Effects of Resource-Island Soils, Competition, and Inoculation with *Azospirillum* on Survival and Growth of *Pachycereus pringlei*, the Giant Cactus of the Sonoran Desert

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Abstract

Resource-island soils formed by some plants in arid lands are capable of supporting certain plants that do not normally establish in surrounding areas free of vegetation. We determined growth responses of *Pachycereus pringlei* (cardon), the giant columnar cactus, whose widespread, finely branched, subsurface root systems stabilize desert soils, to four soils collected from within or outside of resource islands. Traits of cardon grown in soils from mature (MM) or young (YM) *Prosopis articulata* (mesquite), mature *0lnea testosa* (ironwood, MI), or bare areas (BA) were compared, to determine differences between the effects of soils due to the identity or the stage of development of nurse plants. The levels of soil N, P, and C contents were in the order MM >>YM > MI ≥BA. The BA soil had the coarsest and MM soil the finest texture. Cardon was also grown in pot cultures inoculated with the plant-growth-promoting bacterium *Azospirillum brasilense,* or in association with a competing grass, *Sorghum bicolor* (sorghum). Competition did not affect survival rates of cardon in any of the soils after six months of growth, but decreased biomass accumulation by up to 90% in the best (MM) soil. Inoculation of cardon seeds with *A. brasilense* did not affect survival but resulted in significantly better root and shoot growth, and this effect increased linearly as soil nutrients declined. In the best soil (MM), *A. brasilense* had no effect on cardon growth, but in the poorest soil (BA) shoot dry mass was almost 60% and root length over 100% greater as a result of inoculation, with responses in the other two soils intermediate. This effect did not appear to be owing to N_2 fixation, as nitrogenase activity (acetylene reduction) was not detected in any of the treatments. Soil formation by selected nurse trees in arid areas is an important factor in plant establishment and growth, and the present results indicate that these processes can be impeded or facilitated by the introduction of competing or beneficial organisms. The use of beneficial microorganisms associated with roots may accelerate the restoration of disturbed areas.

Introduction

Habitat restoration may make use of plants that stabilize the soil, improve its quality, and in the process provide a favorable microenvironment for desired later successional species (Bradshaw & Chadwick 1980; Marquez & Allen 1996). Such facilitation of plant establishment by nurse plants is particularly prevalent in fragile and harsh environments, such as deserts (Pugnaire & Haase 1996), where the consequences of man's intrusion are particularly serious (Niering et al. 1963; Agnew & Warren 1996).

Perhaps the best-known nurse plant-seedling relationship is the association between legumes and cacti (McAuliffe 1984; Nobel 1988; Valiente-Banuet & Ezcurra 1991; Arriaga et al. 1993). Among cacti, whose seedlings often depend on the habitat-changing activities of other plants (Gurney & Lawton 1996), the giant cactus of the Sonoran Desert, *Pachycereus pringlei* (cardon), stands out as possessing characteristics

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desirable for the stabilization of disturbed arid soils: a widespread, finely branched, shallow root system capable of responding to rare rainfall episodes by rapid regrowth (Bravo-Hollis 1978; Nobel 1996). Among the legumes, *Prosopis* sp. (mesquite) is a well-known facilitator of plant establishment (Callaway 1995). Improvements in nutrient and moisture conditions and an attenuation of temperature extremes have been cited as beneficial nurse-plant effects (Turner et al. 1966; Franco & Nobel 1989; Garner & Steinberger 1989). Exotic plants, introduced initially for commercial purposes, may proliferate in the resource islands (Halvorson et al. 1994) formed by nurse plants, occupying and negating an essential niche for the reestablishment of native species. The islands, formed by processes such as the entrapment of airborne particles by dense plant canopies (Armbrust & Bilbro 1997), the transfer of water and nutrients from deeper strata (Dawson 1993), N_2 fixation (Virginia & Jarrell 1983), and the development of soil-food-web communities (Wardle 1995), become a growth substrate distinct from, and superior to, that of the surrounding plant-free areas. Indeed, the fact that organisms other than plants are also likely to be vital to the restoration process is often ignored (Hobbs & Norton 1996).

