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Restoration of giant cardon cacti in barren desert soil amended with common compost and inoculated with *Azospirillum brasilense*

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Abstract Barren desert soil that otherwise could not support perennial plant growth was amended with six levels of common agricultural compost. Seedlings of the giant cardon cactus, one of the primary plant species responsible for soil stabilization in the southern Sonoran Desert, were inoculated with the plant-growth-promoting bacterium *Azospirillum brasilense* Cd, planted, and grown for 18 months under nursery conditions typical for slow-growth cacti. Control plants were grown without compost amendment, without inoculation (negative control), or in fertile, rare “resource island” soil preferred by cardon seedlings (positive control). During the prolonged growth period, the decisive factor in seedling growth in barren soil was the addition of small amounts of common compost; 6 to 25% of the growth substrate volume gave the best growth response and, to a lesser extent, so did inoculation with *A. brasilense* Cd. Although the bacteria significantly affects plant growth when amended with “resource island” soil and added to barren soil, its effect on plant growth was far smaller than when compost alone was added. Compost added to barren soil significantly increased the dry weight parameters of the plant to almost similar levels obtained by the “resource island” soil; however, the compost amendment supports a more voluminous and greener plant with elevated pigment levels. This study shows that barren soil supplemented with compost can replace the rare “resource island” soil for cardon nurseries destined to abate soil erosion in the desert.

Keywords *Azospirillum* · Bacterial inoculants · Cactus · Compost · Nursery · Plant-growth-promoting bacteria · PGPB · PGPR · Soil erosion

Introduction

Many barren desert soils in the southern Sonoran Desert of Mexico are low in organic matter and available nutrients and prohibit the normal growth of most plants, including local desert plants, even when irrigated (Bashan et al. 2000a; Carrillo-García et al. 2000a). Some perennial plants, particularly legume desert trees, modify the impact of adverse environmental conditions by changing their habitats (Virginia 1986; Gurney and Lawton 1996) by creating “resource islands”. This process of “habitat engineering” (Jones et al. 1997) may be necessary to facilitate the establishment and survival of other plants (nurslings) (Belsky et al. 1989; Pugnaire and Haase 1996). “Resource islands” formed by some perennial nurse plants (Halvorson et al. 1994) are low mounds that originate from the deposition and subsequent stabilization of wind-borne soil particles under mature plant canopies (Armbrust and Bilbro 1997; Carrillo-García et al. 1999, 2000a) and are characterized by fine-textured soils that become habitats for communities of organisms (Burns and Davies 1986) related to their higher fertility characteristics, such as low bulk density, higher organic matter, higher water-holding capacity, better aeration, attenuation of temperature extremes, finer texture, stable aggregate structure, higher nutrient levels than the surrounding areas, and a massive population of arbuscular mycorrhizal (AM) fungi (Turner et al. 1966; Jordan and Nobel 1981; Burns and Davies 1986; Garner and Steinberger 1989; Valiente-Banuet et al. 1991; Callaway 1995; Bashan et al. 2000a; Carrillo-García et al. 1999).

A well-known nurse plant–nursling association, creating “resource islands,” is between leguminous trees and desert succulents (Nobel 1988; Arriaga et al. 1993) where mature mesquite trees (*Prosopis* spp.) play a pivotal role in natural vegetation in the southern Sonoran Desert in Baja California (Carrillo-García et al. 1999), as it does in other arid lands (Barth and Klemmedson 1982; Shearer et al. 1983; Virginia and Jarrell 1983; Lajtha and Schlesinger 1986). The giant cardon cactus (*Pachycereus pringlei*) is one of the most important soil stabilizers of the Sonoran desert (Gibson and Nobel 1986; Bashan et al. 1999) because it has

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a widespread shallow root system that stabilizes top soils for hundreds of years. This cactus is closely associated with mature mesquite trees, forming “resource islands” (Bashan et al. 2000a; Carrillo-Garcia et al. 1999). These “resource island” soils are widely used by gardeners and nurseries and are diminishing in supply, and their collection from natural deserts for large-scale nurseries would deplete the environment and prohibit natural desert revegetation.

