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Cacti–shrub interactions in the coastal desert of northern Sinaloa, Mexico

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Spatial patterns and replacement in ten cacti were studied on an island of the coastal desert of Sinaloa, México. Four platyopuntias had 74–92% of their individuals beneath shrub canopies, whereas three globose cacti, one columnar cactus and two cylindropuntias had similar or higher percentages of individuals in open spaces. This study advances the idea that open-space colonization is enhanced by less harsh physical and biotic conditions in coastal deserts, and by certain morphological and physiological adaptations of cacti. The absence of nurse-shrub replacement is understood as a result of induced co-existence by physical damage from cyclones in the coastal zone.

Keywords: coastal deserts; Sinaloa–México; cacti; nurse effect; stones

Introduction

The vegetation of dry environments in many parts of the world is made up of perennial shrubs more or less spaced, which facilitate recruitment of less stress-tolerant plants like cacti. These shrubs are referred to as 'nurse plants' due to the works of Niering *et al.* (1963), Turner *et al.* (1966, 1969) and Steenbergh & Lowe (1969). The restrictions imposed by water scarcity and high temperatures in this environments can be reduced by nurse-plant canopies (Patten, 1978; Smith *et al.*, 1987), as well as outcrops and stones (Steenbergh & Lowe, 1969; Danin, 1999). In addition, the shrubs can modify other environmental variables such as solar radiation (Franco & Nobel, 1989), soil fertility (García-Moya & McKell, 1970; Franco & Nobel, 1989; Cross & Schlesinger, 1999), mechanical injury and browsing (McAuliffe, 1984*b*; Suzán *et al.*, 1996).

Protection and habitat amelioration by shrubs are underlying causes of clumped distribution of cacti (Vandermeer, 1980; McAuliffe, 1984*a, b*), while negative

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interactions such as competition, browsing, and allelopathy may convert aggregated distributions of plants into random ones, and random distributions into regular ones (Fowler, 1986). Positive and negative interactions are hypothesized as predictable important forces which balance depends on gradients of physical stress and consumer pressure in several environments (Bertness & Callaway, 1994; Hacker & Gaines, 1997). It is suggested that positive interactions are frequent in communities developing under high herbivory and harsh environments, though many other variables like density, size, age, and physiology of interacting species may affect the balance too (Callaway & Walker, 1997). These conceptual ideas has been corroborated in rocky intertidal communities (Bertness *et al.*, 1999); some predictions are concordant in arid systems (Tewksbury & Lloyd, 2001), but other remain to be probed (Tielbörger & Kadmon, 2000).

Besides affecting the spatial pattern of species, positive plant–plant interactions have great potential for increasing biological diversity of plants (Búrquez & Quintana, 1994; Tewksbury & Petrovich, 1994), herbivores and their predators (Hacker & Gaines, 1997). Since woody perennials in dry zones enhance fertility and retain soil moisture, productivity is definitively higher under nurse-shrubs as compared to the open space matrix (Patten, 1978). Successional sequences were unrecognized in early works of desert communities, but during the last 20 years, several authors have pointed out that succession in dry environments occurs at the scale of individual plants by a combined effect of protection (nurse-plant syndrome) followed by a competitive pressure; the open areas in the interstices of the existent vegetation are colonized by highly stress-tolerant plants, later these species serve as sites of establishment for seedlings of several species; eventually, the mature nursed plants displace their benefactors by competition, producing an oscillatory behavior in the population dynamics which ends up in a cyclic succession (Yeaton, 1978; Vandermeer, 1980; McAuliffe, 1988; Yeaton & Esler, 1990; Cody, 1993; Flores-Flores & Yeaton, 2000).

The coastal deserts differ in many aspects from inland deserts. Temperatures tend to be less extreme, specially winter ones, and freezing temperatures are lacking. Furthermore, relative humidity is frequently higher, and water inputs from dew and fog may represent a significant contribution of the water budget for plant communities (Noy-Meir, 1973; Schemenauer & Cereceda, 1991; Vetaas, 1992).

The cacti–nurse association has been documented in the Sonoran and Chihuahuan deserts (Turner *et al.*, 1966; Yeaton, 1978; McAuliffe, 1984*a*, *b*; Yeaton & Romero-Manzanares, 1986; Franco & Nobel, 1989; Suzán *et al.*, 1996), the Tehuacán Valley in central México (Valiente-Banuet & Ezcurra, 1991; Valiente-Banuet *et al.*, 1991*a*, *b*), and the deciduous forest of Southern Baja California (Arriaga *et al.*, 1993); it has not been documented for coastal deserts, where the environment may produce structural/compositional and successional differences from inland deserts.