Since early growth of cardon is slow (Roberts 1989) and subject to competition, especially while growing as a seedling under mesquite (A. Carrillo, unpublished data), plant-growth-promoting microorganisms (PGPM) as soil amendments (Fauci & Dick 1994) may be a key to an artificial acceleration of its development as part of restoration programs. Of particular interest among PGPM are mycorrhizal fungi (Corkidi & Rincón 1997) and diazotrophic bacteria like *Azospirillum brasilense* (Döbereiner & Day 1976), because of their ability to improve plant nutrient status, reduce environmental stresses, and stimulate growth (Bethlenfalvay 1992; Bashan & Holguin 1997; Bashan et al. 1998). Although the roots of mature cardon are colonized by mycorrhizal fungi (Rose 1981), seedlings apparently do not become mycorrhizal for over one year (A. Davis, unpublished data). Among PGPM, however, seed inoculation with strains of *Azospirillum* was shown to enhance the growth of cardon seedlings (Puente & Bashan 1993). Interest in the effects of *Azospirillum* on plants has centered in the past on their potential benefits to agriculture (Bashan & Levanony 1990). In view of inconsistent results in the field, interest has shifted, to some extent, to the use of mixed inoculants (Bashan & Holguin 1997). In combination with other bacteria (Del Gallo & Fredrick 1994), with mycorrhizal fungi (Linderman 1992), or with rhizobia (Plazinski & Rolfe 1985), *Azospirillum* shows enhanced effectiveness in promoting plant growth. This effect is modified by community-level interactions of the soil biota (Janzen & McGill 1995) and is most pronounced in semiarid ecosystems (Zaady et al. 1994).

We have carried out an experiment under screenhouse conditions to determine early survival and growth responses of cardon seedlings: (1) to four different desert soils; (2) to seed inoculation with *A. brasilense*; (3) to a competing non-native grass species; and (4) to colonization by native mycorrhizal fungi contained at different propagule densities in the test soils. The soils were taken from islands of mature or young mesquite plants, from mature ironwood, and from plant-free bare areas that surround these island-forming plants. These soils were chosen to assess differences between cardon responses: (1) to resource-island soils formed by different legume species of the same stage of development (mature trees); (2) to soils from the same legume species but at different stages of development (young and mature trees); and (3) to compare all of these effects with those produced by bare (nonvegetated), non-resource-island soil. These choices were motivated by our own observations and those of others that plant-growth-promoting soil qualities vary with the identity (Barth & Klemmedson 1982) and with the age (Archer et al. 1988) of nurse plants.

Materials and Methods

Study Site, Soils, and Growth Conditions

The study area near La Paz, Baja California Sur, Mexico (24°1N and 110°2W) is an alluvial coastal plain formed by sedimentation and the deposition of granitic rock fragments derived from erosion of the Sierra de la Laguna mountains (Maya & Guzman 1998). The climate is arid with annual mean rainfall of 180 mm, mainly in late summer. Mean monthly temperatures vary from 18 to 30°C. The flora is characterized as a transition between xerophilic matorral and dry tropical forest (León de la Luz et al. 1996). The disturbed area from which soils were collected was cleared by bulldozing for development in the mid 1970s, but many of the trees, arborescent shrubs, and large succulents were left in place for their esthetic value. Vegetation was subsequently permitted to recover.

Twenty sites were selected at random within a 1-ha plot. Of the sites, five each were centered either on a (1) mature *Prosopis articulata* (mesquite) tree; (2) a young mesquite tree; (3) a mature *0lneya testosa* (ironwood) tree; or (4) contained a plant-free bare area (BA). These bare areas surrounded perennial plants and were highly variable in size (2- to 10-m diameter). Roots from adjacent plants penetrated BA soils, but BA surface soils tended to be coarser than sub-canopy soils. Trees of a stem diameter greater than 20 cm were defined as "mature," based on the observation that smaller trees did not support associated seedlings under their canopies (G. J. Bethlenfalvay, unpublished data). Five soil samples (5- to

35-cm depth) were collected from each site at radially increasing distances from the center (tree trunk) of the sites to the edge of the canopy. The replicate samples from each site were mixed, sieved (1-cm screen openings) to remove large roots and rocks, potted (1.5-L pots), arranged at random on screenhouse benches and planted with cardon seedlings.

