	T	++	+	open	loose	5/5	2/7	4/0	19/30
Bignoniaceae	*Tecoma stans*	AS	++	−	open	loose	0	1	1	2
Boraginaceae	*Bourreria sonorae*	S	++	+	closed	dense	9	11	14	39
Burseraceae	*Bursera microphylla*	T	+	+/−	open	loose	3/9	10/3	0/10	20/23
	Bursera hindsiana	T	+	−	open	loose	3/1	6/4	1/0	3/2
Chenopodiaceae	*Atriplex barclayana*	SS	+	−	closed	dense	35	0	0	0
Celastraceae	*Maytenus phyllantoides*	AS	+++	+	closed	dense	2	2	1	19
Cactaceae	*Cochemia poselgeri*	cylS	++++	+	closed	dense	0	0	0	16
	Ferocactus peninsulae	gloS	+++	−	open	open	0	0	0	5
	Lemaireocereus thurberi	colS	+	−	open	open	15/4	0/1	14/2	6/18
	Lophocereus schottii	colS	++++	−	open	dense	41/2	1/0	37/0	22/26
	Machaerocereus gummosus	colS	+	−	open	dense	15/12	1/0	4/0	e/293
	Mammillaria dioica	cesS	+	−	open	open	16	11	20	249
	Opuntia cholla	cylS	++++	+	open	dense	278/25	185/22	102/13	124/307
	Opuntia lindsayi	cylS	++++	−	open	loose	16	18	7	14
	Pachycereus pringlei	colS	+	−	open	open	127/20	20/12	64/29	152/213
Capparidaceae	*Atamisquea emarginata*	AS	+++	+	closed	dense	4	4	3	64
Compositae	*Bebbia juncea*	S	+++	+	closed	dense	0	0	0	17
	Ericameria diffusa	S	++	+/−	open	dense	3	0	0	25
Euphorbiaceae	*Adelia virgata*	AS	+++	+/−	open	loose	0	0	0	22
	Jatropha cinerea	AS	++++	−	open	dense	465/38	390/7	369/18	149/194
	Jatropha cuneata	S	++++	+	closed	dense	122	113	133	76
	Ditaxis lanceolata	S	+++	+	closed	dense	8	13	0	3
	Pedilanthus macrocarpus	S	+++	+	closed	dense	4	1	3	35
Fabaceae	*Caesalpinia pannosa*	S	++++	−	open	loose	65	155	35	25
	Cercidium praecox	T	+++	−	open	dense	1	1	3	4
	Lysiloma candida	T	++++	+	open	loose	5/4	15/25	0/1	25/12
	Olneya tesota	T	++++	+	closed	dense	6/8	3/7	3/0	6/7
	Prosopis articulata	T	++++	+	open	dense	35/16	18/7	12/12	45/97
Fouquieriaceae	*Fouquieria digueti*	AS	+++	+/−	open	loose	10/7	4/2	7/6	12/25
Krameriaceae	*Krameria paucifolia*	SS	++	+	closed	dense	18	23	4	39
Labiatae	*Hyptis laniflora*	S	++	−	open	loose	13	7	0	22
Malvaceae	*Abutilon californicum*	S	++	−	open	loose	22	14	18	8
Phytolaccaceae	*Stegnosperma halimifolia*	S	+++	+	closed	dense	14	7	0	7
Rhamnaceae	*Condalia globosa*	S	+++	+	closed	dense	8	8	3	9
	Ziziphus obtusifolia	AS	+++	+	closed	dense	19	12	9	28
	Colubrina glabra	S	++	+/−	open	dense	0	0	0	7
Sapindaceae	*Cardiospermum corindum*	AS	+++	+	closed	dense	0	0	0	6
Simaroubaceae	*Castella peninsularis*	S	++	+	closed	dense	14	9	3	6
Solanaceae	*Solanum hindsianum*	S	++	−	open	loose	23	15	5	6
	Lycium fremontii	S	+++	+	closed	dense	37	27	2	9
Zygophyllaceae	*Larrea tridentata*	S	++++	+	open	loose	2	2	1	1
	Viscainoa geniculata	AS	++	−	open	loose	0	1	0	2

