Water versus spacing: A possible growth preference among young individuals of the giant cardon cactus of the Baja California Peninsula

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ABSTRACT

Mature columnar cardon (Pachycereus pringlei) and saguaro (Carnegiea gigantea) cacti sometimes grow in very dense stands without apparent effect on growth; their seedlings and young plants are commonly found in clusters under legume nurse trees. The potential preference between space and water of young cardon was quantitatively measured under controlled environments for 30 months. The assessment used two types of experiments, one with different plant densities and the other of two plant densities combined with different irrigation regimes. Increases in population density reduced height and dry weight of the plants, but increased their volume and hydration; the water potential of the plants and the soil was less negative for denser populations. Addition of water above the minimum moisture required for growth made water potential less negative in plants and soil. The denser the population in a pot, the less soil surface was exposed to hot air. We conclude that water evaporation from soil surface from exposure to hot air during cultivation of this cactus was significantly reduced when the population density increased. Since loss of soil water from transpiration by cacti is very limited, evaporation directly from soil surface becomes dominant. With less evaporation under high plant density (shading), more water remains in the plant-soil system to be available for storage in the plant tissue.

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1. Introduction

The two largest columnar cacti of the Sonoran Desert, the giant cardon (*Pachycereus pringlei*) of Baja California and the saguaro (*Carnegiea gigantea*) of Arizona, visibly dominate the landscape and sometimes grow in crowded stands. In many instances, two or several large cacti are growing almost attached to each other for decades or centuries without showing visible signs of stress or any visible effect on their size, compared to the nearby separate cacti of the same species (Fig. 1; McAuliffe and Janzen, 1986; Turner et al., 1966). This happens in a desert that is characterized as an environment with low resources for plant growth that prevents dense plant cover of any species.

The giant cardon cactus is the most massive of all cacti. It is the keystone plant of the southern part of the Sonoran Desert in the Baja California Peninsula, responsible for large scale soil stabilization (Bashan et al., 1999, 2009; Carrillo-Garcia et al., 1999) and soil formation (Bashan et al., 2002; Puente et al., 2004) allowing other desert plants to establish and grow. As a young seedling,

it is relatively small, develops very slowly, and usually needs the support of a mesquite tree in a resource island under its canopy, mostly in initial, crowded stands (Carrillo-Garcia et al., 1999; Bashan et al., 2000a; Suzán-Azpiri and Sosa, 2006). Most seedlings, as is common for most desert cacti, do not survive the first year after germination (Gulmon et al., 1979). The southern Sonoran Desert environment also has numerous seed-eating rodents and long drought periods that affect survival. Early in its life cycle, it is a barrel-shaped seedling that later changes into a columnar form that can reach 10 m, with a few specimens reaching 20 m. The spatial pattern of young (Bashan et al., 2000a), but mainly adult cardon stands, is documented (Medel-Narvaez et al., 2006; Suzán-Azpiri and Sosa, 2006), as are patterns of distribution (open spaces or under the canopy of a nurse plant) of several other columnar cacti in American deserts (Gulmon et al., 1979; Nobel, 1988; Drezner and Lazarus, 2008). However, the distribution of very young seedlings of cardon in their first year of growth under their nurse tree is not, to the best of our knowledge, quantitatively documented.

The relationship of pattern of distribution of columnar cacti and available water for the growing seedlings indicates positive and negative influences. Under the nurse tree and because of the shade more water is potentially available to all plants growing there (Bashan et al., 2000a; Carrillo-Garcia et al., 2000b). Yet, competition with the mature and far larger nurse tree for

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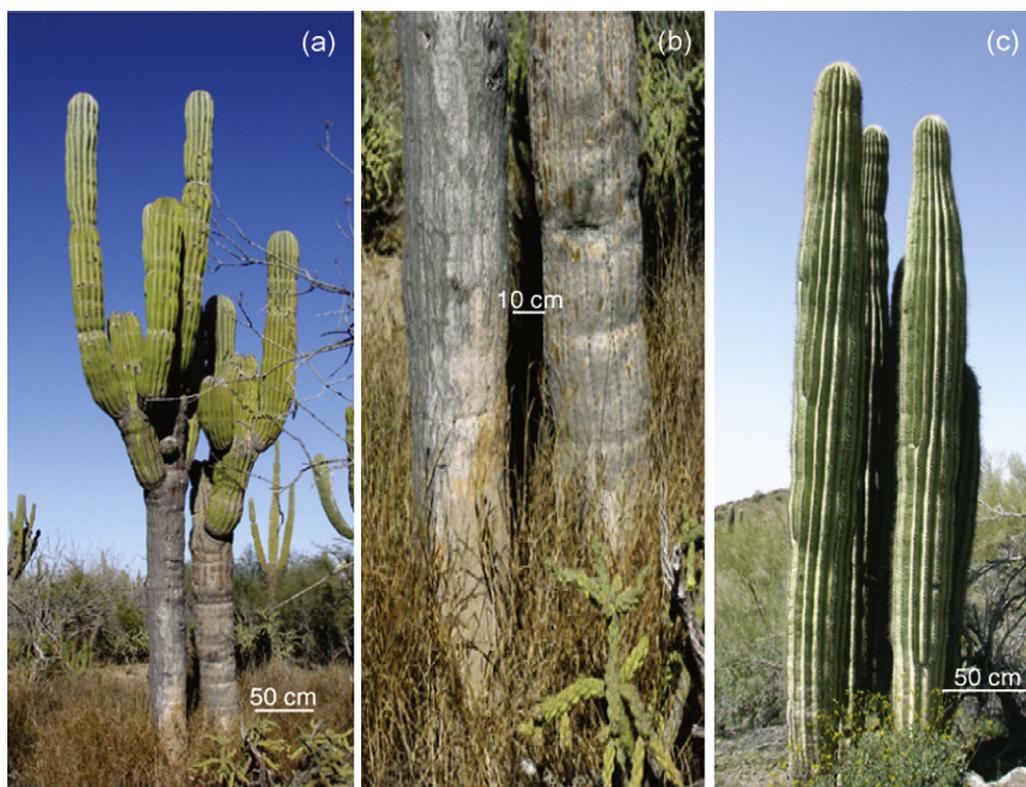E-mail address: bashan@cals.arizona.edu (Y. Bashan).