An appropriate substrate is a pivotal factor for desert plant nurseries, especially cacti, where some species have difficulty growing in commercially mixed substrates (Maiti et al. 2002a,b). In addition, the cardon cactus has a preference for “resource island” soils for initial growth (Carrillo-Garcia et al. 2000a). “Resource island” soils are limited; there is only a handful or two of mature mesquite trees in a hectare of land and each has a limited canopy cover (Carrillo-Garcia et al. 1999). Our hypothesis explored an alternative to primary economic exploitation of this limited, but essential, desert soil. We proposed that the typical, barren desert soil, available in unlimited quantities, can be amended with small amounts of common animal compost and inoculated with the plant-growth-promoting bacteria (PGPB) *Azospirillum brasilense* to support the initial growth of cardon rather than consume the limited enriched desert soils. If demonstrated to produce healthy cardon, amended desert soil would be a valuable resource

as a growth substrate for commercial plant nurseries to avoid depleting deserts of scarce “resource island” soils.

Composts significantly increase the organic matter content of most desert soils, improve soil structure and fertility (El Nadi et al. 1995), protect plants against soil-borne pathogens (Pascual et al. 2002), and stimulate biocontrol-PGPB in the rhizosphere (De Brito Alvarez et al. 1995). Compost can be used by PGPB as a source of nutrients (Bacilio et al. 2003).

The objective of this study was to determine whether inoculation with a common PGPB, the bacterium *A. brasilense* Cd (Bashan et al. 2004), together with amendments of dairy cow compost to eroded, barren desert soil can substitute for “resource island” soils. We have some evidence that soil fertility will be improved to support cardon cacti in nurseries under growth chamber conditions, without using a very limited soil resource.

Materials and methods

Organisms and growth conditions

Seeds of the giant cardon cactus (*P. pringlei*, S. Wats Britt. & Ross) were collected from wild plants (Bashan et al. 2002) in the fall and stored at 4°C until used. Seeds were

Table 1 Composition of growth substrates used in this study

Composition	Resource island soil ^a	Barren soil ^a	Compost	Barren soil–resource island soil mix at 8:1 (v/v) ^b	Barren soil–compost mix at 8:1 (v/v) ^b
Total carbon (mg kg ⁻¹)	6,680	400	115,000	1,235	8,500
Total inorganic carbon (mg kg ⁻¹)	400	400	ND	400	ND
N (mg kg ⁻¹)	340	20	19,200	60	2,400
P (mg kg ⁻¹)	28	12	8,900	13	1,112
K (mg kg ⁻¹)	976	619	8,600	740	1,700
Fe (mg kg ⁻¹)	6.6	7.5	3,100	6.9	390
Mn (mg kg ⁻¹)	15.3	4.4	500	6.2	65
Zn (mg kg ⁻¹)	0.4	0.3	200	0.3	25
Cu (mg kg ⁻¹)	0.8	0.8	ND	0.8	ND
Na	0.6 ^c	0.4 ^c	0.34 ^d	0.42 ^c	0.05 ^d
Ca [cmole (P ⁺) kg ⁻¹]	8	7.8	ND	8	ND
Mg [cmole (P ⁺) kg ⁻¹]	2.2	1.7	ND	2	ND
Cation exchange capacity [cmole (P ⁺) kg ⁻¹]	10.7	8.6	ND	10	ND
Electrical conductivity	0.2 ^e	0.1 ^e	1.13 ^f	0.1 ^e	0.1 ^e
Clay (%)	37	8	ND	12.6	ND
Silt (%)	47	8	ND	13.8	ND
Sand (%)	16	84	ND	73.6	ND
Water-holding capacity (%)	14.6	12	ND	13.8	ND
pH	7.3	7.59	9.5	7.5	7.7

ND Not determined

^aFrom Bashan et al. 2000a; Carrillo-Garcia et al. 2000a,b

^bCalculated

^cCentimole (P⁺) per kilogram [cmol (P⁺) kg⁻¹]

^dPercent (%)

^eSiemens per meter (S m⁻¹)

^fMillisiemens per centimeter (mS cm⁻¹)

disinfected and prepared for inoculation, as described in Puente and Bashan (1993). In brief, after disinfection, they were inoculated with bacteria suspended in liquid 0.06 M phosphate buffer, pH 7.0, supplemented with 0.15 M NaCl at a final concentration of 10^6 cfu ml⁻¹ by the vacuum infiltration method (Puente and Bashan 1993). The plant growth-promoting bacterium *A. brasilense* Cd (DSM 1843, Braunschweig, Germany) served as the standard and was cultivated and prepared for inoculation according to the standard methods of this genus (Bashan et al. 1993).

