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SHORT COMMUNICATION

Responses of native legume desert trees used for reforestation in the Sonoran Desert to plant growth-promoting microorganisms in screen house

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Abstract Three slow-growing legume trees used for desert reforestation and urban gardening in the Sonoran Desert of Northwestern Mexico and the Southwestern USA were evaluated whether their growth can be promoted by inoculation with plant growth-promoting bacteria (*Azospirillum brasilense* and *Bacillus pumilus*), unidentified arbuscular mycorrhizal (AM) fungi (mainly *Glomus* sp.), and supplementation with common compost under regular screenhouse cultivation common to these trees in nurseries. Mesquite amargo (*Prosopis articulata*) and yellow palo verde (*Parkinsonia microphylla*) had different positive responses to several of the parameters tested while blue palo verde (*Parkinsonia florida*) did not respond. Survival of all tree species was over 80% and survival of mesquite was almost 100% after 10 months of cultivation. Inoculation with growth-promoting microorganisms induced significant effects on the leaf gas exchange of these trees, measured as transpiration and diffusive resistance, when these trees were cultivated without water restrictions.

Keywords *Azospirillum* · Desert · Mesquite · Palo verde · *Parkinsonia* · Plant growth-promoting bacteria · PGPB · PGPR · *Prosopis* · Reforestation

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Introduction

Desertification is an increasing phenomenon worldwide reducing arable lands and increasing health risks due to dust pollution (Mctainsh 1986; Wang et al. 2004). Reforestation is one of the common solutions to combat encroaching deserts, and projects can be of very large size (Moore and Russell 1990). Trees destined for reforestation are initially grown in greenhouses or screenhouses and later transplanted to the field. Therefore, effective nursery management and proper growth of the trees there is of outmost importance for reforestation practices.

Among numerous practices of reforestation for timber production, inoculation with plant growth-promoting bacteria (PGPB; Bashan and Holguin 1998), and arbuscular mycorrhizal (AM) fungi is a prospective niche yet to achieve commercial acceptance (Chanway 1997; Perry et al. 1987). Inoculation with PGPB is a contemporary trend in organic and nonorganic agriculture (Bashan and de-Bashan 2005a; Lucy et al. 2004) that is starting to get a foothold in commercial agricultural applications (Bashan et al. 2004). Growth promotion of numerous crops by PGPB, including fruit trees is well known, while inoculation of wild plants is a very recent development. Reforestation with native trees is common (Hooper et al. 2002; Miyakawa 1999).

Apart from agro-forestry trees like oak, eucalyptus, and pine evaluated for their response to PGPB (Domenech et al. 2004; Enebak 2005; Estes et al. 2004; Lucas García et al. 2004; Sastry et al. 2000; Zaady and Perevolotsky 1995), only a handful of wild plants have been inoculated with PGPB; the vast majority were cactus species of the Sonoran Desert (Bacilio et al. 2006; Bashan et al. 1999; Carrillo et al. 2002; Carrillo-Garcia et al. 2000; Puente and Bashan

1993; Puente et al. 2004b) and several other shrubby plant species (Bashan et al. 2000b; Grandlic et al. 2008; Herrera et al. 1993) as well as saltwater mangroves (Bashan and Holguin 2002; Toledo et al. 1995).

The hypothesis of this study was that native desert-legume trees that do not have commercial timber value but are essential for reforestation of eroded lands to prevent soil erosion and dust pollution respond to inoculation with native plant growth-promoting microorganisms in a similar manner as agricultural and agro-forestry trees. Thus, this agricultural technology may be applied also to the propagation of these trees usually done in screen-houses (Bean et al. 2004). Mesquite amargo and yellow and blue palo verde trees are common native trees of the Sonoran desert in the Southwestern USA and Northwestern Mexico. They have extensive deep root systems that enable them to survive in extremely arid habitats (Shreve 1951), and they are consequently wide spread throughout the desert (Roberts 1989). Palo verde species have bark biomass capable of photosynthesis (Adams and Strain 1969), hence, their common name (green tree in Spanish). Wild mesquite wood is intensively harvested, legally and illegally, for charcoal and timber industries. The two wild palo verde species are not harvested but are used in urban settings as ornamental plants that are propagated in nurseries. Because of their outstanding topsoil-holding capacity, these trees prevent soil erosion in their areas of growth. The three tree species are slow growers under native growth conditions.

