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Restoration of eroded soil in the Sonoran Desert with native leguminous trees using plant growth-promoting microorganisms and limited amounts of compost and water

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Dedication: This study is dedicated for the memory of the German/Spanish mycorrhizae researcher Dr. Horst Vierheilig (1960-2011) of CSIC, Spain.

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ABSTRACT

Restoration of highly eroded desert land was attempted in the southern Sonoran Desert that had lost its natural capacity for self-revegetation. In six field experiments, the fields were planted with three native leguminous trees: mesquite amargo *Prosopis articulata*, and yellow and blue palo verde *Parkinsonia microphylla* and *Parkinsonia florida*. Restoration included inoculation with two of plant growth-promoting bacteria (PGPB; *Azospirillum brasilense* and *Bacillus pumilus*), native arbuscular mycorrhizal (AM) fungi, and small quantities of compost. Irrigation was applied, when necessary, to reach a rainy year (300 mm) of the area. The plots were maintained for 61 months. Survival of the trees was marginally affected by all supplements after 30 months, in the range of 60–90%. This variation depended on the plant species, where all young trees were established after 3 months. Plant density was a crucial variable and, in general, low plant density enhanced survival. High planting density was detrimental. Survival significantly declined in trees 61 months after planting. No general response of the trees to plant growth-promoting microorganisms and compost was found. Mesquite amargo and yellow palo verde responded well (height, number of branches, and diameter of the main stem) to inoculation with PGPB, AM fungi, and compost supplementation after three months of application. Fewer positive effects were recorded after 30 months. Blue palo verde did not respond to most treatments and had the lowest survival. Specific plant growth parameters were affected to varying degrees to inoculations or amendments, primarily depending on the tree species. Some combinations of tree/inoculant/amendment resulted in small negative effects or no response when measured after extended periods of time. Using native leguminous trees, this study demonstrated that restoration of severely eroded desert lands was possible.
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1. Introduction

Desertification is an increasingly worldwide problem that leads to soil erosion and flooding, forces migration of rural populations, and increases health risks of the residents from dust pollution (Mctainsh, 1986; Ortega-Rubio et al., 1998; Wang et al., 2004). Natural revegetation in highly-disturbed deserts is very slow. Revegetation of the native flora is one of the proposed solutions to combat encroaching deserts (Moore and Russell, 1990). In North America, desertification is common in northwestern Mexico and reforestation is commonplace only for timber production.

In general, among practices available for reforestation for timber production, inoculation with plant growth-promoting bacteria (PGPB) (Chanway, 1997) and arbuscular mycorrhizal (AM) fungi

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(Perry et al., 1987) is a procedure yet to achieve acceptance. Inoculation with these microorganisms in organic and conventional agriculture (Bashan and de-Bashan, 2005; Lucy et al., 2004) has already reached commercialization (Bashan and Holguin, 2004; Díaz-Zorita and Fernández-Canigia, 2009). As far as we know, revegetation using native plants for recreation, soil reclamation after mining extraction, restoration after fires, and prevention of soil erosion has not used growth-promoting microorganisms (Hooper et al., 2002; Miyakawa, 1999). Apart from agro forestry, trees like oak, eucalyptus, and pine that were evaluated for their response to PGPB (Enebak, 2005; Estes et al., 2004; Garcia et al., 2004; Sastry et al., 2000), only a handful of wild plants have been inoculated with PGPB. The vast majority are cacti of the Sonoran Desert (Bacilio et al., 2006; Bashan et al., 1999, 2009b; Carrillo-Garcia et al., 2000a; Carrillo et al., 2002; Lopez et al., 2011; Puente and Bashan, 1993; Puente et al., 2004a) and several other shrubs (Grandlic et al., 2008; Herrera et al., 1993), as well as mangroves and their associates (Bashan et al., 2000b; Bashan and Holguin, 2002; Toledo et al., 1995). Recently, inoculation with PGPB and AM fungi was demonstrated in greenhouse cultivation of four Sonoran Desert native trees (Bashan et al., 2009a; Solís-Domínguez et al., 2011).

We hypothesized that native leguminous trees, essential for revegetation of eroded desert lands, would respond in the field to inoculation with plant growth-promoting microorganisms in a manner similar to its use in agriculture and agro forestry. In addition, trees planted at high densities can serve as soil stabilizers in their initial years, as do many desert shrubs. This would allow revegetation of severely eroded desert areas that otherwise do not recover. We inoculated three species of native legume trees with two PGPB and AM fungi and supplemented with limited amounts of compost and water. The entire scheme was tested at two plant densities. We assessed revegetation success by measuring survival, height, number of branches, and thickness of the main stem, as indicators of improved survival under desert conditions (Glenn et al., 2001).

2. Materials and methods

2.1. Organisms

We tested three leguminous trees, mesquite amargo *Prosopis articulata* (S. Watson), yellow palo verde or foothill palo verde (*Parkinsonia microphylla* Torr.), and blue palo verde or palo junco (*Parkinsonia florida* (Benth. ex A. Gray) S. Wats). Also, we used the plant growth-promoting bacteria (PGPB) *Azospirillum brasilense* Cd (DSM, 1843; the type strain of *A. brasilense;* Braunschweig, Germany) and *Bacillus pumilus* strain RIZO1 #FJ032016, GenBank of NCBI, National Center for Biotechnology Information (Hernandez et al., 2009; Puente et al., 2004b). The inoculum of arbuscular mycorrhizal (AM) fungi was a pot culture, mainly of *Glomus* spp. and a consortium of unidentified native species found in resource islands (Halvorson et al., 1994) under mesquite trees in the southern Sonoran Desert (Bashan et al., 2000a; Carrillo-Garcia et al., 1999).

2.2. Preparation of the selected site field

The revegetation area was located 17 km northwest of La Paz, Baja California Sur, Mexico at the southern limit of the Sonoran Desert. The climate is arid with mean annual precipitation of 180 mm, mainly in late summer. The surrounding area is a transition between xerophilic scrubland and dry tropical forest (León de la Luz et al., 1996). Geomorphologically, the area is an alluvial coastal plain of alluvium derived from weathered granite eroded from of the Sierra de la Laguna Mountains (Maya and Guzmán, 1998).