Fig. 1. Mature columnar cacti growing in close proximity: (a) two mature giant cardon in the El Comitan federal reserve, La Paz, Baja California Sur, Mexico, (b) close-up of the trunks, (c) five saguaro cacti in Saguaro National Park near Tucson, Arizona. (This figure is presented as a reference for supporting the hypothesis and is not part of the data of this study.)

water markedly reduces growth of nursling seedlings (Franco and Nobel, 1989). Furthermore, this competition may result in a drier environment (lower dew point temperature) under the canopy (Drezner, 2007). Facilitation through improvement of water conditions is known for some desert plants and are also known for dune vegetation, Mediterranean scrubland, tropical savanna, salt marsh, tundra, and temperate grasslands and forests (for reviews: Callaway, 1995; Holmgren et al., 1997), but not for cacti.

This study explored the underlying causes for aggregation and non-random distribution of adult columnar cacti observed in the field among several columnar cactus species (Hutto et al., 1986; Franco and Nobel, 1989; Drezner, 2006). Distribution of these cacti was explained by the existence of islands of favorable soil conditions (Turner et al., 1966; Carrillo-Garcia et al., 1999, 2000a,b), facilitation by nurse plants (McAuliffe, 1984; Franco and Nobel, 1989; Medel-Narvaez et al., 2006) and dispersal of seeds by animals (Nobel, 1988). These options are not mutually exclusive. In this study, an additional option is explored: aggregation of seedlings reduces the fraction of exposed soil and the overall water loss is reduced because evaporation from soil is more important than plant transpiration for water balance at these arid ecosystem dominated by this cactus species. We experimentally tested this mechanical hypothesis, based on earlier quantitative measurements of cardon seedlings growing under a nurse tree (Bashan et al., 2000a; Carrillo-Garcia et al., 1999) and field observations (Fig. 1). We suspected that the initial intraspecific crowded growth of seedlings provides an advantage for acquisition and conservation of scarce water. High density may allow new seedlings to endure the first critical drought and consequently allows successful establishment in this desert, especially in degraded soils. This was done by growing seedlings in natural degraded desert

soil at several densities and irrigation regimes under controlled conditions.

2. Materials and methods

2.1. Plants and soil type

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. The soil for growing plants was an eroded, barren desert soil that does not normally support perennial plant growth, including cardon (Bashan et al., 2000a; Carrillo-Garcia et al., 2000a). The alluvial soil contained 8% clay, 8% silt, and 84% sand; pH 8.1. Water-holding capacity is 12 mg kg^{-1}. Macronutrients (in mg kg^{-1}) are N (24), P (12), and K (620). The soil taken from the field was well stirred and sieved to obtain particles <2 mm to create a homogeneous substrate. This degraded, infertile soil was not able to support normal growth of cardons in the field and consequently, required supplements of organic matter and nutrients to allow extended growth of these plants (Bashan et al., 2009). Application of small amount of compost also relieved the need for fertilization during the long experimental period. Consequently the soil used in these experiments was amended with compost produced from dairy cow manure (ratio of 1:8, compost to soil, v/v) that was previously characterized (Bacilio et al., 2003). This amended soil contained (in mg kg^{-1}) N (2400), P (1100), K (1700) at pH 7.7 and water-holding capacity of 13.8% (Bacilio et al., 2006). We were aware that the addition of compost may indirectly change soil osmotic and physicochemical properties influencing water relations and hydrologic properties, including heating and evaporation rates. Yet, incorporation of compost was essential for plant growth. Because all treatments received the same low doses of

compost, we assumed that this amendment equally affects all treatments.

2.2. Plant growth conditions and planting densities

Cardon seeds were germinated at 25 ± 1 °C and 60% relative humidity by placing them on soil in a dark growth chamber (Conviron TC 16, Controlled Environments, Winnipeg, Canada) for 96 h. Seedlings were grown in 120-ml plastic pots containing 88 g of the processed desert soil. Pots did not have a drainage hole, leaving all water losses to evapotranspiration. The pots had been saturated with distilled water to water-holding capacity and then incubated in a walk-in growth chamber at $30–40 \pm 2$ °C, 40% relative humidity (normal growth conditions of these plants). This setup allowed control of temperature and evaporation in the growth chamber and normal growth of cardon without reaching extreme temperatures.

Equal-size seedlings (10 mm tall) were planted at 3 mm depth at the following densities; 1, 3, 6, 10, 20, 30, 37, and 45 individuals per pot. The number of individuals per pot was chosen to solely reflect increase in plant density. A second experiment to evaluate different water regimes was planted at two densities, 3 and 30 seedlings per pot. Plants were incubated for 30 months to assess the effect of density and 18 months to assess the effect of watering regime. Visually, no differences between the central and peripheral plants were observed. At high plant densities, sometimes a few plants in the center of the pot died possibly as a result of overcrowding. The reported data represent only the remaining live plants.

2.3. Irrigation

In the density experiment, plants were irrigated at weekly intervals with 20 ml distilled water per pot until saturation of the substrate, but not in excess. There was no accumulation of water in the bottom of the pots. In the irrigation experiment, we applied 5, 10, or 20 ml distilled water per pot at weekly intervals.

2.4. Measurements of plant growth

After 18 months (for the water regime experiment) and 30 months (for the density experiment), all plants were measured with a digital caliper (Control Company, model 62379-531, Friendswood, TX) for height and stem diameter. We calculated plant volume in these cylindrical seedlings (Bashan et al., 1999). Data shown indicate the calculated volume of a single plant.

The plants were carefully removed from the soil. The roots from plants in each pot were excised and measured after gently washing 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 was then weighed with an analytical balance (Bashan and de-Bashan, 2005). Each weight measurement indicated the calculated volume of a single plant in a pot. Root and shoot dry weight were measured in the first experiment and only shoot dry weight was measured in the second experiment because the roots were too small for accurate measurement.

Plant-free soil surface in pots was calculated after measuring the diameter of all the plants growing at each density (in four replicates) and subtracting it from the total soil surface area of the pot.

2.5. Water potential

Water potential of the homogenous soil and the plants was measured with a portable meter (model WP4, Decagon Devices, Pullman, WA). This instrument measured the sum of osmotic and matric potential of the sample. It measures water potential from 0 to −60 MPa with an accuracy of ±0.1% MPa from 0 to −10 MPa and ±1% from −10 to −60 MPa. Sample and instrument chamber temperature were carefully equalized.