We attempted to show that the growth of these trees can be enhanced by the use of treatments that previously proved to improve the growth of few desert plants, such as cacti, like inoculation with PGPB (Bashan et al. 1999; Carrillo-Garcia et al. 2000; Carrillo et al. 2002; Puente et al. 2004b), desert AM fungi (Bashan et al. 2000a; Bethlenfalvay et al. 1984; Cui and Nobel 1992; Carrillo-Garcia et al. 1999; Requena et al. 2001;), and the use of small levels of common compost (Bacilio et al. 2006). This has been done to demonstrate the feasibility of enhanced propagation of these plants under screenhouse conditions that are typical to commercial propagation of these trees for future reforestation of eroded desert lands. We have used two types of native microorganisms as inoculants, AM fungi propagated from resource island soil of the Southern Sonoran Desert (Bashan et al. 2000a; Carrillo-Garcia et al. Carrillo-Garcia et al. 1999) and *Bacillus pumilus*, originally isolated from cardon roots of this area (Puente et al. 2004a). This bacterium increased cardon growth in ground rock (Puente et al. 2004b) and also the growth of the freshwater microalgae *Chlorella* sp. (Hernandez et al. 2009). The nonnative diazotrophic bacterium used was the nonspecific PGPB *Azospirilum brasilense* Cd (Bashan et al. 2004).

Materials and methods

Organisms

Legume tree species used were: 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). Microorganisms used were the PGPB *Azospirillum brasilense* Cd (Bashan et al. 2004) and *B. pumilus* strain RIZO1 (EF123224, GenBank of National Center for Biotechnology Information, Bethesda, MD USA) (Puente et al. 2004a). The AM fungi used were a propagated mixture of *Glomus* sp. and unidentified native species found in resource islands under mesquite trees in the Southern Sonoran desert (Bashan et al. 2000a; Carrillo-Garcia et al. 1999).

Microbial cultivation

A. brasilense Cd and *B. pumilus* RIZO1 were cultivated on a trypton-yeast extract glucose medium supplemented with microelements (TYG) for 24 h at 30°C and 120 rpm (Bashan et al. 2002). The two bacterial species were formulated into a dry microbead inoculant preparation made of alginate (Bashan et al. 2002) using specialized equipment (http://www.bashanfoundation.org/bead.html, accessed 15 February 2009).

Production of AM inoculum

AM fungal inoculum used sorghum plants (*Sorghum bicolor* (L.) Moench) as a trap plant for propagation. Plants were cultivated in 10-l commercial plastic pots containing poor desert soil (Bashan et al. 2000a; Carrillo-Garcia et al. 1999). Resource island soil of high AM-fungal infectivity (Carrillo-Garcia et al. 1999) was the inoculum source. Plants were cultivated in a screenhouse at ambient conditions of the Sonoran desert at light intensities approximately one half of full sunlight (1,000 μmole photon m^{-2} s^{-1}) for 6 months and irrigated with tap water when necessary to prevent desiccation. They were fertilized once with 1.5% NPK commercial garden fertilizer but with low P content (0.1%) to enhance AM fungal growth (R. Linderman, personal communication). The plants were senescent at harvest. At harvest, analysis of the roots for the number of spores and AM fungal infection, presence, and frequency was done by the method of measurement of length in random arrangements of lines (Marsh 1971) and by root staining (Vierheilig et al. 1998). Upon excising the stems, the rooted soil clumps were air-dried for 2 weeks before being crumbed for spore counts. Spore numbers were determined by wet-sieving (45-, 75-, 100-, and

200-μm sieve openings), decanting, and sucrose-gradient centrifugation (Brundrett et al. 1994) of the soil samples. Colonization of root fragments used in the inoculum was 54.5%.