During a survey on 1 July 2003 along a dirt access road to the Northwestern Center for Biological Research (CIBNOR) in El Comitan, Baja California Sur, Mexico (24°07′31.91″ N 110°25′41.80″ W) bordering conserved desert forest, we found an area that had been cleared around 1980 for a paved road that was never built. Eight soil samples (about 1 kg each) were taken every 100–150 m along the flat road to a depth of 10–15 cm. The soil was described in detail (Bashan et al., 2000a; Carrillo-Garcia et al., 2000b). To choose a site along this road for the restoration trials, three criteria were considered: light native plant cover, low salinity, and high clay content. These considerations were necessary because part of the cleared area had been used 15 years earlier to dump marine sediments. Clay was analyzed for its potential improvement of water content of the soil (Carrillo-Garcia et al., 2000a, b) and limited plant coverage as an indicator of low fertility. Site 7 was selected because it had low salinity (0.44 dS/m) and relatively high content of clay (20%) and silt (16%). The remaining fraction was sand. The site (75×27 m) is in the CIBNOR ecological and research reserve. When the site was checked on 22 January 2004, it contained three organ pipe cacti/pitahaya dulce (*Stenocereus thurberi* (Engelm.) Buxbaum) (synonym *Lemaireocereus thurberi*), the remnants of an experiment from the 1990s; one small yellow palo verde tree; two medium mesquite amargo trees, nine ashy limberbush/lomboy blanco shrubs *Jatropha cinerea* (Ortega) Müll. Arg. The latter is the most important pioneer plant in the southern Sonoran Desert (Perea et al., 2005). Additionally, there was abundant buffel grass (*Cenchrus cillaris* L.); this exotic and invasive grass was removed by hand in February 2004. Root mats and shoots were burned to avoid dissemination of seeds in the field plots. The three leguminous trees were trimmed to avoid shading the experimental plots. The three pitahaya cacti were left intact. The lomboy blanco were severely trimmed and maintained in the trimmed condition throughout the experiment to prevent interference with the planted trees.

2.3. Culturing microbes

A. brasilense Cd and *B. pumilus* strains were cultivated on tryptic yeast extract–glucose medium supplemented with microelements (TYG) for 24 h at 30 °C on a shaker at 120 rpm (Bashan et al., 2011). The two species were then added to dry alginate micro-bead inoculants, using automated equipment, as described in Bashan et al. (2002).

2.4. Production of AM fungal inoculum

Inoculum was prepared in 10 l pot cultures with sorghum plants (*Sorghum* bicolor [L.] Moench), using consortia of AM fungi from resource island soil obtained from the field experiment. The plants were senescent at harvest, when ~50 roots were analyzed using the line intersects method for the level of colonization by AM fungi with the ink-staining method (Marsh, 1971; Vierheilig et al., 1998). Root colonization was 54.5%.

After excising the stems, the rooted soil clumps were air-dried for 2 weeks before they were broken and separated for spore counts. Spores from the soil samples were collected by wet-sieving (45, 75, 100, and 200-μm mesh), decanting, and sucrose-gradient centrifugation (Brundrett et al., 1994). Typical spore count of the AM fungi in pot culture was 308 spores 100 g^{-1} soil.

2.5. Compost

Compost of cow manure and wheat straw that had been used for cultivating cardon cactus was described earlier (Bacilio et al., 2006). Compost was mixed with soil and added to each planting hole at a proportion of 1:8 (compost:soil, 735 g:10 kg, w/w).

2.6. Application of inoculants

Bacterial inoculant made of alginate micro-beads was attached to the seeds of wild trees, as described for wheat (Bashan et al., 2002), at a level of 1.2×10^6 CFU g^{-1} soil of *B. pumilus* and 1×10^6 CFU g^{-1} soil of *A. brasilense*.

After pot-culturing of AM fungi on sorghum roots, the roots were extracted and cut into short lengths (~0.5 cm). The pieces of root were mixed into the soil. A mixture of soil and root inoculant (213 g) was used to inoculate each leguminous tree. Inoculants and compost for the field experiments were mixed into the soil by hand. The amendment was stored in 30-kg sacks at ambient temperature for about two weeks, until used.

2.7. Collecting seeds and screen house cultivation of seedlings

Seeds of mesquite amargo, yellow palo verde, and blue palo verde were collected from ten native trees (200 g $plant^{-1}$) located in fields surrounding the settlements of El Centenario and El Comitan, 15 km from La Paz, B.C.S., Mexico (24°07′36″N, 110°25′48″W) in July 2003 (Figure S1). Seedlings for transplantation to the field plots were cultivated in pots for 9 months and were of similar height: 20 cm for yellow palo verde and 50 cm for blue palo verde and mesquite amargo (Bashan et al., 2009b).

2.8. Planting procedures

The planting holes were designed to maximize the connection between inoculants and plants, conserve water, and reduce risk of predation by herbivores. Briefly, each transplant was planted in an identical hole excavated by a commercial garden excavator to a depth of 25 cm and a diameter of 30 cm (Truper, Mexico). About 80% of the extracted soil was mixed with the bacterial and AM fungal inoculants and compost (as described earlier) and returned to the hole. Each hole received 6 kg of this inoculated soil on the day of planting (total 180 kg per treatment, 900 kg per experiment). One seedling was planted in the center of each hole and the soil was lightly packed to ~5 cm below the surrounding ground, which created a sunken planting.

2.9. Irrigation

After planting, the holes were filled with tap water until soaked. These experiments were initially devised to use only rainfall for 3 years. In this area, the multi-year average is 180 mm and, in exceptionally rainy years, rainfall can reach 300 mm, mainly from hurricanes and tropical storms during late summer. After greater rainfall, perennial desert vegetation is normally established (Drezner, 2006). Unfortunately, the experiments were conducted in dry years, common to this area, receiving 177 mm in 2004, 58 mm in 2005, and 73 mm in 2006 (Comisión Nacional de Aguas, Mexico). Consequently, rainfall was supplemented by irrigation to achieve an annual 300 mm in amounts and frequencies similar to natural rainfall and according to the multi-year average of monthly precipitation. In the first two years, irrigation was done by adding 1 L of tap water to each planting hole. In the third year, when the planting depressions had almost disappeared, the entire area was surface irrigated by a water tanker, when necessary, equivalent to 10–20 mm rain. The amount of water that the trees received in any given year, either from rainfall or by irrigation, did not exceed 300 mm rain per year.

2.10. Measurement of plant parameters

Measurements of growth (height, number of branches, and survival) were made of all trees at 6 time points at 3, 8, 12, 19, 24 and 30 months after planting. Diameter of the main stem was measured 5 cm above the ground surface at 12, 19, 24, and 30 months. Seedlings had similar stem diameters during the first months after planting.