Plants were grown for six months, from November 1997 through April 1998. Maximum mid-day light intensities were. approximately one-half of full sunlight (900 μmole/m^2 sec), and ambient temperatures were in the range of 20/40, night/day. Cardon seeds were pre-germinated on moist tissue paper (5 d), selected for uniformity, and transferred to the potted soils. Plants were given sufficient tap water once a week to flush the pots, thus avoiding the accumulation of salt.

Experimental Design and Treatment Description

The design was a 3 x 4 factorial. The factors were treatments (3) and soils (4). Each combination was replicated six times, for a total of 72 experimental units. Ten seedlings were planted in each unit (pot) or 60 seedlings per treatment. Seeds of one of the treatments (+Ab) were inoculated with *A. brasilense,* strain ATCC 29710. A bacterial suspension (106 cfu/mL) was grown by standard methods for this genus (Puente & Bashan 1993). Seeds were dipped for five minutes into the suspension under a vacuum of 600 mm Hg, followed by a rapid release of the vacuum to allow bacterial penetration of seed cavities previously filled with air (Puente & Bashan 1993). In the second treatment (+S), a *Sorghum bicolor* (sorghum, cv. Pampa Verde) plant was grown in each pot in association with the 10 cardon seedlings. Sorghum was used, as seeds of the grass *Cenchrus ciliaris,* an exotic competitor of cardon in the study area, were not available. The plants of the control treatment were neither inoculated with *Azospirillum* nor associated with sorghum.

Assays

Surviving plants were counted. Fresh shoot masses were determined immediately at harvest and dry masses after drying (70°C, 3 d), and shoot water content was calculated from the dry and fresh masses. Roots of the control and of the +Ab treatments were separated into two parts. One part was used to measure fresh and dry masses, and the other served to determine nitrogenase activity, root length, and root colonization by mycorrhizal fungi. Cardon and sorghum roots of the +S treatment were inseparably intertwined; cardon roots from this treatment were, therefore, not further analyzed. Clearly distinguishable fragments of sorghum roots, however,

were used in the assessment of mycorrhizal colonization, to ascertain if mycorrhizal propagules were present in all soils.

Unwashed, moist roots with adhering rhizosphere soil were first placed into 25-mL vials, sealed, injected with acetylene (10%, v:v), and incubated at 30°C for two days. Roots not exposed to acetylene under identical conditions were used for comparison. Evolution of ethylene was not detectable with the instrumentation (Varian 6000 gas chromatograph) under the conditions described in detail by Holguin et al. (1992). The roots were next washed and weighed for fresh mass. Root length was determined on this sample by the grid-line intersect method (Giovanetti & Mosse 1980), and mycorrhizal colonization by staining with trypan blue as described by Brundrett et al. (1994). Total root dry mass was calculated from dry/fresh mass ratio of the other root sample. A count of *Azospirillum* in the bulk soil was made by the limited enrichment technique (Bashan et al. 1991) and in the root-rhizosphere by the plate-count method using OAB N-free medium (Bashan & Levanony 1985).

Total soil N (Bremmer & Mulvaney 1982) and C (Nelson & Sommers 1982) were determined by Kjeldahl analysis or dry combustion, respectively, and plant-available (NaHCO$_3$-extractable) P by the molybdate-blue method (Olsen & Sommers 1982). Soil particle analysis was performed according to Gee and Bauder (1986).

Statistics

Results were evaluated by analysis of variance (ANOVA). The significance of differences between treatments or soils was determined by orthogonal contrasts. When only two treatment means were compared, the independent Student's t-test was used. The competitive relationship between cardon and sorghum shoot dry masses of the +S treatment and plant responses to soil characteristics were evaluated by regression analysis (Pearson *r*), as were the percent changes (%0) of plant traits in response to inoculation with *Azospirillum* [100 x (+Ab - Control) / Control]. Actual probability values were presented instead of arbitrary ones ($p \leq 0.05$ or $p \leq 0.01$) to permit the reader to interpret significance (Nelson 1989). We may interpret differences to be significant up to $p = 0.1$.