Substrates for growing plants

Five growth substrates for cardon seedlings were used (Table 1): (a) an eroded, barren desert soil that does not support perennial plant growth (Bashan et al. 2000a; Carrillo-Garcia et al. 2000a), (b) the same desert soil amended with compost produced from dairy cow manure at a ratio of 1:2 to 1:256 (compost to soil, v/v) (Bacilio et al. 2003), (c) “resource island” soil collected under the canopy of a mature mesquite tree located in El Comitán, 17 km northwest of La Paz, Baja California Sur, Mexico (Bashan et al. 2000a; Carrillo-Garcia et al. 2000a), (d) dairy cow manure compost, and (e) barren desert soil similarly diluted with “resource island” soil.

Plant growth conditions

Cardon seeds were germinated at $25 \pm 1^\circ\text{C}$ and 60% relative humidity by placing them on the respective soil substrates (Table 1) in an unlighted growth chamber (Conviron TC 16, Controlled Environments, Winnipeg, Canada) for 96 h. Germination of seeds was considered positive when the seeds started to show visible germination by rupturing of seed coat and emergence of a radicle. Fifteen seeds per pot were initially germinated. After germination, they were thinned to five seedlings per pot. These uniform seedlings were grown in 120-ml plastic pots containing either 100 g of desert soil, 90 g soil–compost mixture, or 45 g compost (same volume). As cardon seedlings are very slow growing, this plant density did not provide any competition among plants during the entire growth period (Bacilio, M., unpublished data). Pots, previously saturated with distilled water to water-holding capacity, were incubated in the same growth chamber at $30\text{--}35 \pm 2^\circ\text{C}$, 40% relative humidity (normal growth conditions of these plants), and $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ light intensity. Plants were irrigated once each week with 5–15 ml distilled water depending on the growth and the type of the substrate, until saturation of the substrate but not in excess.

Measurements of plant growth parameters

After 18 months, all plants were measured with a ruler and the stem diameter with calipers. The plants were carefully removed from the substrate. The roots in each pot were

excised and gently washed with tap water to remove soil and compost particles. Roots and shoots were dried separately in a forced-air oven at 70°C for 2 days. Plants were then placed in a hermetically sealed desiccator to avoid absorption of humidity from the air. Each sample group was then weighed with an analytical balance (Bashan and de-Bashan 2005). Each weight measurement represented the average weight of a single plant in a pot (out of four plants per pot). The volume of the plants was calculated (Bashan et al. 1999) and it represented the average volume of a single plant (out of three plants per pot).

Pigment extraction and determination from plants

Pigments were extracted from plants after 10 months of growth as described by Bashan et al. (2006). In brief, as a precaution to avoid the known degradation of pigments during cold storage at 4°C , samples were taken and pigments were immediately extracted by high-pressure liquid chromatography (HPLC)-grade acetone overnight at -40°C and immediately analyzed without storage. Pigments were detected with the diode array absorbance signal at 440 nm, using a Hypersil C8 column (10-cm length, 0.45-cm diameter). Identification was made by comparing the retention time and the spectral characteristics with commercial pigment standards supplied by DHI (International Agency for ^{14}C Determinations, Denmark). Quantification of results used the pigment response factor (HPLC peak area/pigment mass), obtained from the commercial pigment standards (Mantoura and Repeta 1997). Results are expressed as micrograms of pigment per gram dry weight of plant.

Bacterial isolation and identification

In one experiment (12 months after inoculation), bacteria were isolated (Bashan et al. 1999). Identification of morphotypes resembling *A. brasilense* Cd was done by the fatty acid methyl-ester (FAME) analysis as a commercial service at Auburn University, Auburn, AL, USA.

Experimental design and statistical analysis

The experimental plan has a 2×8 factorial design, with PGPB (inoculated and non-inoculated) and soil (eight dilutions of barren soil diluted with compost or with “resource island” soil) as factors. Controls served as natural, undiluted barren soil (negative) and “resource island” soil or compost (positives). All growth experiments were done in four replicates composed of a pot with five plants per pot. The experiments were repeated, in full, three times ($n=640$ plants per experiment). Each growth experiment was carried out for 18 months. The experiment evaluating pigments was carried out for 10 months. All data were first normalized and the results were analyzed by