2.5.1. Water potential of soil

The soil in every plastic pot, after removal of the plants, was immediately and manually stirred with a spatula under humid conditions equal to the growth chamber to prevent loss of water from the soil. Two samples of each replicate were then used for measuring water potential of soil; there were four replicates for each cardon density experiment. In the irrigation experiment, one sample of each replicate was used, for a total of 20 samples per treatment.

2.5.2. Water potential of plants

After removing the plants from the soil, we cut the spines and the root with a scissors. The cylindrical stem was then cut transversally into 1-mm thin section tissue layers with a scalpel. We then placed a tissue section in a disposable sampling cup, according to the instructions of the manufacturer. In the density experiment, we used two samples from each replicate. In the water regime experiment, we used one sample per replicate, except in the 5-ml irrigation treatment, in which the cardon were smaller and their tissue was not sufficient for the minimum sample required by the equipment. To make one measurement in this treatment, 1 or 2 pots containing 30 plants were used and in the density of three plants, six pots were used per measurement.

2.6. Experimental design and statistical analysis

Two types of experiments were done. In the plant density experiment, the plan had a random design, with four replicates for each plant density, where one pot served as a replicate. The control was natural, barren soil. This experiment lasted 30 months. In the irrigation experiment, we used a factorial design with three levels of irrigation and two cardon densities. The experiment had ten replicates for pots containing 30 cardon and 14, 16, and 18 replicates for pots with three cardon ($n = 1044$ plants per experiment). This experiment lasted 18 months.

All data were first normalized and the results were analyzed by ANOVA and LSD post hoc analysis at $P < 0.05$. The same data were used for linear regressions. All statistical analyses were performed with computer software (Statistica v. 6.0, StatSoft, Tulsa, OK). Graphical data are accompanied by standard error bars. Each experiment was repeated three times ($n = 608$ or 1044 plants per experiment, respectively). Detailed analyses were done for a single trial in the density and irrigation treatment.

3. Results

3.1. Survival of cardon seedlings under increasing plant density

Plant density up to 10 seedlings per pot had no negative effect on the survival rate of the cacti for the 30-month duration of the experiment. All plants survived. Higher initial plant densities (20–45 plants per pot) reduced survival at the end of the experiment to a small degree, where survival rates were: for 20 seedlings per pot, $93.75\% \pm 2.39$; for 30 seedlings, $91.66\% \pm 3.47$; for 37 seedlings, $90.5\% \pm 3.4$; and for 45 seedlings $87.7\% \pm 4.3$.

3.2. Effect of initial plant density on development of cardon seedlings after 30 months

A single plant growing in a pot always had superior growth characteristics to pots containing more than one plant, as determined
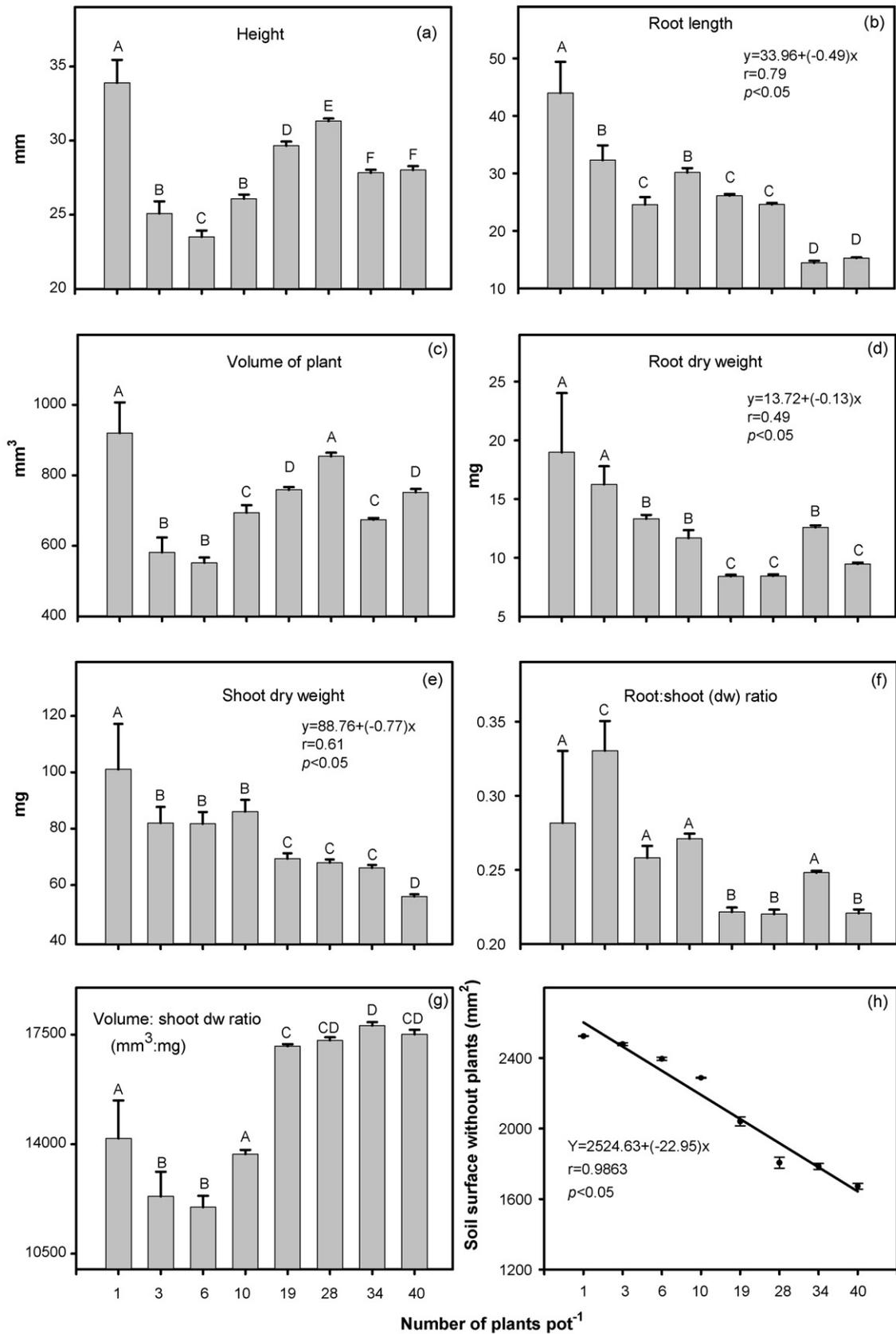
Fig. 2. (a–e) Effect of plant density on development of cardon seedlings after 30 months. (f–g) Correlation between plant parameters. (h) Correlation between soil surface without plants and actual plant density. Number of plants (*x*-axis) corresponds to the number of surviving plants after 30 months. Columns, in each subfigure, denoted with a different letter, differ significantly by one-way ANOVA and the LSD post hoc test at $P < 0.05$. Bars represent SE. Linear correlations in each subfigure for each plant density are presented only as equations and their *r* value for clarity. All correlations were significant at $P < 0.05$.