Results

Survival and Competition

Survival of cardon was not affected by seed inoculation with *Azospirillum* or by competition from sorghum (control versus

+Ab or +S treatments, *p*>0.1 in all soils) over the 6-month experimental period (Table 1). Soil effects were significant in the control (Fig. 1) and +Ab treatments. More cardon plants survived in the mesquite soils of these two treatments than in the bare-area soil. In the +S treatment (Table 1), differences in soil characteristics (Table 2) did not affect survival, because soil effects on cardon were apparently offset by the differences in the sizes of the competing sorghum plants (Fig. 2). Responding to the same soil stimuli as cardon, sorghum plants were larger in the MM and YM soils than in the MI or BA soils, providing for stronger competition in the former and equalizing stress across the spectrum of soil characteristics. Average shoot dry mass was a better indicator of soil effects on cardon than survival (Table 1): individual cardon plants of the two unstressed treatments (control and +Ab) grown in MM soil were larger, and those grown in BA soil smaller, than plants grown in the other soils. As with survival, total dry-mass responses to soil in the +S treatment did not differ significantly, whereas in the non-stressed treatments all differences were large (Table 1).

Differences in shoot water content in response to soils were small, but significant for the comparisons of MM and YM plants with BA plants, whereas hydration status of the stressed plants within the +S treatment were statistically the same (Table 1). Inoculation with *Azospirillum* did not affect shoot water status.

Inoculation Effects

Dry mass and root length of cardon plants (Table 3) increased with improving soil quality (Table 2). Soil traits

and plant responses tended to be more strongly correlated in the control plants than in the +Ab plants (Table 4). Inoculation with *Azospirillum* had no effect on root length in the best (MM) soil, but root development increased significantly in the coarser and more nutrient poor soils (Tables 2 and 3): growth-promotion by *Azospirillum* increased with decreasing soil quality (Fig. 3). This phenomenon was reflected in the negative relationships between the percent change (%Δ) in plant responses and soil quality (Table 4). The %Δ in the responses of the control and +Ab plants increased linearly as soil quality decreased.

Root/shoot ratios increased with decreasing soil quality (Table 3), indicating that root growth relative to shoot growth became greater as soil quality became poorer in nutrients and coarser in texture. The root/shoot ratios of plants growing in MM, YM, and MI soils were significantly smaller than those growing in BA soil.

Incidence of PGPM in the Soil

Propagule densities of mycorrhizal fungi were significantly lower in BA soil [<3 (±1 SE) propagules per 100 g dry soil] than in the soils of the other treatments [>20 (±6 SE) propagules per 100 g dry soil]. However, cardon roots did not become mycorrhizal during the experiment in any of the soils, whereas sorghum roots became highly colonized (>60% of root length) in all soils. The strongly mycotrophic sorghum plants were apparently able to equalize initial differences in propagule densities and developed highly mycorrhizal root systems in the course of the experiment. Colony-forming units of *Azospirillum* were not detected in the bulk soils

Table 1. Plant survival and shoot characteristics of cardon plants grown in different soils.[a,b]

	Survival (%)			Average Dry Mass (g/shoot)			Shoot Dry Muss (g)			Water Content (%)		
	Cont	*+Ab*	*+S*	*Cont*	*+Ab*	*+S*	*Cont*	*+Ab*	*+S*	*Cont*	*+Ab*	*+S*
Soil												
Mature mesquite	9.3	8.7	8.8	0.46	0.45	0.06	4.3	3.9	0.6	96	96	92
Young mesquite	9.3	8.3	7.3	0.22	0.30	0.06	2.2	2.4	0.5	95	94	92
Mature ironwood	7.7	7.7	8.2	0.18	0.25	0.08	1.4	1.9	0.7	94	94	92
Bare area	7.3	6.3	8.0	0.07	0.10	0.04	0.5	0.6	0.3	92	93	91
ANOVA												
(probability numbers)	0.016	0.050	0.697	<0.001	<0.001	0.131	<0.001	<0.001	0.197	<0.001	0.074	0.240
Orthogonal contrasts												
(probability values)												
MM vs. YM	0.998	0.692	0.838	<0.001	<0.001	0.828	<0.001	<0.001	0.729	0.192	0.135	0.663
MM vs. MI	0.032	0.242	0.418	<0.001	<0.001	0.260	<0.001	<0.001	0.477	0.016	0.110	0.586
MM vs. BA	0.012	0.011	0.314	<0.001	<0.001	0.194	<0.001	<0.001	0.151	<0.001	0.010	0.388
YM vs* MI	0.033	0.431	0.542	0.183	0.176	0.183	0.036	0.079	0.259	0.211	0.909	0.907
YM vs. BA	0.014	0.026	0.418	<0.001	<0.001	0.274	<0.001	<0.001	0.265	<0.001	0.080	0.660
MI vs. BA	0.650	0.124	0.838	0.002	0.002	0.021	0.009	<0.001	0.036	0.001	0.263	0.746