2.11. Experimental field design and statistical analysis

Six field experiments were performed and the plants maintained from July 2004 to August 2009 (61 months) within an area of ~2000 m^2. Detailed measurements were taken up to 30 months after planting. Additional measurements of survival were recorded 61 months after planting. The following treatments were used for each experiment: (1) Control trees growing in eroded soil; (2) Trees inoculated with AM fungi; (3) Trees inoculated with a mixture of two PGPB; (4) Trees growing in soil amended with compost; (5) Trees growing in soil amended with compost and inoculated with AM fungi and PGPB. Selection of treatment was based on a screen house study that showed potential benefits of these treatments (Bashan et al., 2009a). All experiments had a design of five blocks each. Each block in the field contained the 5 treatments randomly arranged (Figure S1).

Experiments in low planting density (3): For each of the three tree experiments, each treatment contained 25 trees for a total of 125 trees per experiment. Planting distance between trees was 1.0 m and the holes were dug in a W configuration to minimize competition and provide the same volume of soil for each tree (Figure S1).

Experiments in high planting density (3): The design and treatments were the same as in the low density plantings except for density. Each treatment contained 30 seedlings of a tree for a total of 150 plants. Planting distance was 0.5 m in a zigzag configuration (Figure S1).

Results of all experiments were analyzed by one-way ANOVA and then by Tukey's HSD post-hoc analysis with significance set at $p < 0.05$. Additionally, results of the effect of the treatment on the number of developing branches over time were analyzed by Repeated Measures ANOVA, using Least Square Means (Proc Mixed procedure, SAS system, 2002). Data in percentages were converted to arcsin before analysis. Linear regressions models were used for analysis of height versus time at p levels indicated.

3. Results

3.1. Survival of trees in the field

Survival of the trees was marginally affected by all tested variables. After 30 months, mesquite was the best survivor, regardless of the treatment or the planting density. Survival rate of mesquite at low density was 90–100% (Fig. 1 A; lower case letter analysis and Table 2). At the higher density, inoculation with PGPB or AM fungi reduced survival of mesquite to ~80% (Fig. 1B; lower case letter analysis). Survival of yellow palo verde was 70–95%, similar in all treatments at low density (Fig. 1A; capital letter analysis); at high density, the survival rate increased to 90–100% (Fig. 1B; capital letter analysis). For blue palo verde at low density planting, only inoculation with AM fungi improved survival (98%); survival for other treatments ranged from 58 to 87% (Fig. 1A; italic letter analysis). At high density, survival was higher (70–85%) and best when all the treatments were combined (95%, Fig. 1B; italic letter analysis).

Following survival rates over time, the three species survived well for 12 months at low density (>85% of the trees). At 12–19 months after transplantation, all species lost plants (Fig. 1C–E); the most drastic result occurred among blue palo verde (Fig. 1E). Later, the populations stabilized, with variations depending on treatment (Table 2). At high densities, the only tree species that