Compost

The common dairy-wheat compost used was produced for cultivation of cardon cactus and its composition was described earlier (Bacilio et al. 2006). It was applied at the rate of 1:8 (compost/soil, *v*/*v*).

Preparation of inoculants

Bacterial inoculant made of alginate microbead was attached to the seeds of wild trees as described for wheat plants (Bashan et al. 2002) in the screenhouse experiment 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*. AM inoculant was prepared as follows: after propagation of AM fungi in sorghum roots, roots were separated from the soil. The soil was saved, and the roots were cut into small pieces (<0.5 cm). Then the root pieces were mixed again with the same soil. A mixture of soil and root (213 g) was used to inoculate each pot of the legume trees. The inoculant was placed around the root system of the plants, and the rest of the pot volumes were filled with field soil.

Collection of seeds

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, Baja California Sur, Mexico (24°07′36″ N, 110°25′48″ W) in July 2003 and kept in hermetically sealed boxes at ambient temperature until use (Puente and Bashan 1993).

Screenhouse cultivation

Legume trees were grown in black plastic commercial tubes with drainage for growing plants (50×10 cm in diameter) each containing 2.5 kg soil. Dead mineral soil was collected from desert sites bare of vegetation to minimize its microbial content. It was not autoclaved to avoid possible deleterious effects, such as Mn toxicity. The soil was used sieved to 1 mm (Tyler equivalent 16 mesh No.18 USA standard testing sieve). Seeds were washed with 2% Tween 20 (Polyoxyethylene-sorbitan-monolaurate; Sigma, St. Louis MO, USA) under constant agitation for 5 min, thoroughly washed with tap water, disinfected in 1% (the two palo verde species) and 3% (mesquite) commercial NaOCl under constant agitation for 5 min, thoroughly rewashed with sterile tap water, and soaked in water in a steel strainer at 55°C for 2 min (mesquite) and boiling water for 1 min for the two species of palo verde (Scott 2006). Seeds were germinated on large Petri dishes with moist, sterile filter-paper towels about 1 cm apart and incubated in the dark at 33°C in a growth chamber (Conviron, Model 125L, Manitoba, Canada). Defective seedlings were discarded. Healthy seedlings were transferred to large test tubes (12.5 cm long, 1.5 cm in diameter) containing 10 ml of sterile distilled water for 14 days until they were about 10 cm tall. Seedlings of similar size were planted in pots. All other seedlings were discarded.

Each pot contained initially five seedlings. After 1 month, the pots were thinned to one plant per pot intending to obtain similar sized seedlings in naturally variable native plants. A total of 50 pots per plant species were used (ten per treatment in a completely randomized layout). All plants were grown in a screenhouse on elevated metal net beds at the ambient temperature (15–35°C, night/day) irrigated with tap water twice a week (small plants) and later three times a week. No water stress was imposed on these plants to avoid wilting throughout the experiment and a single fertilization (commercial 0.5% NPK 18:4:18) was given after 10 days. Each experiment (using one tree species) was conducted separately. The three experiments were maintained for 10 months each. Chemicals used for foliar pest control were nonsystemic to avoid influencing the treatments by translocation to the roots. Their use was necessary in these long-term experiments to control the sweet potato whitefly *Bemisia tabaci* (Gennadius), and ants (Hormiga Arriera; *Atta mexicana* Smith). This was done after 3 months of cultivation using a concentration of 1 ml l^{-1} of each of the following insecticides: "Naturales-L" (Troy Biosciences, USA) then with a mixture of Previcur N (Bayer CropScience, Chile) and Derosal (Bayer, Mexico). Second and third applications were given at 10 and 25 days later, respectively. Fumigation was done directly to the leaves avoiding contact with the soil after covering the soil surface with black plastic film. Cover was removed only after insecticides dried out. Fumigations were of low volume and were restricted to the foliage.