A shrubland site selected in the Mazocahui island in Topolobampo includes 11 out of 16 cacti registered for this location by Reyes-Olivas *et al.* (in preparation), and one unidentified platyopuntia. These cacti are the globose *Echinocereus sciurus* var. *floresii* (Backeberg) N. P. Taylor, endemic to Sinaloa and protected under NOM-059-ECOL-2000; *Mammillaria dioica* K. Brandegee; *M. mazatlanensis* K. Schuman, endemic to the Mexican Pacific coast; the giant globose *Ferocactus herrerae* González-Ortega; the columnar *Pachycereus pecten-aboriginum* (Engelmann) Britton & Rose and *Stenocereus thurberi* (Engelmann) Buxbaum var. *thurberi*; the cylindropuntias *Opuntia burrageana* Britton & Rose and *O. fulgida* Engelmann; the platyopuntias *O. rileyi* González-Ortega and *O. spraguei* González-Ortega, endemics to Sinaloa, *O. wilcoxii* Britton & Rose, and *Opuntia* sp. The nurse effect has been observed in *Echinocereus*, *Mammillaria* and *Ferocactus* (McAuliffe, 1984*b*; Franco & Nobel, 1989; Valiente-Banuet *et al.*, 1991*a*, *b*), *S. thurberi* (Arriaga *et al.*, 1993), in cylindropuntias (Cody, 1993) and platyopuntias (Yeaton, 1978; Yeaton *et al.*, 1983; Yeaton & Romero-Manzanares, 1986); however, some species growing in the coastal shrubland of Topolobampo, which are sheltered by shrubs in other dry zones (Cody, 1993; Arriaga *et al.*, 1993), appear to occupy the interstices among shrubs under more benign conditions.

The objective of this research is to evaluate the nurse effect for cacti in the coastal desert of northern Sinaloa, and to explore their relationships with soil factors such as depth, texture, temperature, moisture, fertility, pH, salinity, and water regime inputs by dew and fog during winter. In the associated cacti, we analyse some evidences related to the presence or absence of nurse-shrub replacement.

Materials and methods

Study area

The Mazocahui island is located in northern Sinaloa at 25°34′08″N, 109°00′44″W, 65 m elevation, and has an area of 1·5 km^2. This basaltic outcrop dates back to Pleistocene or to mid-Cenozoic (Phleger & Ayala-Castañares, 1969), and it is surrounded by the Ohuira Bay, which covers 125 km^2 (Fig. 1). The bay was the water course of an ancient main channel of the Fuerte river, which continued through the Topolobampo Bay at a time of lowered sea level, 6000–7000 years B.P.; the island was formed as the Sea of Cortez level increased 10–15 m to reach the actual level about 2000–2500 years B.P. (Phleger & Ayala-Castañares, 1969). The soil is shallow, 7–16 cm depth, clayish–loamy, 50–60% stone cover, which includes frequent rock outcrops. The climate is characterized by a mean annual precipitation of 240 mm, which falls mainly in July–September, and a mean annual temperature of 24°C (García, 1973). The winter season is dry, with a high relative humidity at night. The sea breeze blows from the west–north-west in October to May and influences the frequency of fog and dew, 81 and 133 days per year, respectively. The vegetation is a xerophyllous shrubland (Rzedowski, 1978), 10–80% cover, with predominance of *Euphorbia californica* Benth. 'zipehui' and *Bursera laxiflora* S. Watson 'copal'.

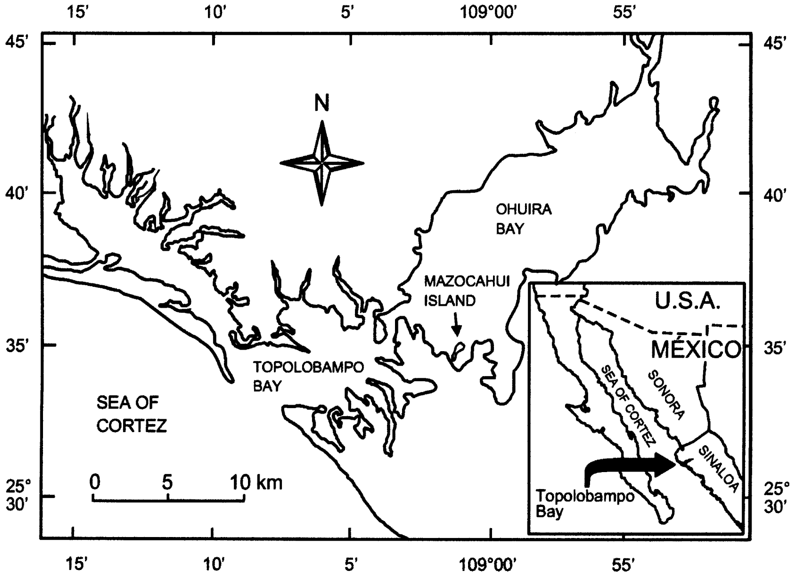

Figure 1. Location of Mazocahui island, the study area, in the Topolobampo coastal desert, Sinaloa, México.