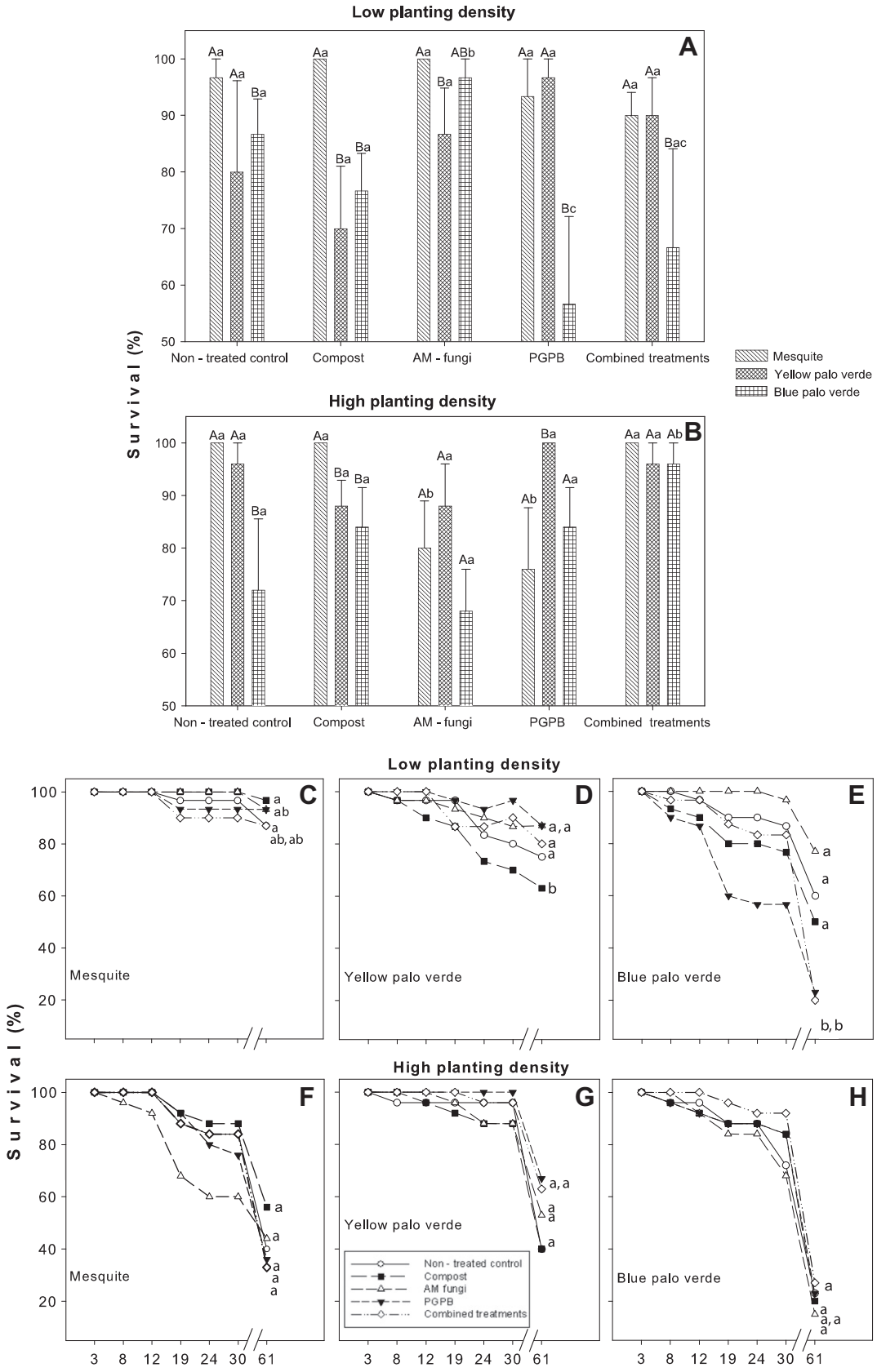

Fig. 1. Survival of mesquite amargo, yellow palo verde, and blue palo verde in the field for 61 months after transplantation and inoculation with PGPB, AM fungi, and supplemented with compost at two plant densities (A, B). Columns of the same tree species denoted by a different letter of different types lower case letters (mesquite); capital letters (yellow palo verde) and italics (blue palo verde; representing comparison among treatments carried out on the same tree species) differ significantly at $p < 0.05$ by one-way ANOVA. Bars (absent for columns representing 100% survival) represent standard error (SE). (C–H) show survival of trees, with time after planting. Lines in each subfigure separately denoted by a different lower case letter differ significantly at $p < 0.05$ by one-way ANOVA. Analysis is presented for data after 61 months (without SE to enhance clarity).

Table 1
Linear regression models between height of trees and time. Trees were measured after 3, 8, 12, 19, 24 and 30 months.

Treatment	Regression model	r^2	p
Low plant density			
Mesquite amargo			
Untreated control	y = 36.21−0.24x	0.75	0.027
Compost	y = 28.69−0.16x	0.19	ns
AM-fungi	y = 39.78−0.29x	0.76	0.024
PGPB	y = 50.59−0.31x	0.62	ns
Combined treatment	y = 34.75−0.23x	0.19	ns
Yellow palo verde			
Untreated control	y = 41.4 + 0.38x	0.68	0.043
Compost	y = 36.2 + 0.46x	0.75	0.027
AM-fungi	y = 43.35−0.008x	0.001	ns
PGPB	y = 37.76 + 0.55x	0.95	0.0008
Combined treatment	y = 33.1 + 0.39x	0.99	0.00007
Blue palo verde			
Untreated control	y = 71.56 + 3.19x	0.82	0.013
Compost	y = 60.9 + 3.44x	0.86	0.008
AM-fungi	y = 53.13 + 3.4x	0.95	0.001
PGPB	y = 57.9 + 2.77x	0.83	0.01
Combined treatment	y = 68.38 + 3.07x	0.77	0.021
High plant density			
Mesquite amargo			
Untreated control	y = 34.58 + 0.14x	0.05	ns
Compost	y = 20.68 + 0.45x	0.54	ns
AM-fungi	y = 23.2 + 0.51x	0.71	0.036
PGPB	y = 31.86 + 0.37x	0.47	ns
Combined treatment	y = 40.5−0.1x	0.34	ns
Yellow palo verde			
Untreated control	y = 42.69−0.08x	0.11	ns
Compost	y = 42.08 + 0.03x	0.05	ns
AM fungi	y = 36.24 + 0.16x	0.21	ns
PGPB	y = 35.9 + 0.17x	0.49	ns
Combined treatment	y = 31.94 + 0.14x	0.26	ns
Blue palo verde			
Untreated control	y = 77.19 + 1.33x	0.56	ns
Compost	y = 69.49 + 1.77x	0.80	0.016
AM fungi	y = 64.54 + 1.3x	0.67	0.046
PGPB	y = 63.58 + 1.56x	0.75	0.026
Combined treatment	y = 71.56 + 1.83x	0.65	0.05

ns = not significant ($p > 0.05$).

survived well was yellow palo verde, with survival rates similar or higher than low density plantings; all trees inoculated with PGPB in the high density treatment survived (Fig. 1G, compared with Fig. 1D). Survival of the mesquite was less at high density with a similar decline in population at 12–19 months after planting, as happened in low density plots (Fig. 1C, F). At high density, mesquite inoculated with AM fungi had the lowest survival (~60%), while trees in the other treatments had higher survival (>75%; Fig. 1F). At 12–19 months, blue palo verde inoculated with PGPB had the poorest survival at low density (Fig. 1E) and higher survival (>85%) at high density treatments (Fig. 1H).

At 61 months after planting, survival declined in most of the treatments; however, measurements of survival clearly showed differences between low and high planting densities. At low density, survival of mesquite amargo was not affected by the additional months (Fig. 1C). Survival of yellow palo verde declined slightly and treatments with compost had the lowest survival (>60%) of the three species (Fig. 1D; 61 months). Blue palo verde declined significantly under all treatments; treatments with PGPB and the combined treatment had the lowest survival (~20%) of the three species (Fig. 1E). A major decline in survival at 61 months was detected for high density plantings of all species and for all treatments (Fig. 1F–H). In mesquite amargo, survival was reduced from ~90% at low density to 30–60% at high density. In yellow palo verde, survival was reduced from 70 to 90% at low density to 40–70% at high density. In blue palo verde, survival was very low for high density plantings, regardless of treatment, reaching 10–30% of the original plantings.

3.2. Effects on tree height

Height varied because some branches normally dry out under severe drought and then re-grow when water is available; this produced shorter trees for the longer growth period. The results varied by species (Table 2). Among mesquite, height was not affected by plant density. The trees grew faster in the first 3 months and mostly maintained their height (within a range of 30–50 cm) for the next 27 months (Fig. 2 A, B) and differed only in branching (described later). Application of compost in the planting hole had a negative effect on plant height for 24 months. Inoculation with PGPB significantly enhanced tree height at the low density (Fig. 2A) and had a lesser effect at high density, with a significant difference occurring 24 months after planting (Fig. 2B). Inoculation with AM fungi had a positive effect on growth for the first 19 months at low density, but the effect later diminished (Fig. 2A); there was no effect of AM fungi on height at the high density (Fig. 2B). The combination of all variables as one treatment sometimes enhanced plant height, but had no lasting effect after 30 months at either density (Fig. 2A, B).

Height of yellow palo verde under low density planting was not affected by any treatment (Fig. 2C), largely because this tree has a mostly horizontal growth as a shrub during its first years. Only at high planting density was height significantly affected after 30 months by inoculation with AM fungi and application of compost after 3 months, but to a small degree (Fig. 2D). Similar to mesquite, yellow palo verde grew quickly during the first 3 months (Fig. 2C, D) and maintained its height at high density planting (30–45 cm) for the next 27 months (Fig. 2D). Height increased at the lower density from 40 to 55 cm, on average, over the course of the experiment (Fig. 2C).