Table 1
Effect of initial plant density on water potential of cardon seedlings (a) and the potting soil (b) after 18 months. Values, in each column, with a different letter, differ significantly by ANOVA and LSD post hoc test at $P < 0.05$. ± represents standard error.

Plants per pot	Water potential (MPa)	
	Plant	Soil
1	$-0.99 \pm 0.04a$	$>-60a$
3	$-0.90 \pm 0.11a$	$>-60a$
6	$-0.60 \pm 0.10b$	$>-60a$
10	$-0.45 \pm 0.06bc$	$>-60a$
19	$-0.33 \pm 0.05c$	$-53.82 \pm 12.98b$
28	$-0.36 \pm 0.08c$	$-45.54 \pm 13.94bc$
34	$-0.26 \pm 0.05c$	$-25.05 \pm 8.66c$
40	$-0.39 \pm 0.08bc$	$-48.46 \pm 6.74b$

by measurements of height, volume, root length, and dry weight of roots and shoots (Fig. 2a–e; ANOVA analyses). Notwithstanding, increases in plant density improved height and volume of the plants up to a density of 28 surviving seedlings per pot (Fig. 2a and c; ANOVA analyses), while linearly decreasing root length and dry weight of roots and shoots (Fig. 2b, d and e; ANOVA analyses and linear regression analyses). Root:shoot ratio (dry weight) decreased for densities of three to 19 plants per pot and was lower at higher densities (Fig. 2f). Volume:shoot ratios showed the opposite trend, with 19 plants per pot as the inflection point and the ratio stayed high afterwards (Fig. 2g). These measurements of growth are comparable to measurements of normal growth of cardon seedlings under nature conditions (Suzán-Azpiri and Sosa, 2006).

Seedlings of cardon have a barrel shape with many long, dense spines (Vazquez-Yanez, 1997). Each seedling covers part of the soil surface, reducing evaporation from the surface of the pot. A linear and significant direct negative correlation was found between the area of the plant-free, unshaded soil surface and plant density, with higher density, the area of plant-free, unshaded soil surface was less (Fig. 2h). The difference in plant-free, unshaded soil surface between the high-density pots (40 plants per pot) and the pots with one plant was 33.39% (average of 1700 mm^2 versus 2500 mm^2). The enhanced shading of the dense spines was not measured, but was observed.

3.3. Effect of initial plant density on water potential of seedlings and the potting soil after 18 months

Water potential of seedlings increased linearly (less negative) with increasing densities of seedlings from one (highest) to 19 (lowest) and remained stable at higher densities (Table 1). The water potential of the soil was less negative up to densities of 34 plants per pot (Table 1).

3.4. Effect of irrigation on plant growth in low and high density plantings

As expected, higher levels of irrigation over 30 months linearly and significantly increased plant growth of the two tested plant

densities, affecting height, volume, and dry weight (Fig. 3a–c; linear regression analyses). For the lowest irrigation regime (5 ml weekly), plant density had no effect for any plant parameter (Fig. 3a–c; ANOVA analyses). Irrigation with 10 and 20 ml of water each week significantly increased plant height at the lower density (Fig. 3a; ANOVA analyses, comparison of pairs at each irrigation level). At the lower plant density with increasing irrigation, plant volume significantly increased (Fig. 3b; ANOVA analyses, comparison of pairs at each level of irrigation). Increased irrigation, up to 20 ml water, increased the dry weight of the plants, but this was independent of the plant density (Fig. 3c; ANOVA analysis). The volume:shoot ratio (dry weight) significantly increased with the higher level of irrigation (to 10 ml weekly); this was also more significant for plants in the low density treatment. Higher levels of irrigation, up to 20 ml weekly had no effect on the volume:shoot ratio at high plant density and a negative effect on low plant density (Fig. 3d; ANOVA analyses, comparison of pairs at each irrigation level).

3.5. Effect of increased irrigation on water potential of plants and potting soil at low and high plant densities

Higher levels of irrigation had significant effects on water potential of plants and soil, since both were more hydrated (Table 2). The lowest level of irrigation had a greater negative water potential in plants and soils. Plants were significantly more hydrated with irrigation up to 10 ml weekly, but doubling this level had no additional effect on hydration. The density of the plants had no effect on the water status of the plants at higher levels of irrigation (Table 2; ANOVA analysis). The water potential of the soil was less negative with increased irrigation and was significantly less negative for the higher plant density (Table 2; ANOVA analysis, comparison of pairs at each irrigation level). Survival of the plants after 18 month decreased in pots with 30 cardon receiving 5 ml of water weekly (survival of 78% ± 5.19); at 10 ml, survival was 50% ± 4.36; and at 20 ml, survival was 82.30% ± 2.71.

4. Discussion

This study assesses the fundamental question of the possible causes of aggregation of adult columnar cardon cacti observed in the field in relation to water availability and its conservation at the seedling stage. Competition among plants can be above ground for sunlight or below ground for available soil resources, including water (Van Auken and Bush, 1997; O'Brien et al., 2005; Weigelt et al., 2007). Below ground competition is the principal form of competition occurring in arid lands or other systems with extremely low plant densities (Fowler, 1986; Goldberg and Barton, 1992; Casper and Jackson, 1997). For resource-mediated competition below ground, a plant must have a negative effect on the availability of a below ground resource to which neighboring plants show a positive response in growth, survival, or reproduction (Goldberg, 1990). Nonetheless, several species of columnar cacti of the Sonoran Desert and even smaller cacti are capable of growing in dense stands for a long time and apparently are less affected by possi-

Table 2
Effect of two plant densities (3 and 30 plants per pot) and three levels of weekly irrigation (5, 10, and 20 ml per pot) on water potential of cardon seedlings (a) and the potting soil (b) after 18 months. Values in two columns (for plants and soil, separately) with a different letter differ significantly by ANOVA and the LSD post hoc test at $P < 0.05$. ± represents standard error.