Field sampling

The northern slope of the island, at 50–60 m elevation, was chosen to lay out a 0·25 ha plot. Half of the plot is an open low shrubland with $<15\%$ cover; the other half is a dense tall shrubland with 80% cover. All the shrubs of the plot were identified, and the major and minor canopy diameters measured. Cover by species was derived from the mean canopy diameter (d) assuming circular canopies:

$$\text{cover} = \sum_{i=1}^{n} [0{\cdot}25\pi d_i^2],$$

where n is the number of individuals of the ith species. Associated and non-associated individuals of target species were counted to estimate the observed frequencies in order to compare with those expected under the hypothesis of random distribution; individuals rooted under the shrubs canopies were assumed associated.

The hypothesis of equality between the observed and expected frequencies of cacti under shrubs was tested by the G statistic (Sokal & Rohlf, 1981), complemented by the adjusted residuals (d_{ij}) between the observed and expected frequencies for each shrub. Since the adjusted residuals are approximately normally distributed with mean 0 and variance 1, the $d_{ij} > 1{\cdot}96$ indicate that the observed frequencies differ significantly from the expected ones at 5% level. Adjusted residuals were obtained from a χ^2 since the equality $d_{ij} = \sqrt{\chi^2}$ is verified (Sokal & Rohlf, 1981).

Once the association of platyopuntia–shrubs was revealed, we proceeded to look for evidence of replacement. The cladodes of these cacti range from decumbent to erect, thus height does not reflect their size. We attempted to estimate a total length index (TL) based in the length of the main axis (LMA) and the number of branches (NB). The index was adjusted by linear regression through the origin in two species of platyopuntia with 15 observations each. The adjusted models served to derive the total length in 427 individuals of *O. rileyi* and 49 individuals of *O. spraguei*. Effects of shade from shrubs and size of platyopuntias on their frequencies were analysed with independence log-linear models (Agresti, 1990), and the G statistic was used as a test. The effects of size (and hypothetically the age) of *Desmanthus covillei* (Britton & Rose) Wiggins ex Turner var. *covillei* and *O. rileyi* on the percentage of dead basal area of *Desmanthus*, were studied with the aid of a two-way ANOVA. The number of *Desmanthus* stems ranged from 2 to 46 per individual, and dead basal area was estimated from the stem diameter at 20 cm above-ground.

Some environmental variables were registered in the field and others were determined from soil samples at 0–5 cm depth following a random stratified sampling method. The soil depth was measured with a screw auger. Soil surface temperatures were recorded hourly on August 29, 1999, with TGL 40–336 thermometers, one on bare ground and two under shrubs of *Haematoxylon brasiletto* Karst. and *E. californica*. Temperature was recorded for a 13-h period, from 0700 h to 1800 h.

Dew and fog are difficult to separate. For practical purposes, dew was considered as the water collected in pairs 95 cm^2 disks of Whatman filter paper no. 1 on polyethylene plates; 10 plates were placed beneath the shrubs and 14 in the open on one occasion in January 17, 2000, from 1900 h to 0700 h. The paper disks were picked up in Ziploc plastic bags and taken to the laboratory for weighing accumulated water. Fog-measuring gauges, designed to be used in cloud forests by Vogelmann (1973), were modified to be used in dry environments. Vogelmann's gauges were made from 1 liter oil cans with one end removed. The inside and outside were sprayed with white enamel. The inside of the can was marked off into 50 ml divisions, and then fitted with a cylinder of aluminum window screen, which protruded 17 cm above the rim. In our modified gauges, the oil cans were cut into half and transformed into funnels supported by wire legs, which conducted water toward a 50 ml container lined with dry ice. The window screen was replaced by a cylinder made of polyethylene pieces attached to a wire frame with silicone rubber. Six 'fog meters' under shrubs and six on the open were left on the field for two 20–day periods; two drops of oil were added to each container to reduce evaporation.

Laboratory methods

On April 1999 (dry season), soil samples from 0–5 cm depth were collected to determine physical–chemical properties, excepting soil moisture, which was determined on samples collected on September 4, 3 days after a 19-mm rainfall. Soil samples from under *H. brasiletto*, *D. covillei* var. *covillei*, *B. laxiflora* and *E. californica* var. *californica* (five from each species) were obtained to a maximum distance of 0·5 radii from the shrub stem.