Blue palo verde was the only species that increased its height during 2.5 years (Fig. 2E, F). The lower density plantings yielded taller trees, averaging 1.5 m (Fig. 2E), but with individuals up to 2.8 m tall; high density plantings yielded shorter plants, averaging 1.1 m tall (Fig. 2F). None of the treatments had any effect on the height of blue palo verde (Fig. 2E, F).

Change in height was one of the most obvious parameters in the field. Correlation between time after planting and plant height was performed for all treatments 30 months after inoculation. The strength of the correlations differed, depending on the density of planting (Table 1). At low density, linear growth correlations were found mainly in the non-inoculated controls of the three species and in all the treatments with blue palo verde, a species that did not respond to any treatment, and in yellow palo verde (except for the AM-fungi treatment), while mesquite showed linear correlation only to the treatment with AM fungi (Table 1). At high density, no correlation was found between any treatment or non-inoculated control of yellow palo verde and mesquite (the latter only had a growth correlation with the AM fungal treatment). Blue palo verde maintained its growth correlations regardless of the treatment, as happened at low density (Table 1).

3.3. Effects on branch development

The number of branches was expected to indicate development of the tree. Analysis of the effect of time on branching showed clear differences in the number of branches produced by each species at low and high densities ($P < 0.0001$, details in Table S1, supplementary material). Even when low and high densities were not statistically compared, low density plantings yielded more

Table 2
General evaluation of promoting growth by inoculation with growth-promoting microorganisms and supplement of compost after 3 and 30 months of cultivation in an eroded field.

Parameter and plant species	Compost				AM fungi				PGPB				Combined treatment			
	Low density		High density		Low density		High density		Low density		High density		Low density		High density	
	3	30	3	30	3	30	3	30	3	30	3	30	3	30	3	30
Survival																
Mesquite	N	↔	N	↔	N	↔	N	↓	N	↔	N	↓	N	↔	N	↔
	A		A		A		A		A		A		A		A	
YPV	N	↔	N	↔	N	↔	N	↔	N	↔	N	↔	N	↔	N	↔
	A		A		A		A		A		A		A		A	
BPV	N	↔	N	↔	N	↑	N	↔	N	↓	N	↔	N	↔	N	↑
	A		A		A		A		A		A		A		A	
Height																
Mesquite	↓	↔	↓	↓	↑	↔	↓	↓	↑	↑	↔	↔	↑	↔	↑	↓
YPV	↔	↔	↑	↔	↔	↔	↓	↑	↔	↑	↓	↓	↓	↔	↓	↓
BPV	↓	↔	↔	↔	↓	↔	↓	↓	↓	↓	↓	↔	↓	↔	↓	↔
No. branches																
Mesquite	↔	↔	↓	↓	↑	↓	↓	↔	↑	↓	↓	↔	↑	↔	↓	↓
YPV	↔	↔	↔	↔	↑	↔	↓	↔	↓	↔	↓	↓	↓	↔	↔	↓
BPV	↓	↔	↔	↑	↓	↓	↓	↔	↓	↓	↓	↔	↓	↓	↓	↔
Thickness of stem																
Mesquite	N	↑	N	↔	N	↔	N	↓	N	↑	N	↔	N	↑	N	↔
	D		D		D		D		D		D		D		D	
YPV	N	↔	N	↓	N	↑	N	↔	N	↑	N	↓	N	↔	N	↔
	D		D		D		D		D		D		D		D	
BPV	N	↔	N	↓	N	↓	N	↓	N	↓	N	↓	N	↓	N	↓
	D		D		D		D		D		D		D		D	

YPV = Yellow palo verde BPV = Blue palo verde ↔ = no significant effect
↑ = Significant positive effect ↓ = Significant negative effect
Dark gray areas had a significant positive effect after 3 months. White square areas had a significant positive effect after 30 months. NA (Not applicable because survival after 3 months was 100% in all treatments.) ND (Not determined; young plants)

branches at most sampling times for all species (Fig. 3A, B, C). At low density, measurements after 12 and 30 months showed markedly more branches for yellow and blue palo verde, but not for mesquite (Fig. 3A, B, C). When analyzing the effect of various treatments on branching, only yellow palo verde showed significant differences among treatments for low ($p < 0.0158$) and high ($p < 0.0089$) planting densities (Fig. 3D, E, F; more details in Table S1, Supplementary material). In yellow palo verde, adding AM fungi produced the greatest number of branches at low density; the untreated control and the compost application were in an intermediate position, and the bacteria and combined treatments produced the lowest number of branches (Fig. 3E). At high density, the pattern was different; the untreated control produced the greatest number of branches, followed by the compost treatment. The treatment with mycorrhiza was in an intermediate position and the combined treatments and bacteria (by itself) produced the fewest branches (Fig. 3E).

3.4. Effects on main stem diameter

The diameter of the main stem of trees was first measured one year after planting; the diameters did not differ in younger trees. Generally, stem diameter of mesquite at low density increased with most treatments except inoculation with AM fungi. This was especially apparent after 30 months (Fig. 4A). Only inoculation with PGPB increased stem diameters at high density for up to 24 months, but the effect diminished after 30 months (Fig. 4 B). At low density, but to a lesser degree, diameter of yellow palo verde stems increased when inoculated with the PGPB and after 30 months by inoculation with AM fungi (Fig. 4C). At high density, all treatments had negative effects on the diameter of stems (Fig. 4 D). Similarly, all treatments had negative effects on the diameter of blue palo verde stems, regardless of plant density (Fig. 4E, F).

3.5. General analysis of the effects of amendments on plant growth

Table 2 presents a general analysis of performance of the six field trials for all treatments after 3 and 30 months of cultivation. Survival was only marginally affected by any treatment. Only blue palo verde, which generally did not respond to any treatment, survived better in two combinations. Mesquite and yellow palo verde significantly responded (height, number of branches, diameter of stems) to several treatments, but usually each species responded differently to each treatment (compare treatments with ↑ symbol in Table 2). Only inoculation with PGPB for the low density plantings provided a positive and similar response in height and stem diameter in two species. Some of the treatments caused negative effects on plant parameters; these depended mainly on the species and treatment.

A survey of the roots after 24 months for AM fungi colonization revealed that the 50 tested plants (10 per treatment), including plots that had not been treated and controls that were not inoculated, were colonized by AM fungi (detailed data not shown).