[a]Total dry mass reflects the biomass of all surviving plants; soils were taken from mature mesquite (MM), young mesquite (YM), mature ironwood (MI), and bare areas (BA) in a disturbed desert area.
[b]Seeds of the +Ab treatment were inoculated with *Azospirillum brasilense,* whereas those of the controls (cont) were not; controls were also grown in association with sorghum (+S).
[c]Orthogonal contrasts evaluate differences between soil effects.

Table 2. Soil characteristics of four different microsites within a disturbed desert area.

	Soil Nutrients (g/kg)			Soil Texture (mm)				
	N	P	C	<0.004	0.004 to 0.04	0.04 to 0.25	0.25 to 2.0	>2.0
Soil								
Mature mesquite	0.340	0.0045	6.68	27.7	9.2	47.4	15.2	0.5
Young Mesquite	0.312	0.0032	4.16	15.0	11.9	34.7	31.2	7.2
Mature Ironwood	0.296	0.0026	4.43	10.2	5.0	29.8	45.7	9.5
Bare Area	0.248	0.0028	3.63	8.2	6.9	37.5	39.9	7.2
ANOVA (p values)	0.042	0.032	0.003	<0.001	0.001	<0.001	<0.001	<0.001
Orthogonal contrasts (p values)								
MM vs. YM	0.391	0.069	0.004	0.013	0.020	0.089	0.040	0.180
MM vs. MI	0.327	0.015	0.013	0.001	0.063	0.023	0.001	0.077
MM vs. BA	0.006	0.007	0.001	0.001	0.485	0.176	0.003	0.176
YM vs. MI	0.902	0.364	0.666	0.305	<0.001	0.491	0.061	0.630
YM vs. BA	0.052	0.525	0.290	0.166	0.005	0.699	0.244	0.988
MI vs. BA	0.068	0.784	0.529	0.702	0.218	0.288	0.433	0.640

or in the rhizosphere of any of the treatments at harvest, six months after inoculation.

Discussion

The responses of our cardon seedlings to soil in the absence of drought or temperature stresses showed the nature of the growth substrate alone to be an important factor for plant establishment (Callaway 1995). In the field, competing or facilitating plant associates (Callaway & Walker 1997) affect these responses to soil quality (Doran & Parkin 1994) by modifying factors such as water availability, light intensity, and soil structure (Noy-Meir 1973). Survival is much more difficult to evaluate in the field than in pot cultures, making it essential that soil variables be monitored for their contributions to the plant establishment (Hobbs & Norton 1996). The contribution of our study to improving restoration practices, therefore, lies in the demonstration that the nature of the growth substrate that receives the seedlings matters to their survival, and that poor substrates may be improved by the application of plant-growth-promoting soil organisms. Naturally available substrates, like resource-island soils, may perhaps be used in limited amounts to facilitate plant survival during the most critical, early growth phase.

Figure 1. Pachycereus pringlei (cardon) seedlings grown for six months in resource-island soils of mature *Prosopis articulata* (mesquite), young mesquite, and mature *Olneya testosa* (ironwood), and in soils from plant-free bare areas.

Soil effects on cardon in our experiment were modified by competing sorghum plants. The competitor eliminated the beneficial effects of higher soil nutrient and carbon contents and of finer soil texture on the cactus seedlings. Although it did not lower survival rates
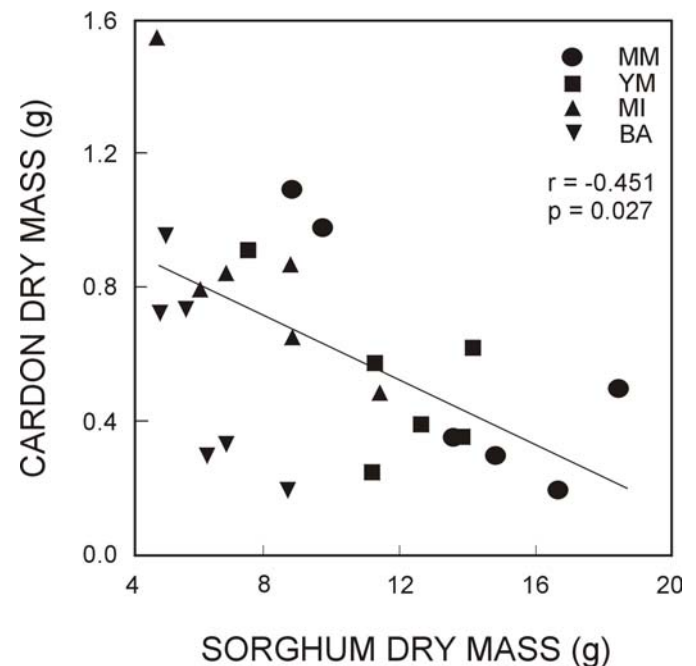