Measurement of plant parameters

The plant parameters measured were plant height, trunk diameter (0.5 to 1 cm above soil level; Bowers and Turner 2001), number of developing branches, and survival after 150 days and additional measurement after 300 days. At the end of the experiments after 10 months, dry weight (40°C, 72 h) of foliage was determined (Bashan and de-Bashan 2005b). After 270 days of cultivation, the following gas-exchange parameters were measured using a portable Porometer LI-1600 (LI-Cor, Lincoln, Nebraska, USA):

diffusive resistance (seconds per centimeter), and transpiration (microgram per square centimeter per second). These measurements were done only on mesquite amargo and yellow palo verde because the leaf structure of blue palo verde (needles) was incompatible with the equipment used.

Experimental design and statistical analysis

Screenhouse experiments were conducted in a completely randomized design, one tree per pot and a total of ten trees per treatment and 50 trees per experiment. The treatments were: inoculation with AM fungi, inoculation with PGPB, soil supplement with compost, all the three treatments combined, and nontreated control trees. A wooden construction ensured equal distance between the pots to provide similar competition for space and light when the trees grew larger.

All experiments were analyzed statistically and were repeated. After normalization of the data, results of all experiments were analyzed by one-way ANOVA and then by Tukey's HSD post hoc analysis at the significance level of $P \leq 0.05$. Data in percentage were converted to arcsin before analysis. All statistics use Statistica software (Statsoft™, Tulsa, OK, USA).

Results

Effect of inoculation with PGPB and AM fungi on plant form and function

The height of trees was not promoted in the three tree species apart from a small but significant ($P \leq 0.05$) increase in mesquite amargo treated with AM fungi. Addition of compost reduced plant height in all species (Fig. 1a). Mesquite amargo responded positively to all treatments by increasing the number of branches per tree. Yellow palo verde responded positively only to addition of compost or the combined treatment, while blue palo verde did not respond positively to any treatment (Fig. 1b). Only the compost treatment affected stem thickness of the two palo verde species as did the combined treatment for yellow palo verde (Fig. 1c). Survival of all mesquite amargo trees, untreated control trees included, was almost 100%. Similar survival occurred with control trees of blue palo verde or those treated with AM fungi. Untreated yellow palo verde survived less well (about 80%); therefore, application of compost, AM fungi, and all the treatments combined significantly enhanced survival (Fig. 1d). When all the trees were harvested, only the dry weights of mesquite amargo (in all treatments) and yellow palo verde (in combined treatment) were significantly increased (Fig. 1e). Several of the treatments had small negative but significant ($P \leq 0.05$) effects on plant growth and none of the treatments, except those of AM fungi on trunk thickness, had a positive effect of blue palo verde trees. When another identical evaluation of these parameters was done after 300 days of growth, no difference in survival and the number of branches was detected with only minimal increase in plant height (data not shown).

Effect of inoculation with PGPB and AM fungi on leaf gas exchange of mesquite amargo and yellow palo verde trees

Treatments with PGPB, AM fungi, and compost-affected leaf gas exchange in these two tree species. In yellow palo verde, inoculation with AM fungi reduced transpiration and increased diffusive resistance over untreated control trees (Fig. 2). PGPB and compost amendment had the opposite effect; they reduced diffusive resistance and increased transpiration (Fig. 2). The combined treatment had no effect on gas exchange.

A different pattern was observed in mesquite amargo where compost increased diffusive resistance and had no effect on transpiration. This effect was opposite to that in yellow palo verde. AM fungi increased transpiration and reduced diffusive resistance (also opposite to what was observed in yellow palo verde). Inoculation with PGPB had no effect, and combined inoculation created similar effects as inoculation with AM fungi (Fig. 3). It was noted that transpiration rates in yellow palo verde were much higher than those in mesquite amargo.

Discussion

Reforestation of severely degraded areas of the Sonoran Desert with shrubs, trees, and cacti is always difficult and, in many cases, unsuccessful (Bashan et al. 1999; Bean et al. 2004). This happens because the nurse tree system governing natural revegetation in deserts is often destroyed; the topsoil together with its beneficial microorganisms is eroded by wind and water; organic matter is scarce; and water, by default, is usually in short supply. Therefore, any attempt to restore a desert with trees and long-lived cacti should also consider to restore the beneficial microflora associated with these plants and to provide some source of organic matter (Bacilio et al. 2006; Grandlic et al. 2008).