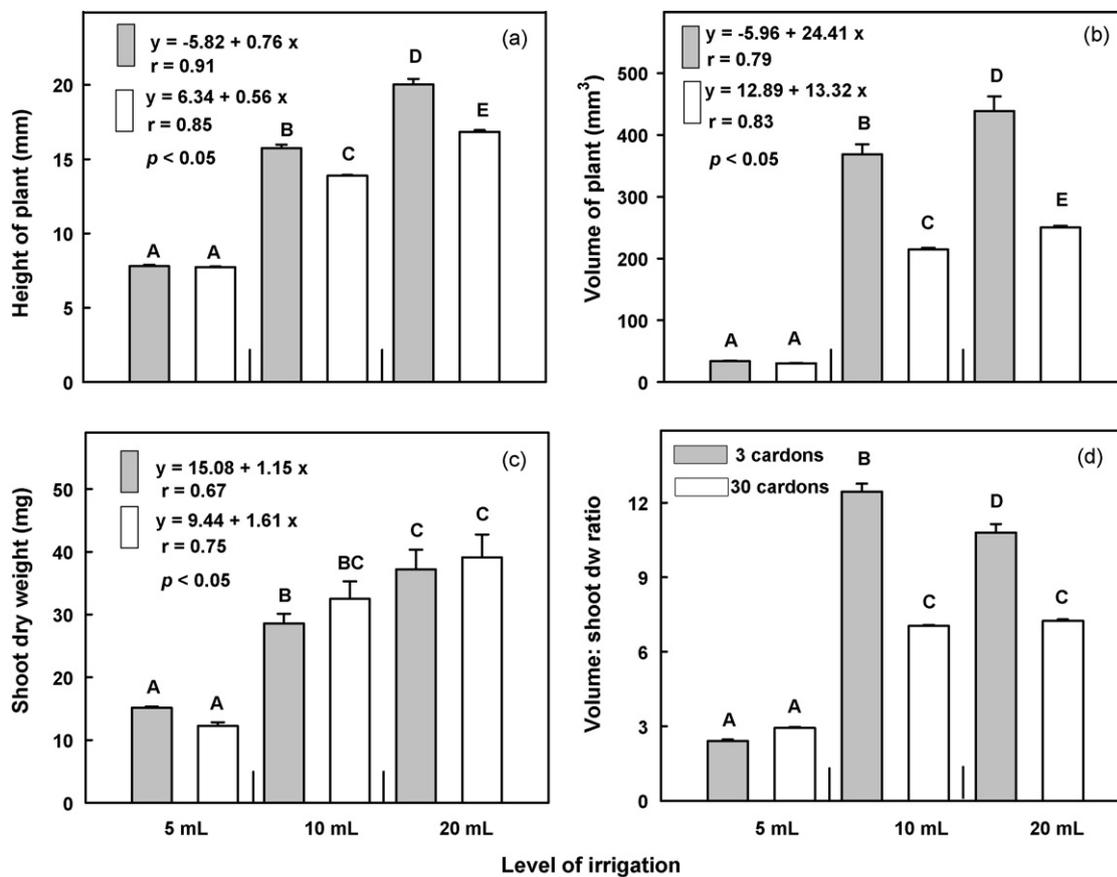| Irrigation per pot (ml)	Water potential (MPa)			
	Plants		Soil	
	3 plants	30 plants	3 plants	30 plants
5	$-4.09 \pm 0.76a$	$-3.21 \pm 0.54b$	$>-60a$	$>-60a$
10	$-0.91 \pm 0.11c$	$-0.55 \pm 0.05c$	$-20.59 \pm 1.15b$	$-6.08 \pm 0.76c$
20	$-0.57 \pm 0.09c$	$-0.57 \pm 0.06c$	$-1.47 \pm 0.14cd$	$-0.22 \pm 0.06d$

Fig. 3. Effect of two plant densities (3 and 30 plants per pot) and three levels of weekly irrigation (5, 10, and 20 ml per pot) on development of cardon seedlings after 18 months (a–c) and the ratio between volume and shoot dry weight (d). Columns with a different letter in each subfigure differ significantly by one-way ANOVA and the LSD post hoc test at $P < 0.05$. Bars represent SE. Linear correlations in each subfigure for each plant density are presented only as equations and their r value for clarity. All correlations were significant at $P < 0.05$.

ble competition of individuals of their own species; clusters of two to five large adult cacti, and many more in case of smaller cacti are commonplace (Fig. 1; López et al., 2009; Turner et al., 1966). Aggregation of many species of cacti seedlings under the canopy of nurse plants is the rule, rather than the exception (Bashan and de-Bashan, 2010; Valiente-Banuet and Ezcurra, 1991; Valiente-Banuet et al., 1991). This study demonstrated that this aggregating phenomenon can be reproduced and maintained for cardon cacti under controlled conditions for 2.5 years. All plants showed no signs of distress.

Commonly, competition is among different plant species, not among individuals of the same species. Classical models for agricultural crops and associated weeds demonstrate negative effect (Harper, 1977; Inouye and Schaffer, 1981; Park et al., 2003). In natural environments, and especially in arid lands, two major approaches to study plant communities prevail. (1) Studies of specific mechanisms, such as competition for available soil resources (Carrillo-Garcia et al., 2000a; Gebauer et al., 2002) and allelopathy (Rice, 1984). (2) Facilitation of growth on resource islands (Hunter and Aarssen, 1988; Valiente-Banuet and Ezcurra, 1991; Callaway, 1995; Carrillo-Garcia et al., 1999; Suzán-Azpiri and Sosa, 2006).