[a]Habit of growth: acaS, acaulescent succulent; AS, arborescent shrub; cesS, cespitose succulent; colS, columnar succulent; cylS, cylindrical succulent; gloS, globose succulent; S, shrub; SS, subshrub; T, tree.
[b]Percentage of root colonization by AM fungi: +, <10%; ++, 10 to 40%; +++, 40 to 70%; ++++, >70%).
[c]Island formation (IF) as presence (+) or absence (−) of mounds below a canopy. +/− indicates occasional to frequent IF.
[d]D, disturbed; U, undisturbed. Arborescent plants are shown as "small/large" (small, <20 cm; large, >20 cm stem diameter).
[e]Rooting of prostrate stems by *M. gummosus*, in dense stands at site 4, did not permit a count of independent small plants.

Appendix 2. Observed and expected numbers of nurse-dependent plants growing under mesquite, ironwood or on total plot area in disturbed and undisturbed plots. The significance of differences between observed and expected numbers is evaluated by the *G*-test of significance.

	Mesquite versus Total Area Comparisons[a]						*Mesquite versus Ironwood Comparisons*				
	Ls	Pp	Mg	Lt	Ad		Ls	Pp	Mg	Lt	Ad
Plot 1 (disturbed)											
Mesquite area (790 m^2)						Mesquite area (790 m^2)					
Observed	38	122	8	18	84	Observed	38	122	8	18	84
Expected	3	7	1	1	39	Expected	27	80	5	12	152
Total plot area less mesquite area (12210 m^2)						Ironwood area (426 m^2)					
Observed	3	5	7	0	559	Observed	3	1	0	0	150
Expected	38	120	14	18	604	Expected	14	43	3	6	82
p-value	<0.001	<0.001	<0.001	<0.001	<0.001	*p*-value	<0.001	<0.001	<0.001	<0.001	<0.001
Plot 2 (disturbed)											
Mesquite area (366 m^2)						Mesquite area (366 m^2)					
Observed	33	59	7	14	42	Observed	33	59	7	14	42
Expected	1	2	0	0	4	Expected	22	35	5	8	48
Total plot area less mesquite area (12634 m^2)						Ironwood area (249 m^2)					
Observed	4	5	3	0	92	Observed	4	0	1	0	39
Expected	36	62	10	14	130	Expected	15	24	3	6	33
p-value	<0.001	<0.001	<0.001	<0.001	<0.001	*p*-value	<0.001	<0.001	0.073	<0.001	0.192
Plot 3 (disturbed)											
Mesquite area (328 m^2)						Mesquite area (328 m^2)					
Observed	1	16	1	0	178	Observed	1	16	1	0	178
Expected	0	1	0	0	19	Expected	1	15	1	0	296
Total plot area less mesquite area (12634 m^2)						Ironwood area (249 m^2)					
Observed	0	4	0	0	578	Observed	0	1	0	0	152
Expected	1	19	1	0	737	Expected	0	2	0	0	34
p-value	<0.001	<0.001	<0.001	—	<0.001	*p*-value	0.773	0.539	0.773	—	<0.001
Plot 4 (undisturbed)											
Mesquite area (3895 m^2)						Mesquite area (3895 m^2)					
Observed	19	104	—	2	496	Observed	19	104	—	2	496
Expected	7	46	—	1	316	Expected	19	99	—	2	572
Total plot area less mesquite area (9105 m^2)						Ironwood area (252 m^2)					
Observed	5	48	—	2	558	Observed	1	1	—	0	112
Expected	17	106	—	3	738	Expected	1	6	—	0	37
p-value	<0.001	<0.001	—	0.437	<0.001	*p*-value	0.846	0.008	—	0.846	<0.001

[a]Nurslings are: Ls, *Lophocereus schottii;* Pp, *Pachycereus pringlei*; Mg, *Machaerocereus gummosus*; Lt, *Lemaireocereus thurberi*; Ad, *Agave datylio.*