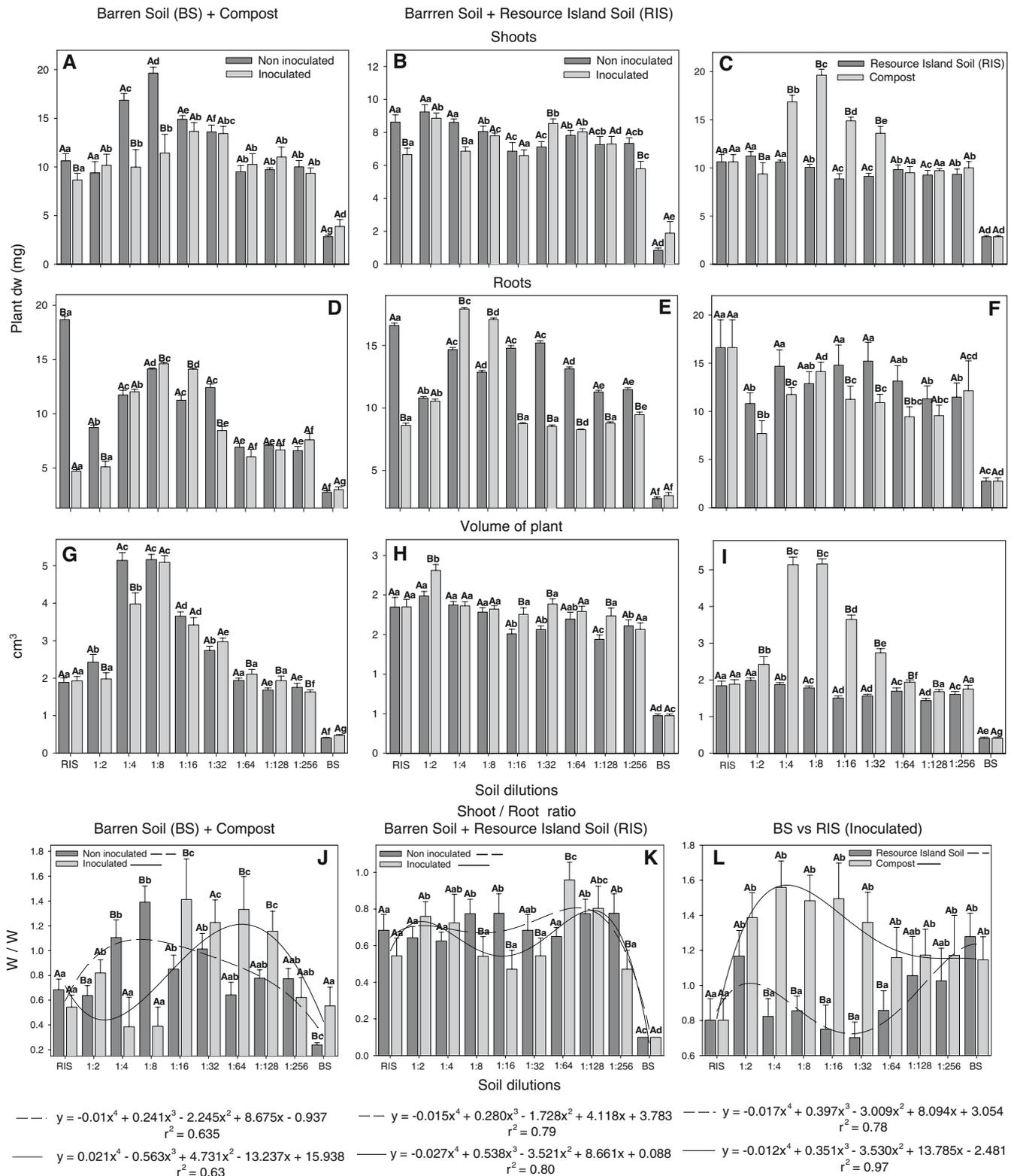


Fig. 1 Growth response of cardon plants to inoculation with the PGPB *A. brasilense* Cd and of those grown in barren desert soil amended with compost (a, d, g) or “resource island” soil (b, e, h). Comparison of growth response of cardon plants grown in barren desert soil amended with compost or “resource island” soil (c, f, i). Shoot-to-root ratio of cardon plants growing in these soils (j, k, l). Values in each subfigure for inoculated and non_inoculated plants or for each soil type, denoted separately by a different lower case letter, differ significantly at $P \leq 0.05$ using one way ANOVA. Pairs of columns at each soil dilution, denoted by different capital letters, differ significantly at $P \leq 0.05$ using Student’s *t* test. Bars represent standard error (SE). Absence of a bar indicates negligible SE. Lines in each of subfigure j, k, l indicate the calculated fit of the data to a polynomial of the fourth order. $n=1,920$ plants