4. Discussion

Restoration with shrubs, trees, and cacti of severely degraded areas of the Sonoran Desert is always difficult and, in many cases,

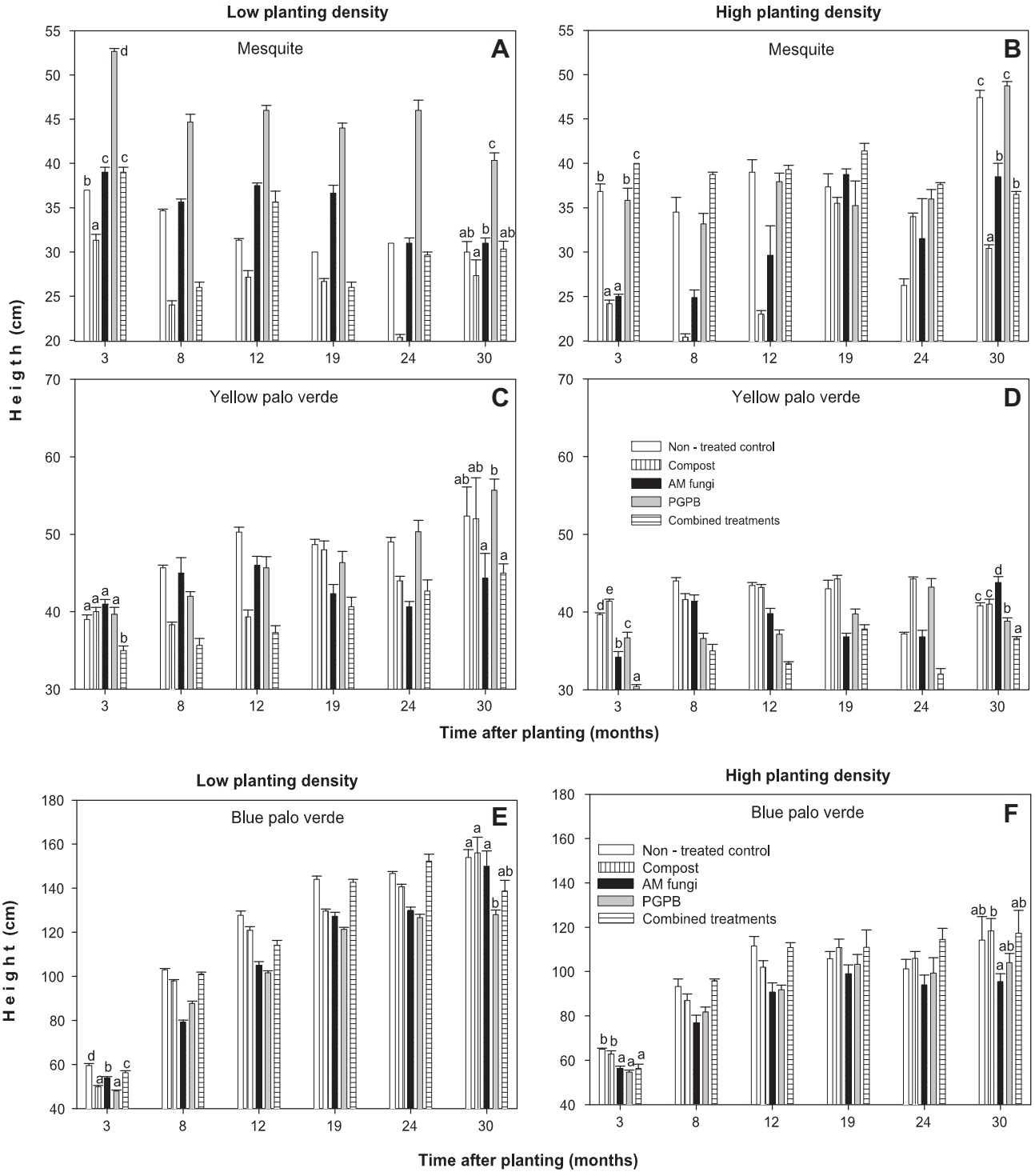

Fig. 2. Effect of inoculation with PGPB, AM fungi, supplementation with compost, and combined treatments on the height of mesquite amargo, yellow palo verde, and blue palo verde planted at two plant densities. Groups of 5 columns denoted by a different lower case letter differ significantly at $p < 0.05$ by one-way ANOVA. Bars represent standard error (SE).

only marginally successful (Banerjee et al., 2006; Bean et al., 2004; Glenn et al., 2001; Roundy et al., 2001). The nurse tree ecosystem governing natural vegetation in deserts is often destroyed, and the topsoil, with its beneficial microorganisms, is removed by wind and water erosion. Organic matter is very low, and water is usually in short supply. Therefore, any attempt to restore a desert with native plants should consider restoring the beneficial microflora associated with these trees and shrubs and provide a source of organic matter (Bacilio et al., 2006; Bashan and de-Bashan, 2010; Grandlic et al., 2008).

PGPB and AM fungi are beneficial in harsh and limiting environments because of their role in alleviating stress in plants (Sylvia and Williams, 1992). PGPB of the genus *Azospirillum* exert their main growth-promoting effects when plants are stressed by