Facilitative and competitive mechanisms do not act in isolation from each other in nature and, as they are simultaneously occurring within the same community and even between the same individuals, they may produce complex and variable effects (Callaway and Walker, 1997; Holmgren et al., 1997). It is assumed that competition increases in importance in productive niches of the environment, whereas facilitation is more important under harsh environmental conditions, such as deserts, where most stud-

ies were conducted (Bertness and Callaway, 1994). In the desert, nurse plants, usually a shrub or tree that creates a soil resource under its canopy, are a major factor (Bashan and de-Bashan, 2010). Mature cardon serving as a nurse plant for younger cacti has not been reported and are uncommon in the southern Sonoran Desert (Bashan et al., 2000b). Consequently, young cardon commonly occur in relatively dense stands under the partial shade of the canopy of a mesquite tree (Bashan et al., 2000a; Carrillo-Garcia et al., 1999), similar to densities tested in the controlled experiments in this study.

To explore the relative roles of water and spacing (plant density), our strategy was to use seedlings growing under controlled conditions rather than wild population under natural conditions for the following practical reasons. (1) In nature, cardon are very slow growers (∼1–3 cm per year) and outlasting a typical human lifespan. With low mortality, this makes natural cardon populations impractical for precise experimentation of growth. (2) Cardon grows only during a very short and unreliable rainy season (∼1–3 months per year). (3) The natural habitat of cardon on the Baja California Peninsula has been overgrazed by livestock for four centuries, making it impossible to obtain pristine large stands of small, dense populations of cardon growing for years under undisturbed conditions, although groups of a very few mature cardon are commonplace. (4) Controlled conditions balance desert extremes of temperature and radiation and allow isolation of one factor, water in this study, from the other commonly associated variables used in competition studies in desert environments: nutrition, temperature, and light. The controlled setup included temperature kept at a normal high level of the desert, but without extreme episodes;

nutrients supplied at a slow rate by the addition of compost to nutrient-poor desert soil, and irrigation by pulse irrigation because this type of rainfall is common in the desert during the summer. As one major factor involved in competition is soil nutrients, addition of necessary small doses of compost, sufficient for the entire experimental period, reduced or eliminated its effect. Because all cardon were of similar size when planted, we eliminated size as a factor because this would introduce competition for light. Finally, the plastic pots limited water loss to evapotranspiration. This strategy allowed us to determine whether high-stand density is beneficial for young seedlings and its affect on the water status of the plant, which is a crucial parameter of survival of young cacti in the natural environment (Gibson and Nobel, 1986).

Normally, an increase in plant density results in lower survival and growth (Yeaton and Cody, 1976; Inouye, 1980; Phillips and MacMahon, 1981), but this is not the case for cacti. Cardon under controlled conditions had excellent survival and growth, comparable to growth rates of cardon under natural conditions (Gibson and Nobel, 1986; Nobel, 1988; Suzán-Azpiri and Sosa, 2006), although root development (length, weight and root:shoot ratio) was negatively affected with increased density. Similarly, for the cactus *Copiapoa cinerea* v. *columna-alba* of the Atacama Desert, which grow in extensive, relatively dense, monospecific stands, no evidence of competition from stand density was observed (Gulmon et al., 1979). According to Briones et al. (1998), in the Chihuahua Desert, competition among three dominant perennial species (a grass *Hilaria mutica*, a shrub *Larrea tridentata*, and a cactus *Opuntia rastrera*) is absent or very low in years of low precipitation.

We chose water relations of cacti as a facilitating factor because most plant ecologists working in arid lands assume that the principal form of competition among plants is competition for water and that limited water is one of the most important determinants of the ecological structure of desert plant communities (McAuliffe and Janzen, 1986; Weigelt et al., 2005). Perhaps because it seemed obvious and intuitive for so long (Spalding, 1905), the number of studies directly supporting this hypothesis is relatively low, mostly decades old (Turner et al., 1966; Nobel, 1977; Fonteyn and Mahall 1981; Robberecht et al., 1983; Ehleringer, 1984). Still, a large body of work has demonstrated that plants in arid regions are often under water stress. Irrigation or rainfall generally increases growth and survival rates, confirming that it is a limiting resource (Inouye et al., 1980). A reduction in the intensity of competition, in addition to increased plant size, survival, or fecundity is also associated with improvements in water status of plants (Fonteyn and Mahall, 1978, 1981; Phillips and MacMahon, 1981) or an increase in soil water content (Robberecht et al., 1983).

What we demonstrated is the crucial positive effect of high plant density of seedlings on water conservation of cacti. Although cacti at higher densities accumulated less biomass (dry weight), as was expected, each plant accumulated more water in their tissues and the adjacent soil was more hydrated. Further and indirectly, we demonstrated that the barrel shape of the cacti, at higher densities, acts as a reducer of evaporation from the soil surface, since less soil surface is exposed to hot air. Consequently, denser stands, at least under controlled conditions, conserve water in the soil for longer periods, which allows a longer period of growth for these slow-growing plants; hence, the seedlings receive an advantage over similar seedlings growing in drier soil. The need to increase the volume of seedlings, that is, more stored liquids, is fundamental for survival of young barrel cacti after germinating in the wet season and then facing with a long drought in their first year. Larger volume generally increases survival of the seedling (Gibson and Nobel, 1986). Calculation of ratios indicates possible translocation of resources (water) among plant parts (Bashan and Dubrovsky, 1996), in this case. The ratios of volume and dry weight demon-

strated that plants growing at higher densities have a volume advantage over those growing in low densities.

However, when the cacti mature after many years of growth, the effect of crowdedness might be negative. McAuliffe and Janzen (1986) found that water–plant interaction of mature saguaro cacti in the northern Sonoran Desert growing in a densely clumped distribution lowered the relative amount of stored water, rate of water uptake, apical growth, and reproductive patterns of individual saguaros and might influence patterns of its distribution and abundance. This happens because extreme water loss leads to death of saguaros during droughts, but precipitation is the key parameter allowing survival of seedlings and young individuals (Jordan and Nobel, 1982). Considering theoretical tradeoffs of early versus later-in-life, clustering helps when plants are young, despite negative effects when plants are older is still an open question for cardon cacti. In our controlled experiments, because cacti grow very slowly, the 2.5-year experiment did not reveal any negative effect on growth under crowded conditions.