Although all trees share the same habitat, they responded differently to the various treatments. Because height was not a good parameter for evaluation for any of the species, an increase in stem diameter is an indication of the good health of these trees (Bowers and Turner 2001) as was demonstrated for some treatments of mesquite amargo and yellow palo verde. On the other hand, the other two species showed growth-promotion effects such as an increase in the

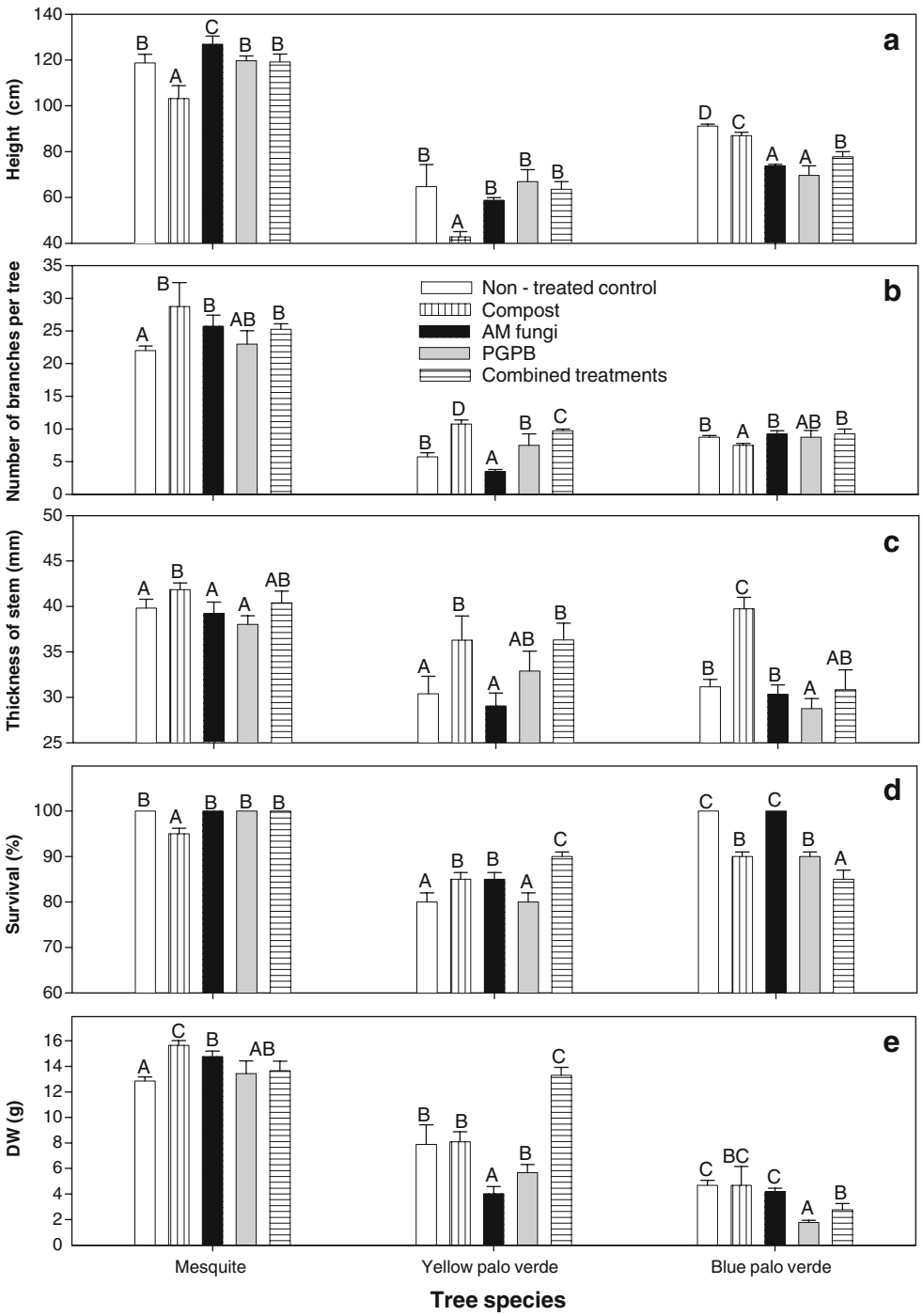

Fig. 1 Effect of inoculation with PGPB and AM fungi and supplementation of compost on growth parameters of three native legume trees in a screenhouse. Each group of *columns separately denoted by different letters* differ significantly at $P \leq 0.05$ using one-way ANOVA. *Bars* represent standard errors. **a** Height. **b** Number of branches per tree. **c** Thickness of stem. **d** Survival. **e** Dry weight

number of branches and dry weight in response to different treatments, while survival was relatively high (>80%) for all trees. Mesquite amargo was the most robust