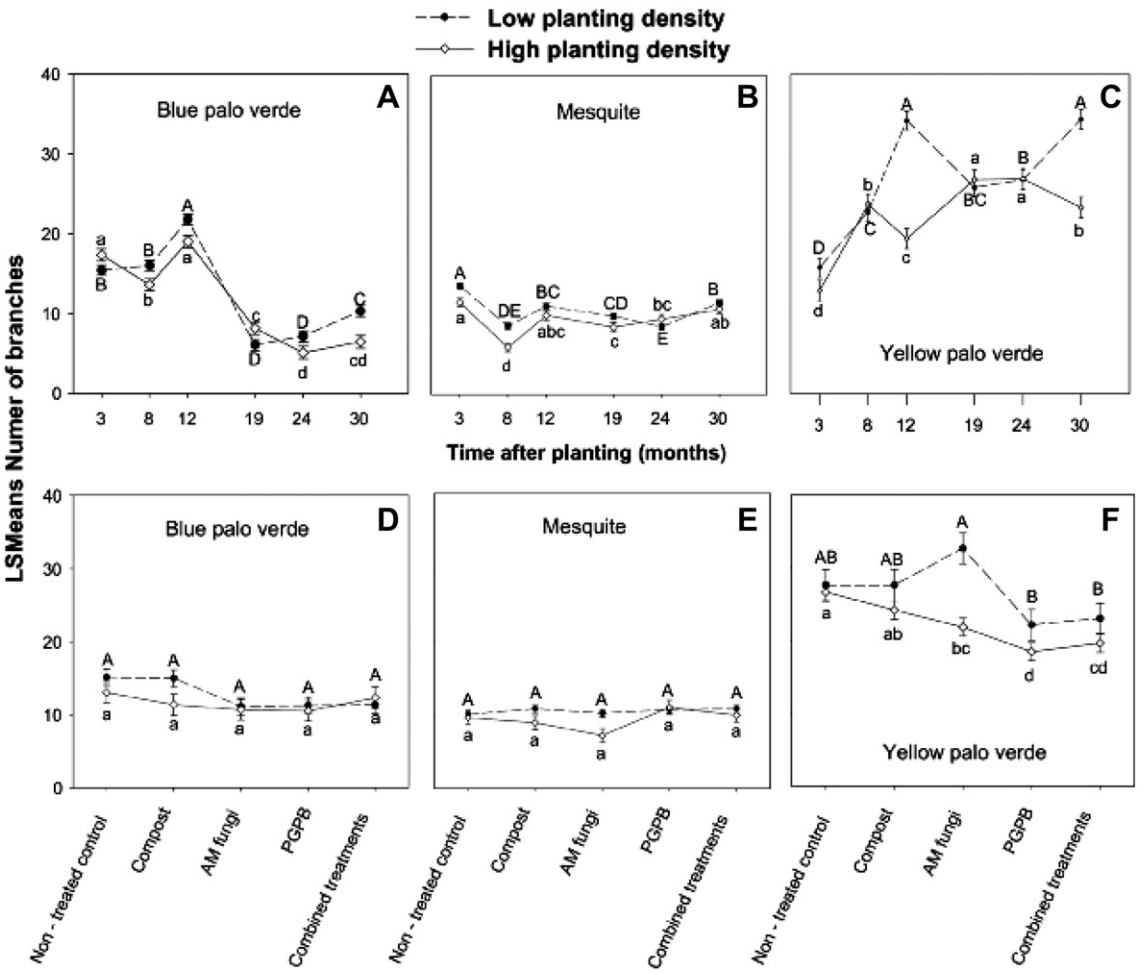

Fig. 3. Least square means generated by Proc-Mixed-ANOVA for the number of branches produced in yellow palo verde, blue palo verde, and mesquite amargo under five treatments, six time measurements, and two levels of planting (low and high density). Effect of time on the production of branches (A, B, C). Overall effect of treatments (C, D, E). At low density of planting, significant differences in time or treatments are indicated with different capital letters ($p < 0.05$). At low density of planting, significant differences in time or treatments are indicated with different lower case letters ($p < 0.05$).

salinity (Bacilio et al., 2004), drought (Creus et al., 1997), excessive humic acids (Bacilio et al., 2003), extreme pH (de-Bashan et al., 2005), and heavy metals (Belimov and Dietz, 2000). PGPB for environmental purposes is solely at the experimental level (de-Bashan et al., in press). Hyphae of AM fungi permeate large volumes of soil and interconnect the roots of adjacent plants; this facilitates exchange of nutrients between them, and contributes to plant growth and soil structure because of their intimate association with the living cells within roots and soil (Bethlenfalvay and Schüepp, 1994; Bethlenfalvay et al., 2007). AM fungi are essential components of plant-soil systems in deserts (Bashan et al., 2000a; Bethlenfalvay et al., 1984; Carrillo-Garcia et al., 1999; Cui and Nobel, 1992; Nobel, 1996; Requena et al., 2001).

One of the fundamental theories about the constant failure of natural revegetation in eroded desert areas and why re-vegetating arid regions with planting or seeding native plants is difficult is that the topsoil has lost its beneficial plant-associated microorganisms; hence, part of its fertility and growth potential. Even during the occasional years of greater rainfall, when desert plants more likely become established (Drezner, 2006), water alone cannot substitute for the loss of soil fertility, including its microbial communities. Theoretically, at least some essential plant growth-promoting microorganisms should be re-introduced to enhance establishment and growth.

This field study attempted to enhance revegetation by inoculation with PGPB and AM fungi and small amounts of compost. Previously, this was shown to produce a significant positive effect on establishing cardon cactus (Bacilio et al., 2006; Bashan et al., 2009b). Limited amounts of water, not exceeding natural rainfall of an average rainy year, were also supplied to the test field that consisted of eroded soil that had constantly failed to re-vegetate with pioneer native trees since about 1975.

Several studies (Carrillo-Garcia et al., 1999, 2000a, b; Reyes-Reyes et al., 2002) show that natural desert vegetation can be re-established on resource island soils under the canopies of some legume trees and shrubs, mainly mesquite. Resource island soils are in relatively short supply. This environment is destroyed when the soil beneath the mesquite is removed or disturbed. Hence, the use of the soils of resource islands is impractical for desert vegetation restoration. Low levels of compost supported growth of cardon cacti similar to or even better than resource island soil. In this case, it stabilized the soil, retained more water, and provided small but essential plant nutrition during the first year (Bacilio et al., 2006; Bashan et al., 2009b). Inoculation with plant growth-promoting microbes is the biological component that was added to this restoration technology. We used native AM fungi and one native PGPB because we assumed that they are adapted to local conditions; additionally, no commercial AM fungi or PGPB product, known to be effective on desert plants, were known at the time of