Samples on bare ground (12) were collected in sites closest to the previous ones but at $>1{\cdot}5$ radii distance. The percentages of sand, silt and clay were determined by the hydrometer method, organic matter by Walkley–Black method, total N by the C/N empirical ratio (Cajuste, 1977), available P by colorimetry trough the extract solution of Olsen (Olsen & Dean, 1965), and K by flame photometry. The electrical conductivity was determined with a conductivity meter, and pH with a potentiometer. Since environmental data did not show normality, the hypothesis Ho: $\mu_1 = \mu_2$ was tested with the Wilcoxon Rank Sum statistic (Gibbons, 1985).

Results

Distribution and abundance of cacti

The number of platyopuntia individuals beneath shrubs was statistically greater than that expected by chance (*G* test, df. = 1, $p<0{\cdot}01$). This means that *O. riley*, *O.*

Table 1. *Observed and expected numbers of cactus individuals beneath shrubs and in the open spaces of Mazocahui island in Topolobampo, Sinaloa*

Cacti	Beneath shrubs		Open spaces		*G*
	Observed	Expected	Observed	Expected	values
Echinocereus sciurus var. *floresii*	124	179·5	207	151·5	37·5**
Mammillaria dioica	63	53·7	36	45·3	3·6
M. mazatlanensis	169	178·9	161	151·1	1·2
Ferocactus herrerae	3	4·3	5	3·7	0·9
Stenocereus thurberi var. *thurberi*	14	36·9	54	31·1	32·4**
Pachycereus pecten-aboriginum	5	3·3	1	2·8	2·3
Opuntia burrageana	13	23·9	31	20·1	11·0**
O. fulgida	2	9·2	15	7·8	13·6**
O. rileyi	400	237·5	38	200·5	290·6**
O. spraguei	109	64·5	10	54·5	80·4**
O. wilcoxii	37	27·1	13	22·9	8·3**
O. sp.	54	35·3	11	29·8	24·2**

G test values with ** indicate significant differences at $p<0{\cdot}01$ and df. = 1 between the observed frequencies and those expected under the hypothesis of a random pattern.

spraguei, *O. wilcoxii* and *Opuntia* sp. have a clumped pattern under the shrub canopies (Table 1).

Echinocereus sciurus and *Stenocereus thurberi*, *O. burrageana* and *O. fulgida*, show significant *G* values. Their observed frequencies are lower than the expected ones, suggesting an aggregated pattern in open spaces. *Mammillaria dioica* and *M. mazatlanensis* have non-significant values, which indicates a random distribution relative to shrub cover.

Seven out of the 27 species of shrubs included in the analysis have a higher number of associated platyopuntia individuals than expected at random ($d_{ij} < 1{\cdot}96$, $\alpha = 0{\cdot}05$; Table 2). Comparisons per species of the observed and expected numbers of cacti individuals growing under the shrub canopies reveal that *H. brasiletto* has three associated species of cacti. *Opuntia wilcoxii* grows under *B. laxiflora* and *Diphysa occidentalis* Rose. Furthermore, *O. spraguei* is significantly associated to *E. californica* var. *californica* and *D. occidentalis*; *O. rileyi* is associated with *D. covillei* and three non-legumes: *B. laxiflora*, *Agave angustifolia* Haw. and *E. californica*; *Opuntia* sp. grows associated to *Stenocereus thurberi* and *A. angustifolia*. Table 2 shows that there are proportionately more individuals of platyopuntias under legumes than under other shrubs: *D. covillei* and *H. brasiletto* have 3·8 and 2·8 times the expected frequencies of cacti, whereas the non-legumes, *B. laxiflora* and *E. californica*, have 1·7 and 1·6 times the expected frequencies, respectively. The hypothesis Ho: the number of platyopuntias under legumes and non-legumes is proportional to their canopy covers, was rejected with $p < 0{\cdot}001$ ($G = 33{\cdot}5$, df. = 1).

Replacement analysis

The size index of *O. rileyi* was $\mathrm{TL} = 0{\cdot}82\,\mathrm{LMA} + 35\,\mathrm{NB}$ ($r^2 = 0{\cdot}95$), and that of *O. spraguei* was $\mathrm{TL} = 0{\cdot}67\,\mathrm{LMA} + 29\,\mathrm{NB}$ ($r^2 = 0{\cdot}97$). The regression coefficients of both models differ significantly from zero ($p < 0{\cdot}05$, *t*-test).

Five nurse-shrub pairs from Table 2 were selected to explore replacement patterns: *A. angustifolia–O. rileyi*, *B. laxiflora–O. rileyi*, *D. covillei–O. rileyi*, *E. californica–O. rileyi* and *E. californica–O. spraguei*. The low number of cases for other pairs did not allow proper statistical analysis. Results are shown in Table 3. The *G* values for the log-linear independence models of two factors were non-significant ($p > 0{\cdot}05$).