one-way ANOVA at $P \leq 0.05$ and Student's t test at $P \leq 0.05$ after combining the results of the three repetitions ($n=12$ replicates). This was done because all the growth experiments showed similar growth responses when analyzed separately. All statistical analyses were carried out with "Statistica" software (StatSoft, Tulsa, OK, USA). Graphic data are accompanied by standard error bars. Line fit was done with CurveExpert 1.2 software (Hyams, Central, SC, USA).

Results

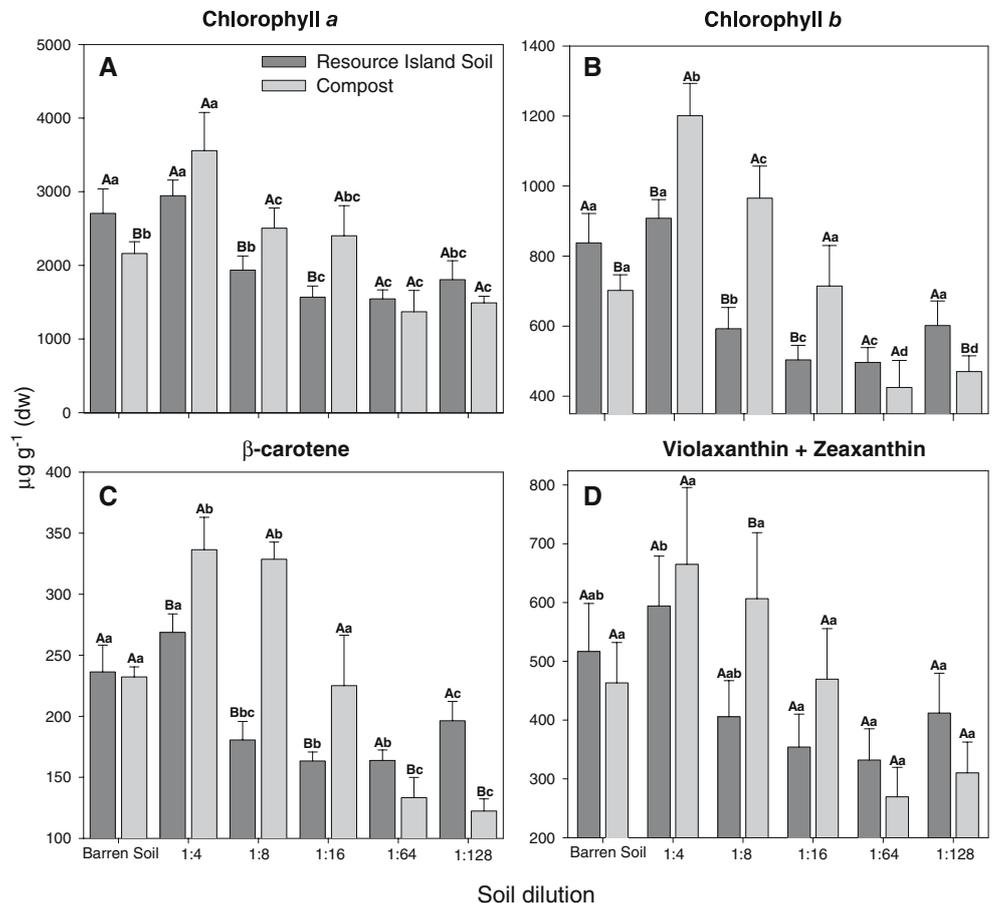
In general, after the long growth period, the effect of inoculation with the PGPB seems small in the growth parameters, dry weight (DW) of roots and shoots, and volume of the plant. Poor plant development occurred on barren soil (Fig. 1, all BS columns). When barren soil was modified with compost, no growth promotion was observed at almost all soil dilutions because of PGPB inoculation, except for a few isolated and small cases, and sometimes some decline in plant growth even occurred (capital letters in t -test analyses) (Fig. 1a,c,e). In barren soil amended with "resource island" soil, inoculation with PGPB was somewhat more pronounced but nevertheless limited. Shoot DW was positively affected only in the barren soil and 1:32-dilution treatments (Fig. 1b), whereas root DW was enhanced only in the barren soil (0 "resource

island" soil) and 1:4- and 1:8-dilution treatments, with negative effects on the other soil dilution treatments (Fig. 1d), where the volume increased in a small, but significant, manner only in four dilutions (Fig. 1f).