Figure 2. Correlation of cardon and sorghum shoot dry masses. Plants were grown in pot cultures in four different soils. MM, mature mesquite; YM, young mesquite; MI, mature ironwood; BA, bare area. Cardon dry masses reflect the survivors of 10 plants per pot versus one sorghum plant per pot.

Table 3. Plant (shoot and root) dry mass, root length, and root/shoot ratio of Pachycereus pringlei (cardon) plants grown in soils taken from different microsites of a disturbed desert area [a-b]

	Total Plant Dry Mass (g)			Root/Shoot Ratio			Root Length (m)		
	Control	+Ab	t-test[c]	Control	+Ab	t-test[c]	Control	+Ab	t-test[c]
Soil									
Mature Mesquite	4.6	4.2	0.182	0.082	0.090	0.114	11.6	11.2	0.873
Young Mesquite	2.3	2.7	0.025	0.108	0.125	0.083	5.5	9.5	0.091
Mature Ironwood	1.5	2.1	0.058	0.114	0.154	0.044	2.8	5.0	0.008
Bare Area	0.6	0.8	0.070	0.166	0.256	0.097	1.9	3.4	0.025
ANOVA (p values)	<0.001	<0.001		0.022	0.006	<0.001	0.007		
Orthogonal contrasts (p values)									
MM vs. YM	<0.001	<0.001		0.330		0.539	<0.001	0.435	
MM vs. MI	<0.001	<0.001		0.248		0.315	<0.001	0.012	
MM vs. BA	<0.001	<0.001		0.003		0.001	<0.001	0.002	
YM vs. MI	0.026	0.075		0.850	0.689	0.013	0.063		
YM vs. BA	<0.001	<0.001		0.024		0.006	0.002	0.013	
MI vs. BA	0.007	<0.001		0.038	0.014	0.418	0.462		

[a]Seeds of the +Ab treatment were inoculated with the diazotrophic bacterium *Azospirillum brasilense*; those of the controls were not so treated.
[b]ANOVA and contrasts evaluate plant responses to soils treatments vertically.
[c]Control- versus + Ab-treatment comparisons are by independent t-test.

of cardon, at least within the time frame of this experiment, it curtailed shoot biomass accumulation by almost 90% in the best (MM) soil. Thus, long-term survival of seedlings at sites dominated by such exotic plant competitors may be jeopardized (Eliason & Allen 1997). This was the case for cardon in the field, where the resource islands of mature mesquite trees did not support cactus seedlings when choked by *C. ciliaris* (G. J. Bethlenfalvay, unpublished data). This grass, introduced originally for grazing, was largely eliminated by cattle in unprotected areas, but persists and interferes with plant establishment in disturbed areas protected by fencing for restoration. In this study, one mechanism of competition appeared to be the induction of drought stress, as shown by the lowering of hydration of the associated cardon-grown plants in the MM soil.