The two-way ANOVA of *D. covillei* dead basal area revealed that this variable has a significant relation with shrub size ($F = 2{\cdot}64$, $p = 0{\cdot}05$), but a non-significant relation with (a) the presence of *Opuntia* ($F = 0{\cdot}21$, $p = 0{\cdot}65$) and (b) the interaction between its presence and shrub size ($F = 0{\cdot}19$, $p = 0{\cdot}9$; data not shown).

Relationships with the environmental variables

The analysis of soil samples revealed that soil under leguminous shrubs has 7·34% organic matter and 0·37% nitrogen, as compared with 6·0% and 0·3% under non-legumes (data not shown). However, differences between both perennials are non-significant for these variables, as well as in the remainder ones (normal approximation to the Wilcoxon Rank Sum test, $p > 0{\cdot}05$).

Table 4 shows the mean values of the analysed variables for both conditions. The mean soil temperatures with full sun and under shrubs are significantly different ($Z = -3{\cdot}91$, $p < 0{\cdot}001$). The mean temperature on August 22 from 0700 h to 1900 h was $45{\cdot}4 \pm 2{\cdot}4$°C with full sun and $32{\cdot}9 \pm 0{\cdot}3$°C under the shrubs. As shown in Fig. 2, the maximum temperature was 56°C and 36°C, respectively. The greater difference between the extremes occurs at 1400 h with 19°C beneath *H. brasiletto*, and 22°C beneath *E. californica*.

Table 2. *Observed and expected frequencies of platyopuntias beneath different shrub species*

Species	Cover (%)	*Opuntia rileyi*			*Opuntia spraguei*			*Opuntia wilcoxii*			*Opuntia* sp.		
		Obs	Exp	d_{ij}	Obs	Exp	d_{ij}	Obs	Exp	d_{ij}	Obs	Exp	d_{ij}
AGA ANG	4·2	41	18·5	5·3	7	5·0	0·9	2	2·1	−0·1	10	2·8	4·5
BUR LAX	14·8	122	64·8	7·7	25	17·6	1·9	18	7·4	4·2	8	9·6	−0·6
COU GLA	1·5	0	6·4	−2·6	2	1·7	0·2	1	0·7	0·3	0	1·0	−1·0
DES COV	3·8	95	16·6	19·6	1	4·5	−1·7	0	1·9	−1·4	2	2·5	−0·3
EUP CAL	12·4	68	54·3	2·0	43	14·8	7·9	10	6·2	1·6	9	8·1	0·4
EUP HIN	3·4	0	14·7	−3·9	3	4·0	−0·5	0	1·7	−1·3	0	2·2	−1·5
DIP OCC	2·4	9	10·4	−0·4	7	2·8	2·5	4	1·2	2·6	0	1·5	−1·3
HAE BRA	2·6	33	11·4	6·5	12	3·1	5·1	0	1·3	−1·2	6	1·7	3·4
IPO ARB	4·2	26	18·3	1·8	3	5·0	−0·9	0	2·1	−1·5	4	2·7	0·8
JAT CUN	1·5	0	6·3	−2·5	0	1·7	−1·3	0	0·7	−0·9	0	0·9	−1·0
STE THU	1·4	1	6·2	−2·1	3	1·7	1·0	1	0·7	0·3	12	0·9	11·6
Other nine shrubs	1·3	2	5·8	−1·6	3	1·6	1·1	1	0·7	0·4	3	0·9	2·3
Other seven crassicaules	1·0	3	4·4	−0·7	0	1·2	−1·1	0	0·5	−0·7	0	0·7	−0·8
Open space	45·6	38	199·8	−15·5	10	54·3	−8·2	13	22·8	−2·8	11	29·7	−4·7

The d_{ij} values >2 indicate significant deviation of the observed frequencies from those expected under the hypothesis of a random pattern (normal distribution) at 5% level. AGA ANG = *Agave angustifolia*, BUR LAX = *Bursera laxiflora*, COU GLA = *Coursetia glandulosa*, DES COV = *Desmanthus covillei* var. *covillei*, EUP CAL = *Euphorbia californica* var. *californica*, EUP HIN = *Euphorbia californica* var. *hindsiana*, DIP OCC = *Diphysa occidentalis*, HAE BRA = *Haematoxylon brasiletto*, IPO ARB = *Ipomoea arborescens*, JAT CUN = *Jatropha cuneata*, STE THU = *Stenocereus thurberi* var. *thurberi*.