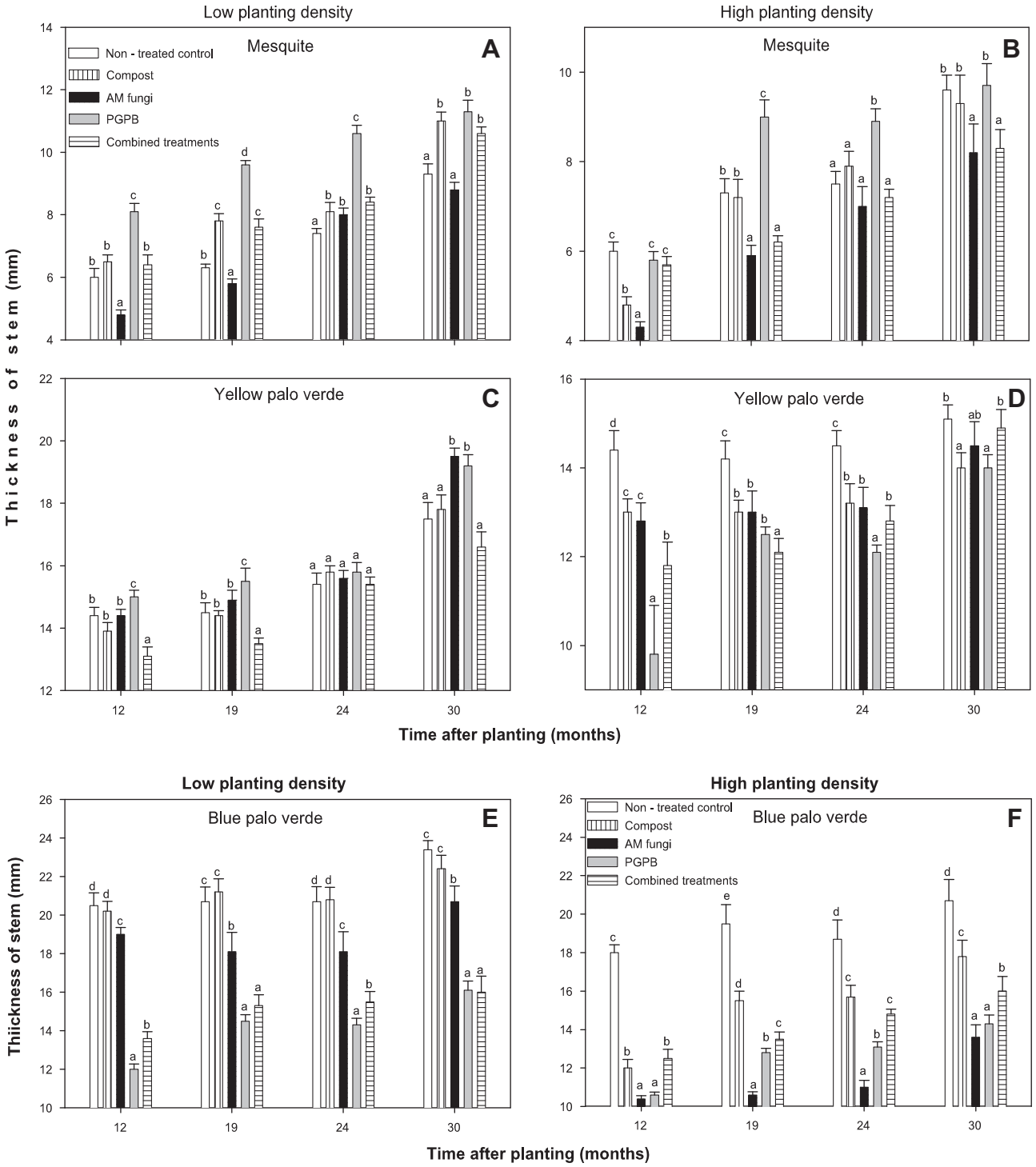

Fig. 4. Effect of inoculation with PGPB, AM fungi, supplementation with compost, and combined treatments on the stem diameters of mesquite amargo, yellow palo verde, and blue palo verde planted at two densities. Groups of 5 columns denoted by a different lower case letter differ significantly at $p < 0.05$ by one-way ANOVA. Bars represent standard error (SE).

the trials in 2004. Inoculation of Mediterranean oak and pine trees with PGPB was previously attempted under nursery conditions (Garcia et al., 2004), as have the three native legume trees used in this study under screen house conditions (Bashan et al., 2009a).

Direct seeding is commonly used for revegetation of abandoned lands in North American deserts and abandoned desert farmlands (Banerjee et al., 2006) and revegetation with annuals in rangelands in these areas (Munda and Pater, 2003). Transplantation combined with drip irrigation, although a more expensive practice, proved more useful on a relatively large expanse of former crop land in Arizona, leading to higher survival and lower densities of weeds than direct seeding of native plants (Bean et al., 2004). Our approach was similar, since we used screen house-propagated transplants, but replaced the drip irrigation by microorganisms that, in theory, potentially enhances drought resistance of plants and by maintaining irrigation practices that substitute for rainfall.

This was done because irrigation is not widely available for restoration work in remote areas with erratic and limited summer rainfall (Glenn et al., 2001; Roundy et al., 2001). Water shortages are especially common in large parts of the southern Sonoran Desert, where almost all precipitation comes from a very few late summer tropical storms.

AM fungi and PGPB were not periodically monitored during the 3-year field trial because the effect of typical PGPB, and especially *Azospirillum,* is short. This PGPB serves mainly as a booster for plant growth during its initial life stages (Bashan and Holguin, 2004). Furthermore, *Azospirillum* spp. does not survive for long periods in dry soils (Bashan, 1999; Bashan et al., 1995, 1999). Additionally, this soil had sufficient AM inoculum potential for AM colonization of most plants over time (Bashan et al., 2000a), even if not directly inoculated, as was also demonstrated in our study. Therefore, it was easier to assess success of the treatments under real field conditions by measuring survival and growth parameters of plants.

Adding each soil amendment separately in these trials did not consistently demonstrate that one amendment is superior and should be used in future revegetation programs. Rather, the usefulness of each amendment was mainly related to particular species. Each combination of a species and an amendment should be analyzed and used separately, as shown in our general analysis (Table 2). Application of a mixture of all amendments as a single treatment did not yield, as was initially assumed, synergistic or cumulative effects. Thus, it is unlikely that a single, multi-amendment treatment will play a role in future restoration in this arid environment. Selective effects of particular combinations of a species and a microbe also occurs when conifers and hardwoods in Canada were inoculated with several mycorrhizal fungi at the nursery (Quoreshi et al., 2008) and in a restoration program with cardon cacti of the Baja California Peninsula (Bashan et al., 2009b).

Mesquite trees in this arid area are known for salt and drought resistance and production of high biomass under desert conditions (Felker et al., 1981, 1983). Establishment of leguminous trees, especially mesquite, as nurse plants can help revegetation efforts when long term soil stabilization with cardon cactus is attempted (Bashan et al., 2009b). This is also true for other nurse plants, The shrub *Salvia lavandulifolia* supports establishment of native pine seedlings during rainless summers in Spain, which leads to improvement in the water status of seedlings and reduces summer mortality from drought (Castro et al., 2002). Even though mesquite amargo and yellow palo verde are very spiny during their early years, they are attractive candidates for desert restoration when stabilization and revegetation of soil are the main objective.

In summary, we demonstrated that three leguminous trees can be established in areas of severely eroded soil when irrigation did not exceed average rainy year. Plant density is the crucial parameter for long term survival. Plant growth-promoting microorganisms enhance plant growth for two species of legume tree in several combinations of treatments only for relatively short periods.

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Appendix. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jenvman.2011.12.032.

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