This study cannot directly extrapolate or precisely explain real field conditions because it is likely that the soil can be extremely dry for prolonged periods and most growth occurs during the brief periods when subject to rainfall. During these short periods, soil evaporation is perhaps less important than the dense population of plant absorbing water during the dry periods that are present most of the year. At the typical locations where cardon and other cactus species grow under nurse trees, the soil retains more moisture for longer periods (Turner et al., 1966; Valiente-Banuet and Ezcurra, 1991; Valiente-Banuet et al., 1991; Carrillo-Garcia et al., 1999, 2000a,b; Bashan et al., 2000a), parallel to the prolonged growth conditions occurring in this study. Our results suggest that higher densities of seedlings and young cacti provide a possible mechanism that enhances survival and growth of this species of cactus.

In summary, higher plant densities facilitate the initial growth of cardon seedlings under controlled conditions by improving their water status by shading the soil surface and that close spacing is less important as a growth factor during the early stages of growth. The controlled experiments support the thesis that high plant density provides an advantage for initial growth of barrel-shaped, columnar cactus seedlings. Nonetheless, these results should be tested and re-evaluated under natural conditions.

Acknowledgements

References

Bacilio, M., Hernandez, J.-P., Bashan, Y., 2006. Restoration of giant cardon cacti in barren desert soil amended with common compost and inoculated with *Azospirillum brasilense*. Biol. Fertil. Soils 43, 112–119.

Bacilio, M., Vazquez, P., Bashan, Y., 2003. Alleviation of noxious effects of cattle ranch composts on wheat seed germination by inoculation with *Azospirillum* spp. Biol. Fertil. Soils 38, 261–266.

Bashan, Y., Davis, E.A., Carrillo-Garcia, A., Linderman, R.G., 2000a. Assessment of VA mycorrhizal inoculum potential in relation to the establishment of cactus seedlings under mesquite nurse-trees in the Sonoran Desert. Appl. Soil Ecol. 14, 165–176.

Bashan, Y., de-Bashan, L.E., 2005. Fresh-weight measurements of roots provide inaccurate estimates of the effects of plant growth-promoting bacteria on root growth: a critical examination. Soil Biol. Biochem. 37, 1795–1804.

Bashan, Y., de-Bashan, L.E., 2010. Microbial populations of arid lands and their potential for restoration of deserts. In: Dion, P. (Ed.), Soil Biology Series 21. Springer, Berlin, pp. 109–137 (Chapter 6).

Bashan, Y., Dubrovsky, J.G., 1996. *Azospirillum* spp. participation in dry matter partitioning in grasses at the whole plant level. Biol. Fertil. Soils 23, 435–440.

Bashan, Y., Gonzalez, L.E., Toledo, G., Leon de La Luz, J.L., Bethlenfalvay, G.J., Troyo, E., Rojas, A., Holguin, G., Puente, M.E., Lebsky, V.K., Vazquez, P., Castellanos, T., Glazier, E., 2000b. A proposal for conservation of exemplary stands of the giant cardon cactus (*Pachycereus pringlei* [S. Wats Britt. & Ross]) in Baja California Sur, Mexico. Nat. Areas J. 20, 197–200.

Bashan, Y., Li, C.Y., Lebsky, V.K., Moreno, M., de-Bashan, L.E., 2002. Primary colonization of volcanic rocks by plants in arid Baja California, Mexico. Plant Biol. 4, 392–402.

Bashan, Y., Rojas, A., Puente, M.E., 1999. Improved establishment and development of three cacti species inoculated with *Azospirillum brasilense* transplanted into disturbed urban desert soil. Can. J. Microbiol. 45, 441–451.

Bashan, Y., Salazar, B., Puente, M.E., Bacilio, M., Linderman, R.G., 2009. Enhanced establishment and growth of giant cardon cactus in an eroded field in the Sonoran Desert using native legume trees as nurse plants aided by plant growth-promoting microorganisms and compost. Biol. Fertil. Soils 45, 585–594.

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9, 191–193.

Briones, O., Montana, C., Ezcurra, E., 1998. Competition intensity as a function of resource availability in a semiarid ecosystem. Oecologia 116, 365–372.

Callaway, R.M., 1995. Positive interactions among plants. Bot. Rev. 61, 306–349.

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78, 1958–1965.

Carrillo-Garcia, A., Bashan, Y., Bethlenfalvay, G.J., 2000a. Resource-island soils and the survival of the giant cactus, cardon, of Baja California Sur. Plant Soil 218, 207–214.

Carrillo-Garcia, A., Bashan, Y., Diaz-Rivera, E., Bethlenfalvay, G.J., 2000b. Effects of resource - island soils, competition, and inoculation with *Azospirillum* on survival and growth of *Pachycereus pringlei*, the giant cactus of the Sonoran Desert. Restor. Ecol. 8, 65–73.

Carrillo-Garcia, A., León de la Luz, J.L., Bashan, Y., Bethlenfalvay, G.J., 1999. Nurse plants, mycorrhizae, and plant establishment in a disturbed area of the Sonoran Desert. Restor. Ecol. 7, 321–335.

Casper, B.B., Jackson, R.B., 1997. Plant competition underground. Ann. Rev. Ecol. Syst. 28, 545–570.

Drezner, T.D., 2006. Plant facilitation in extreme environments: The non-random distribution of saguaro cacti (*Carnegiea gigantea*) under their nurse associates and the relationship to nurse architecture. J. Arid Environ. 65, 46–61.

Drezner, T.D., 2007. An analysis of winter temperature and dew point under the canopy of a common Sonoran Desert nurse and the implications for positive plant interactions. J. Arid Environ. 69, 554–568.

Drezner, T.D., Lazarus, B.L., 2008. The population dynamics of columnar and other cacti: a review. Geog. Compass 2, 1–29.

Ehleringer, J.R., 1984. Intraspecific competitive effects on water relations, growth and reproduction in *Encelia farinose*. Oecologia 63, 153–158.

Fonteyn, P.J., Mahall, B.E., 1978. Competition among desert perennials. Nature 275, 544–545.

Fonteyn, P.J., Mahall, B.E., 1981. An experimental analysis of structure in a desert plant community. J. Ecol. 69, 883–896.

Fowler, N., 1986. The role of competition in plant communities in arid and semiarid regions. Ann. Rev. Ecol. Syst. 17, 89–110.