Table 3. *Results of* G *tests on log-linear models of independence of two factors (size classes and associated/non-associated conditions of platyopuntias)*

Condition	Size classes (m)				G values	p
	0–1	1–2	2–3	>3		
Opuntia rileyi						
Non-associated	18	33	8	4		
Associated with:						
Agave angustifolia	9	39	12	1	6·26	0·0997
Bursera laxiflora	16	53	19	4	3·97	0·2649
Desmanthus covillei	39	86	12	1	6·44	0·0922
Euphorbia californica	16	52	5	1	6·14	0·1049
Opuntia spraguei						
Non–associated	4	7	1	0		
Associated with:						
Euphorbia californica	22	14	1	0	3·10	0·2122

The p values are $>0{\cdot}05$ and indicate non-significant interaction between both factors. Hence, there is no evidence of shrub replacement by cacti.

Soil depth was 15·7 cm under the shrubs and 11·7 cm in the open, but the difference is non-significant ($Z = 1{\cdot}74$, $p = 0{\cdot}08$). Deeper soils under the shrub canopies may capture more water and may be more protected against evaporation. Soil moisture 3 days after 19 mm rainfall was double (17·7%) that registered in the open (8·2%) ($Z = 4{\cdot}36$, $p < 0{\cdot}01$). Soil texture under the shrub canopies in the island is sandier and has less silt than in the open ($p < 0{\cdot}05$), whereas the clay ratio is similar in both conditions. The percentages of organic matter and nitrogen are significantly greater under shrubs (6·7 ± 0·6%, and 0·33 ± 0·03%) than in the open (2·8 ± 0·2%, and 0·14 ± 0·01%); likewise assimilable potassium (0·56 ± 0·03 *vs.* 0·47 ± 0·02 meq$(100\,\mathrm{g\,soil})^{-1}$, $p < 0{\cdot}05$). As in other deserts (Nobel, 1989), phosphorus is not significantly greater beneath the shrubs than in the open (12·6 ± 2·0 *vs.* 11·0 ± 1·5 p.p.m., $p > 0{\cdot}05$). Soil pH and electrical conductivity are not significantly different in sun and shade.

The amount of water collected on the paper disks was 0·68 ± 0·19 g under shrubs canopies and 3·07 ± 0·09 g in the open ($Z = -4{\cdot}07$, $p < 0{\cdot}001$). The mean water accumulated in the fog meters for 20 days was 0·05 ± 0·03 g under shrubs and 1·12 ± 0·21 g in the open ($Z = -3{\cdot}99$, $p < 0{\cdot}001$). The evaporation in a control container without screen was 3·4 g for the same period, indicating that most of the water collected by fog meters was evaporated.

Discussion

The spatial distribution of cacti in Topolobampo, with the exception of the platyopuntias, differs from the pattern associated to shrubs reported in other arid and semi-arid environments (Niering *et al.*, 1963; Turner *et al.*, 1966, 1969; Yeaton *et al.*, 1977, 1983; McAuliffe, 1984*a*, *b*; Nobel, 1989; Franco & Nobel, 1989; Cody, 1993; Valiente-Banuet & Ezcurra, 1991; Valiente-Banuet *et al.*, 1991*a*, *b*; Arriaga *et al.*, 1993).

The platyopuntias of Mazocahui island are associated with eight of the 27 shrubs investigated. The density of individuals is greater under the legume canopies than

Table 4. *Mean values of environmental variables under shrub canopies and in the open*

Variables	Means		*Z* values	*p*
	Beneath shrubs (N_1)	Open spaces (N_2)		
Soil surface temperature (°C)	32·88	45·15	−3·91	0·000
Soil depth (cm)	15·73	11·67	1·74	0·080
Soil moisture (%)	17·10	8·20	4·36	0·000
Sand (%)	22·30	16·50	2·41	0·020
Silt (%)	36·35	43·83	−2·64	0·010
Clay (%)	41·90	39·92	0·92	0·360
Organic matter (%)	6·66	2·76	4·25	0·000
Total nitrogen (%)	0·33	0·14	4·25	0·000
Soluble phosphorus (p.p.m.)	11·00	12·58	−0·84	0·400
Assimilable potassium (meq $(100\,g)^{-1}$)	0·56	0·47	2·25	0·020
pH	5·95	5·87	0·41	0·680
Electrical conductivity (mmho cm^{-1})	0·20	0·18	0·77	0·440
Dew accumulation (g)	0·68	3·07	−4·07	0·000
Fog condensation (g)	0·05	1·12	−3·99	0·000

The *Z* values are a normal approximation of the Wilcoxon Rank Sum test for Ho: the means are the same. N_1 and N_2 are the sample sizes. Temperature: $N_1 = 26$, $N_2 = 13$; soil depth and moisture: $N_1 = 15$, $N_2 = 15$; dew accumulation: $N_1 = 10$, $N_2 = 14$; fog condensation: $N_1 = 12$, $N_2 = 12$; rest of variables: $N_1 = 20$, $N_2 = 12$.