plant tested; almost all plant survived the growing season. It also responded better to inoculation and compost treatments. Therefore, it should be considered as a candidate for reforestation trials in the field even if it is considered a pest in rangeland by cattle ranchers in the southern USA but not in Mexico. Because both species of palo verde have high ornamental value and public acceptance, albeit one species responded less than mesquite and the other did not respond at all, they nevertheless merit further long-term evaluation upon transplanting to the field. This study demonstrated that native desert trees respond to inoculation with growth promoting microorganisms in a manner resembling agricultural crops and cacti (Bashan and

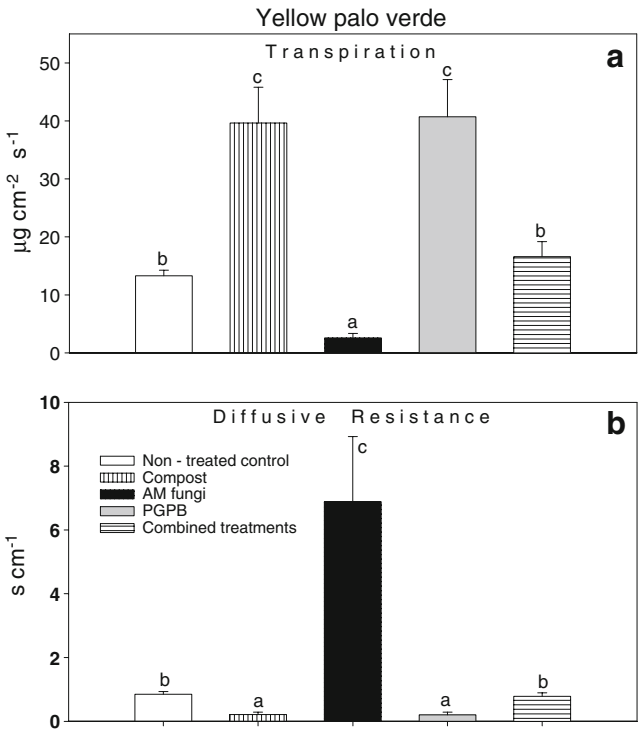

Fig. 2 **a**, **b** Effect of inoculation with PGPB and AM fungi and supplementation of compost on transpiration and diffusive resistance of yellow palo verde leaves. *Columns denoted by different letters* differ significantly at $P \leq 0.05$ using one-way ANOVA. *Bars* represent standard errors