Cardon plants growing in any of the barren soils amended with "resource island" soil showed significantly improved plant growth parameters over those grown in ordinary barren soil (Fig. 2). Pronounced positive effects were recorded for dry weight of roots and shoots in soil dilutions ranging from 1:4 to 1:32 (Fig. 2a,b). Barren soil amended with compost had a similar positive effect on all plant parameters, similar to the effects of a "resource island" soil amendment. Pronounced effects occurred in the volume of plants in 1:4- to 1:32-dilution treatments with a peak at the 1:8 dilution (Fig. 2c). By visual inspection, these plants were far larger than any plants in these experiments. There was a major effect of compost additions on the dry weight of roots and shoots compared to barren soil, but the effect was somewhat smaller than the effect of dilution with "resource island" soil (Fig. 2a-c). Inoculation with *A. brasilense* Cd, although changing the values to a small degree, had no significant effect on the trends described above (data not shown).

Three shoot-to-root ratio analyses confirmed the above results. In barren soil amended with compost and inoculated with the PGPB, results showed that (1) in the "poorer" created soils (lower levels of compost), inoculation with the PGPB enhanced plant growth, and (2) in

Fig. 2 Changes in the quantities of chlorophyll *a*, chlorophyll *b*, β -carotene, and the photo-protective pigments violaxanthin and zeaxanthin in the shoots of cardon cactus grown in different substrates. Values in each sub-figure for each soil type, denoted by a different lower case letter, differ significantly at $P \leq 0.05$, using one-way ANOVA. Pairs of columns, denoted by different capital letters, differ significantly at $P \leq 0.05$, using Student's t -test. Bars represent standard error



“richer” soils (higher levels of compost, dilutions of 1:4 and 1:8), the effect diminished, and the dominant effect was the compost amendment (Fig. 1j). In barren soil amended with “resource island” soil, the effect of the created soil was greater than the effect of inoculation with the PGPB, but only at soil dilutions of 1:8 to 1:32 (Fig. 1k). The similar fitting curves of inoculated and non-inoculated plant (both statistically significant) showed that, in these created soils inoculated with *A. brasilense* Cd, the bacterium played no role. Finally, comparing the two soil amendments for their effect on plant growth showed superiority of compost amendment over amendment with “resource island” soils, especially at higher concentrations of the supplement (Fig. 1l, dilutions 1:4 to 1:64, capital letter analysis). The effect disappeared when the amount of each amendment was small (dilution 1:128 to 1:256, Fig. 1l). Although both fitting curves are statistically significant, the fitting curve of the compost has a higher determination coefficient ($r^2=0.97$).

More than 95% of the cardon plants grown in any of the soil dilutions survived the 18-month experiment (data not presented). Only cardon plants growing in pure compost without soil had a very low survival rate (5%). After 12 months, several *Azospirillum*-like colonies (Bashan et al. 1993) were isolated from cardon roots. However, FAME analysis failed to confirm these morphotypes as *A. brasilense* Cd.

All plants growing in barren soil diluted at 1:4 to 1:8 with compost were visibly greener (photo not shown). An analysis of five major pigments of cardon plants showed that chlorophyll *b*, β -carotene, and zeaxanthin + violaxanthin increased in dilutions 1:4 and 1:8, but no difference in chlorophyll *a* concentrations occurred (Fig. 2a–d, lower case statistics). Generally, the amount of each plant pigment at high soil dilutions (1:64 and 1:128) was greater when the barren soil was amended with “resource island” soil than when amended with compost (Fig. 2, capital letter analysis). Yet, these values were lower than the values for plants growing in barren soils (dilution 0) (Fig. 2a–d), which exhibited poor plant development, as explained earlier.

Discussion

Giant cardon cacti in the southern Sonoran Desert of Mexico were and still are clear-cut to make room for agricultural and urban developments (Bashan et al. 2000b). Failed developments are abandoned, creating severe dust pollution that affects human health (Ortega-Rubio et al. 1998; Servin and Tejas 1991; Strannegaard and Strannegaard 1990). Restoration of cardon and other native desert plants are a priority for protecting the desert for its natural and human inhabitants. This environmental concern initiated our interest in this applicative study.