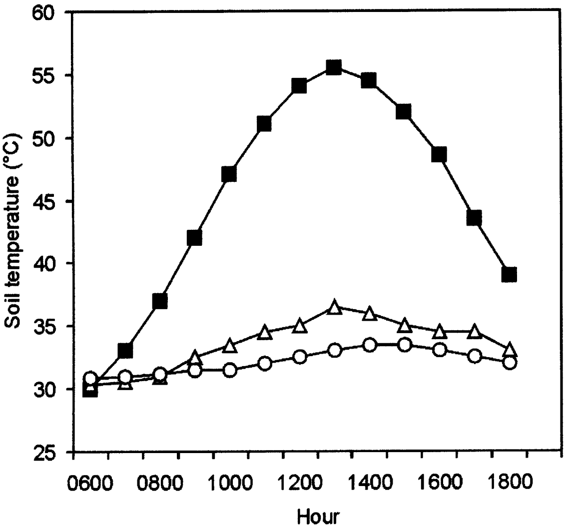

Figure 2. Soil surface temperature beneath the 'brasil' *Haematoxylon brasiletto* (Δ), the 'zipehui' *Euphorbia californica* var. *californica* (○) and in open spaces (■) for a 13–hour period in August 29, 1999. Soil extreme temperatures of 56 °C in open spaces, as well as high solar radiation could confine propagation of prickly pear cacti to shaded places of Mazocahui island.

under the non-legumes. However, soil fertility is not different in both perennials, as occurs with fertility data obtained in other deserts (García-Moya & McKell, 1970; Barth & Klemmedson, 1978; Virginia & Jarrell, 1983). The difference in nurse effectiveness among shrubs and cacti species may indicate some specific biotic relationship; perhaps allelopathy contributes to the non-proportional distribution of the platyopuntias.

There are few studies related to prickly pear cacti–nurse shrub interactions, the following being the most important: Yeaton *et al.* (1983) on the distribution of *O. littoralis* (Engelmann) Cockerell in southern California, Yeaton & Romero-Manzanares (1986) on the replacement of *Acacia schaffneri* (S. Watson) F. J. Herm by *O. streptacantha* Lem., Mandujano *et al.* (1998) on the sexual and clonal recruitment of *O. rastrera* Weber in the southern Chihuahuan Desert, and Flores–Flores & Yeaton (2000) on the associational dynamics of *O. streptacantha* with several species in the Mexican Central Plateau.

The replacement of *A. schaffneri* is hypothetically mechanical, since the cacti open the shrub canopy and expose the lower branches to desiccation (Yeaton & Romero-Manzanares, 1986). Significant relationships have also been observed between the size of *O. streptacantha* and branch mortality of *Larrea tridentata* Sessé & Moc. ex DC. and *Prosopis laevigata* (Willd.) M. C. Johnst. (Flores-Flores & Yeaton, 2000). In the coastal desert of Topolobampo, there was no evidence of shrubs replacement by *O. rileyi* and *O. spraguei*. The dead basal area of *Desmanthus* was significantly related to its own size, but not with the presence or absence of *O. rileyi*, nor with the interaction; the *G* values for independence log-linear models were non-significant for both *Opuntia* species. An explanatory hypothesis is that vigor of the platyopuntias diminishes periodically due to mechanical injury by cyclones affecting the Sinaloa coastal region; their stems break, reducing their competition with *Desmanthus* and other nurse plants. The decumbent stems of the platyopuntias associated with shrubs break off easily, enhancing their propagation. Stems exposed to sunlight and high soil temperature dehydrate and die, whereas those that fall under shrubs produce new individuals. Likewise, the lack of overlap between roots of *Opuntia* and those of their nurse plants, enhances co-existence (Yeaton & Cody, 1976; Briones *et al.*, 1996).

Recruitment by clonal propagation in *O. rastrera* Weber has been recognized as dominant in intercanopy areas of nopaleras (vegetation dominated by platyopuntias), whereas sexual reproduction predominates under dense shade in grasslands (Mandujano *et al.*, 1998). The relative importance of both processes is unknown in the coastal desert. For prickly pear cacti 74–92% of individuals are found growing under shrubs on Mazocahui island. Individuals are rare in the open, and their development is poor; there are evidences of dead tissues, and frequently, there are live and dead cladodes and branches on the ground (pers. obs.). Direct solar radiation, as well as soil temperature rising to 56°C in August may be critical for clonal propagation in open spaces; furthermore, stone coverage does not allow adequate contact between the cladodes and the soil. The results from other works support this idea also. The surface area/volume ratio of cladodes is greater than that of globose or cylindrical stems; thus they warm up more rapidly under direct solar radiation and have greater water losses per unit of tissue volume (Gibbs & Patten, 1970; Hadley, 1972). Yeaton *et al.* (1983) reports that individuals of *O. littoralis* growing under shade in the coast of southern California have 92% live cladodes, whereas those growing on full sunlight have 75%.