Franco, A.C., Nobel, P.S., 1989. Effect of nurse plants on the microhabitat and growth of cacti. J. Ecol. 77, 870–886.

Gebauer, R.L.E., Schwinning, S., Ehleringer, J.R., 2002. Interspecific competition and resource pulse utilization in a cold desert community. Ecology 83, 2602–2616.

Gibson, S.L., Nobel, P.S., 1986. The Cactus Primer. Harvard University Press, Cambridge, MA.

Goldberg, D.E., 1990. Components of resource competition in plant communities. In: Grace, J.B., Tilman, D. (Eds.), Perspectives on Plant Competition. Academic Press, San Diego, pp. 27–65.

Goldberg, D.E., Barton, A.M., 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. Am. Nat. 139, 771–801.

Gulmon, S.L., Rundel, P.W., Ehleringer, J.R., Mooney, H.A., 1979. Spatial relationships and competition in a Chilean desert cactus. Oecologia 44, 40–43.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, New York.

Holmgren, M., Scheffer, M., Huston, M.A., 1997. The interplay of facilitation and competition in plant communities. Ecology 78, 1966–1975.

Hunter, A.F., Aarssen, L.W., 1988. Plants helping plants. Bioscience 38, 34–40.

Hutto, R.L., McAuliffe, J.R., Hogan, L., 1986. Distributional Associates of the Saguaro (*Carnegiea gigantea*). Southwest Nat. 31, 469–476.

Inouye, R.S., 1980. Density-dependent germination response by seeds of desert annuals. Oecologia 46, 235–238.

Inouye, R.S., Byers, G.S., Brown, J.H., 1980. Effects of predation and competition survivorship, fecundity, and community structure of desert annuals. Ecology 61, 1344–1351.

Inouye, R.S., Schaffer, W.M., 1981. On the ecological meaning of ratio (De Wit) diagrams in plant ecology. Ecology 62, 1679–1681.

Jordan, P.W., Nobel, P.S., 1982. Height distributions of two species of cacti in relation to rainfall, seedling establishment, and growth. Bot. Gaz. 143, 511–571.

López, B.R., Bashan, Y., Bacilio, M., De la Cruz-Agüero, G., 2009. Rock-colonizing plants: abundance of the endemic cactus *Mammillaria fraileana* related to rock type in the southern Sonoran Desert. Plant Ecol. 201, 575–588.

McAuliffe, J.R., 1984. Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. Oecologia 64, 319–321.

McAuliffe, J.R., Janzen, F.J., 1986. Effects of intraspecific crowding on water uptake, water storage, apical growth, and reproductive potential in the Sahuaro cactus, *Carnegiea gigantea*. Bot. Gaz. 147, 334–341.

Medel-Narvaez, A., Leon de la Luz, J.L., Freaner-Martínez, F., Molina-Freaner, F., 2006. Patterns of abundance and population structure of *Pachycereus pringlei* (Cactaceae), a columnar cactus of the Sonoran Desert. Plant Ecol. 187, 1–14.

Nobel, P.S., 1977. Water relations and photosynthesis of a barrel cactus, *Ferocactus acanthodes*, in the Colorado Desert. Oecologia 27, 117–133.

Nobel, P.S., 1988. Environmental Biology of Agaves and Cacti. Cambridge University Press, Cambridge, UK.

O'Brien, E.E., Gersani, M., Brown, J.S., 2005. Root proliferation and seed yield in response to spatial heterogeneity of below-ground competition. New Phytol. 168, 401–412.

Park, S.E., Benjamin, L.R., Watkinson, A.R., 2003. The theory and application of plant competition models: an agronomic perspective. Ann. Bot. 92, 741–748.

Phillips, D.L., MacMahon, J.A., 1981. Competition and spacing patterns of desert shrubs. J. Ecol. 69, 97–115.

Puente, M.E., Bashan, Y., Li, C.Y., Lebsky, V.K., 2004. Microbial populations and activities in the rhizoplane of rock-weathering desert plants, I. Root colonization and weathering of igneous rocks. Plant Biol. 6, 629–642.

Rice, E.L., 1984. Allelopathy, 2nd ed. Academic Press, Orlando, FL.

Robberecht, R., Mahall, B.E., Nobel, P.S., 1983. Experimental removal of intraspecific competitors-effects on water relations and productivity of a desert bunchgrass, *Hilaria rigida*. Oecologia 60, 21–24.

Spalding, E.S., 1905. Mechanical adjustment of the sahuaro (*Cereus giganteus*) to varying quantities of stored water. Bull. Torrey Bot. Club 32, 57–68.

Suzán-Azpiri, H., Sosa, V.J., 2006. Comparative performance of the giant cardon cactus (*Pachycereus pringlei*) seedlings under two leguminous nurse plant species. J. Arid Environ. 65, 351–362.

Turner, R.M., Alcorn, S.M., Olin, G., Booth, J.A., 1966. The influence of shade, soil, and water on saguaro seedling establishment. Bot. Gaz. 127, 95–102.

Valiente-Banuet, A., Ezcurra, E., 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. J. Ecol. 79, 961–971.

Valiente-Banuet, A., Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Nunez, H., Barnard, G., Vazquez, E., 1991. Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. J. Veg. Sci. 2, 15–20.

Van Auken, O.W., Bush, J.K., 1997. Growth of *Prosopis glandulosa* in response to changes in aboveground and belowground interference. Ecology 78, 1222–1229.

Vazquez-Yanez, C., 1997. Extraordinary water administrators (Extraordinarias administradoras de agua). In: Valles Septien, C., Rodriguez Perez, L. (Eds.), *Suculentas mexicanas, Cactaceas*. CVS publicaciones, Mexico, pp. 49–53.

Weigelt, A., Schumacher, J., Walther, T., Bartelheimer, M., Steinlein, T., Beyschlag, W., 2007. Identifying mechanisms of competition in multi-species communities. J. Ecol. 95, 53–64.

Weigelt, A., Steinlein, T., Beyschlag, W., 2005. Competition among three dune species: the impact of water availability on below-ground processes. Plant Ecol. 176, 57–68.

Yeaton, R.I., Cody, M.L., 1976. Competition and spacing in plant communities: the northern Mohave desert. J. Ecol. 64, 689–696.