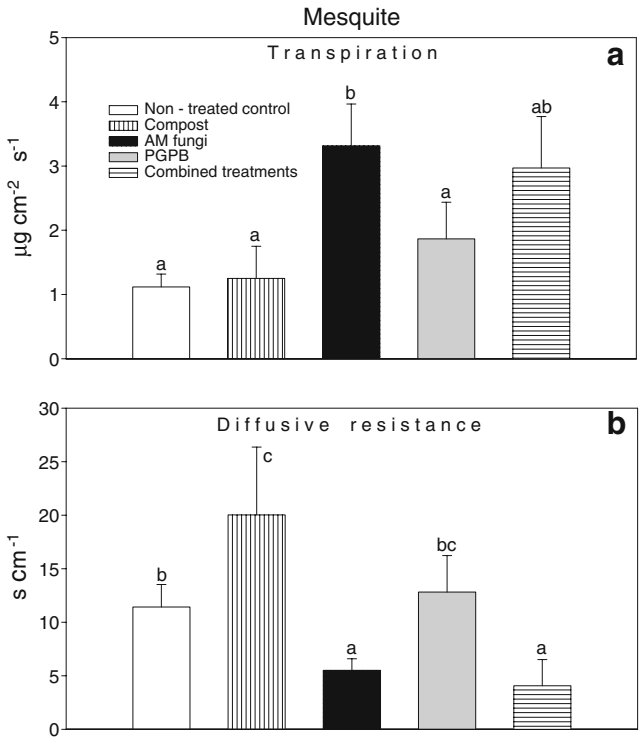

Fig. 3 **a**, **b** Effect of inoculation with PGPB and AM fungi and supplementation of compost on transpiration and diffusive resistance of mesquite amargo leaves. *Columns denoted by different letters* differ significantly at $P \leq 0.05$ using one-way ANOVA. *Bars* represent standard errors

de-Bashan 2005a); therefore, these technologies are worth further evaluation and can be developed into screenhouse production schemes for these plants.

Although *P. articulata* used in this study is known for its salt and drought resistance (Felker et al. 1981), production of significant biomass under desert conditions (Felker et al. 1983), and as an excellent nurse tree of the Southern Sonoran Desert (Carrillo-Garcia et al. 1999), one should note that this species, and also yellow palo verde, are very spiny plants at young age. Perhaps this technology should be also appropriate for other less spiny mesquite species of other deserts. Additionally, these experiments were carried out in eroded desert soil having very low microbial populations (Bashan et al. 2000a) and soil-borne pathogens are not known as a limiting growth factor for these trees. Thus, the addition economical burden of soil sterilization is unjustified for a nursery. Consequently, other soil microbes such as native rhizobia may interact with the legume trees. Although a possibility to consider for future studies, these potential effects were not evaluated in this study.

When the two responding trees—mesquite and yellow palo verde—were evaluated for leaf gas-exchange capacity, they significantly differed in their response although both are drought resistant. Transpiration is a common parameter to measure leaf gas exchange. Lower rates of transpiration are due to a leaf water deficit-related closure of the stomata which control diffusive resistance. Leaf diffusive resistance provides an index of the permeability of the leaf to a given gradient of carbon dioxide or water vapor concentration and thus is used to refer to either the photosynthetic or the hydrological characteristics of the plant (Grace et al. 1975). In nature, leaves of palo verde form during the rainy season and are shed in the dry season to conserve water (Barth and Klemmedson 1986; Whittaker and Niering 1975). When water shortage becomes extreme, palo verde drops its leaflets and twigs but not mesquite (Bowers and Turner 2001). This may explain the large difference in transpiration rates between the two plant species. Historically, it is known that a yellow palo verde (*P. microphylla* formerly known as *P. torreyana*) has high transpiration rate possibly because its leaf structure continuously losing water (Spalding 1906).

Azospirillum spp. and other PGPB are known for the alleviation of water stress in plants (Bashan and Dubrovsky 1996; Creus et al. 1996). *Azospirillum* spp. is especially effective on plants during droughts (Sarig et al. 1992) and so AM fungi (Bethlenfalvay and Lindeman 1992; Levy and Krikun 1980; Perry et al. 1987). Consequently, one of their modes of action is participation in water translocation in plants (Augé 2001, 2004; Bashan et al. 2004). A plausible

explanation why the combination of inoculation with PGPB, compost, and AM fungi did not enhance transpiration in yellow palo verde may be that PGPB and compost vs. AM fungi induced similar opposite transpiration reactions by the plants and consequently cancel one another. While in mesquite, the response of transpiration to AM inoculation was higher than that of PGPB and, therefore, when inoculated together, the combined treatment performed similar to AM inoculation alone.

In sum, the use of AM fungi, PGPB, and compost are parameters that can affect the propagation of some native trees destined for reforestation and positively but selectively can enhance them. The physiological effect of these treatments was on leaf gas exchange.

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