Earlier studies showed that cardon seedlings and transplants responded positively to inoculation with the PGPB *A. brasilense* in desert soils (Puente and Bashan 1993; Bashan et al. 1999; Carrillo–Garcia et al. 2000b).

The combination of compost amendments and inoculation of cacti seeds with PGPB is an uncommon practice. Yet, separately, both are common practices in modern agriculture (Hoitink and Fahy 1986; van Elsas and Heijnen 1990; Bashan 1998). Recently, related studies showed that inoculation with *A. brasilense* can alleviate humic acid toxicity in soil (Bacilio et al. 2003), reduce salt stress in agricultural plants growing in desert soils (Bacilio et al. 2004), and attenuate other stressors for plants (for review, Bashan et al. 2004). For cardon nurseries, the combination of compost amendments and inoculation with PGPB demonstrated that compost has a greater role than inoculation, even though inoculation with the PGPB helped cactus development. When compost is applied to barren soil at low dilutions, creating a soil with high organic matter and, hence, higher water-holding capacity, availability of water apparently has greater significance for plant development than the possible attribution of plant hormones normally contributed by *Azospirillum* sp. inoculation (Bashan et al. 2004). Thus, when the soil is “richer” in organic matter and minerals, either by adding compost or by adding “resource island” soil (serving as a positive control to barren soil amended with compost), the effect of inoculation with PGPB is smaller and the reverse, as demonstrated in this study, particularly in the shoot-to-root ratio analysis. The effects of *A. brasilense* Cd on cardon growth in poor or “resource island” desert soils has been documented (Carrillo–Garcia et al. 2000b) and, therefore, it was not the main objective of this study.

Another effect on plant development by amending soil with compost might be the positive effects of humic and fulvic acids, abundantly present in the compost we used (Bacilio et al. 2003) and affecting numerous physiological mechanisms of plants (Malcolm and Vaughan 1979; Mylonas and McCants 1980; Hartwigsen and Evans 2000). Humic acid effects are dose–response effects (Mylonas and McCants 1980). Although the direct effects of humic and fulvic acids on cardon growth has never been tested, it is plausible that their presence in high concentrations (dilutions 1:2 of soil and compost) somewhat inhibited cardon growth, similar to the effects in wheat plants (Bacilio et al. 2003). At lower concentrations (higher dilutions of compost), these acids probably function as growth promoters, as known for other plants (Evans and Lee 2003).

Although the composition of the soil amended with compost only resembled “resource island” soil, being richer in nutrients and organic matter content, the effect on plant growth was similar. Yet, the plants were slightly less dense (lower dry weight, but more voluminous and greener). The volume of cactus seedlings is a crucial parameter for surviving the first dry season in the desert. The initial growth of seedlings is in the rainy season, thereafter facing a long (10–11 months) period of drought. A more voluminous seedling, storing sufficient liquids, has a better chance to survive the forthcoming drought (Gibson and Nobel 1986). The greater quantities of pigments may indicate a potential for higher photosynthetic capacity (Bashan et al. 2006). The slightly smaller effect of the compost–amended barren soil on cardon dry weight,

compared to cardon growing in undiluted “resource island” soil, might be explained by the role of natural microflora, mainly a massive AM fungi (Carrillo-Garcia et al. 1999; Bashan et al. 2000a), which commonly participate in nutrient transport below ground and were not present in the compost–barren soil mix.

FAME analysis failed to detect the inoculated bacteria a year after inoculation. This may be explained in several ways: barren soil contains larger quantities of sand that is deleterious to *Azospirillum* survival (Bashan and Vazquez 2000) or *A. brasilense* Cd is known to be adsorbed strongly to sand particles (Bashan and Levanony 1988). Although *A. brasilense* survived similar periods in roots of medium-sized cardon in the same soil in the field (Bashan et al. 1999), larger plants growing in the field have a much larger rhizosphere than the small cardon seedlings (with very small root systems and rhizospheres) grown in this study. This might limit the survival of the PGPB in this study. It is well established that *A. brasilense* have low survival rates in soil without plant rhizosphere (Bashan et al. 1995; Bashan 1999).

In general, we propose using infertile desert soils amended with common animal compost as a substitute for the limited “resource island” soil used in nurseries undertaking reforestation programs with giant cardon cacti intended for abating soil erosion in the desert.

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