The salient result of our study was the relationship of cardon responses to *Azospirillum* with soil quality. There was no plant response to *Azospirillum* in the best (MM) soil, but the responses increased with declining soil quality in the poorer soils. Such a response pattern had not been reported previously in nonagricultural soils, although high yield responses have been recorded from field plots that had low yields without inoculation with *Azospirillum* (Jagnow 1987). The only data that relate plant response to *Azospirillum* to a specific soil characteristic deal with N fertilization: high yield responses were consistently obtained when soil N was suboptimal (Mertens & Hess 1984; O'Hara et al. 1987). Our results showed plant response to *Azospirillum* to be significantly affected by a number of soil traits: lower nutrient status and coarser texture favored better plant growth re-

Table 4. Regressions between soil characteristics and actual or derived plant parameters.[a,']

	Soil Nutrients						Soil Texture			
	N		P		C		<0.004		>0.25	
Parameter	r	p	r	p	r	p	r	p	r	p
Plant dry mass										
+Ab	0.955	0.045	0.870	0.130	0.908	0.092	0.940	0.060	-0.838	0.162
Control	0.929	0.071	0.948	0.052	0.949	0.051	0.988	0.012	-0.915	0.085
Root length										
+Ab	0.912	0.088	0.833	0.167	0.774	0.226	0.889	0.111	-0.843	0.157
Control	0.807	0.193	0.984	0.016	0.933	0.067	0.999	0.001	-0.962	0.038
Percentage change[b]										
Plant dry mass	-0.917	0.083	-0.957	0.043	-0.891	0.109	-0.983	0.017	0.949	0.051
Root length	-0.878	0.122	-0.981	0.019	-0.940	0.060	-0.999	<0.001	0.956	0.044

[a]Numbers are probability values.
[b]Percent change [100x (+Ab - Control) /Control] reflects the response to inoculation with *Azospirillum brasilense* relative to the noninoculated controls.
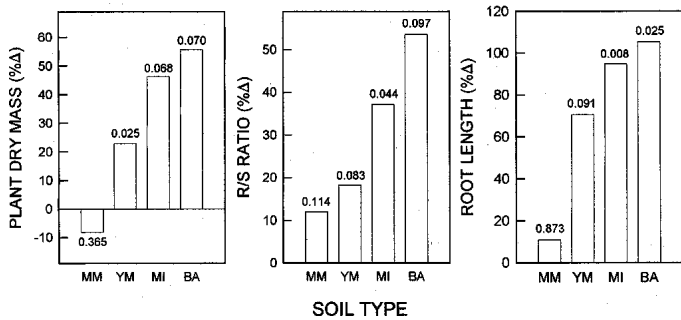
Figure 3. Percent change (%Δ) in plant traits as a result of seed inoculation with *Azospirillum brasilense.* Plants were
grown in pot cultures in four different soils: MM, mature mesquite; YM, young mesquite; MI, mature ironwood; BA, bare area. Numbers above bars are probability values, and represent the significance of differences between control and +Ba treatments.

sponses. *Azospirillum* may affect plant development by improving plant nutrition though N_2 fixation or owing to the production of phytohormones (Jagnow et al. 1991). In our study, the latter mechanism appeared to be operative.

These relationships offer an explanation for the often-observed unpredictability of obtaining positive growth effects with the application of *Azospirillum* (Bashan & Holguin 1997). Some soils, apparently, have characteristics (MM in our case) that permit a plant, like cardon, to achieve good growth without help from microbial soil inoculants. In contrast, for other soils, like our YM, MI, and especially BA soils, inputs by *Azospirillum* were important enough to enhance growth. Mycorrhizal fungi are soil microorganisms that are also known to improve plant development in growth-limiting soils (Bethlenfalvay 1992), but they did not colonize our cardon roots. The mechanism of this exclusion phenomenon is obscure.

The effects of soil components, such as texture, pH, and nutrients, on the survival of *Azospirillum* are small and may be positive or negative (Bashan et al: 1995) and those of soil structure are marginal at best (Y. Bashan, unpublished data). However, *Azospirillum* does not survive well in bulk soil, whereas it persists in the rhizosphere (Bashan et al. 1995). A disappearance of inoculated azospirilla in soils where they are exotic, as was the case in our experiment, has been reported elsewhere (Albrecht et al. 1983; Smith et a1.1984).

The development of soils capable of supporting biological micro-communities by some plants is a natural self-restoring activity in arid environments. It can also serve as a model for restoration efforts. In such desert environments, knowledge of the best island-forming and soil-building plants, and of the time span required by each to sufficiently improve the soil to enhance seedling establishment is important, as documented in this study with cardon in the Sonoran Desert of Baja California. Efforts of restoring disturbed desert areas may be accelerated by the use of selected plant-growth-promoting

microorganisms and impeded by an injudicious introduction of exotic plants.

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