In the study site, a higher soil moisture under shrubs than in full sunlight suggests more availability of water for the platyopuntias. Organic matter and nutrients, mainly nitrogen, are generally scarce in deserts (Noy-Meir, 1973). In Topolobampo, sarcocaulescent shrubs and legumes contribute with litter which accumulates under their canopies. The nitrogen under shrubs of Mazocahui island was double, and potassium was 1·2 times that found in open spaces. The concept of ‘islands of fertility’

(García-Moya & McKell, 1970; Cross & Schlesinger, 1999) applies to the coastal shrubland of Topolobampo, though it is more fertile than interior deserts. Rapid growth succulents as the platyopuntias can increase dry matter as nitrogen increases up to 0·3% in the soil. Nobel (1988) reports that *O. phaeacantha* Engelmann and *O. rastrera* increased their dry weight by 20 times increasing soil nitrogen from 0·05% to 0·3%.

Values of pH about 5·0 reduce stem and root growth of *A. deserti* by 88% and 86%, as compared to values of pH at 6–8 (Nobel & Hartsock, 1986). Thus, pH values around 6 in sun and shade on the island may have no limiting effects on cacti distribution. Salinity seems unimportant for Mazocahui cacti; electrical conductivity values were relatively low, and the differences in sun and shade conditions are not significant. Salt concentrations of 128 p.p.m. in shade and 115 p.p.m. in sun are significantly lower than those reported by Sánchez & Nolasco (pers. comm.) for a population of *E. sciurus* five times greater than ours. A 50% growth reduction in *O. ficus-indica* (L.) Mill. has been reported by Nobel (1988) with concentrations of 4 091 p.p.m. (= 70 mM NaCl).

As a difference from the platyopuntias, 62·5% individuals of the globose *E. sciurus*, 70·5% and 88·2% of *O. burrageana* and *O. fulgida*, and 79·4% of the columnar *S. thurberi*, are found in open spaces (45·6% of the total space) of the shrubland. The observed percentages of the globose *M. dioica* and *M. mazatlanensis* do not differ from the expected 45·6%. The evidences indicate a negative association with, or an independence from the shrubs, but it cannot be concluded that shading is not necessary for these cacti. Their distribution may be caused by a combination of morphological and physiological adaptations with physical and biological factors of the coastal desert, including shading by stones.

Sensitivity analysis of energy budget models in cacti indicate that air and soil temperatures, shielding spines, stem shape, and plant size are the most influential factors on stem surface temperatures (Nobel, 1978, 1988). Temperatures are greatest for the smallest seedlings, primarily because of the high temperatures and low wind speed near the soil surface. Shading is crucial for protecting seedlings, but it competes with growth. A critical shading occur below which growth rate do not permit seedlings escape from this stage. Environmental conditions would be more benign in the northern slope of the island because of the sea breeze and lower solar radiation. In *M. dioica*, the dense spines maintain apical temperatures 2·4°C warmer in winter and 7·3°C cooler in summer than would be expected in absence of spines, clearly indicating that variation in spines may account for ecological boundaries of this genus (Nobel, 1978). Since heat convection depends on the square root of the diameter of cylinders and spheres (Nobel, 1988), thin cylindrical stems are more heat sensitive, but they are cooled off faster by the wind. When the air temperature is 44°C, thin stems of the cylindropuntia *O. parryi* Engelmann reach a maximum of 32°C, whereas those of the platyopuntia *O. littoralis* reach 40°C (Yeaton *et al.*, 1983). Physiological differences also exist among cacti, barrel cacti being most heat tolerant, followed by columnar, globose, platyopuntia, and cylindropuntia (Smith *et al.*, 1984).

Previous works in deserts underline the importance of herbivory for nursing of small globose cacti as *E. engelmannii* (Parry ex Engelmann) Rümpler, *M. microcarpa* Engelmann (McAuliffe, 1984*b*) and *M. dioica* (Cody, 1993). In contrast, *M. gaumeri* Orcutt on the Yucatán coast is distributed equally under shrub canopies and in open spaces, where herbivory is insignificant (Leirana-Alcocer & Parra-Tabla, 1999). This coastal dune scrubland receives <700 mm average annual rainfall, but seedlings of this species have greater survivorship under the shrub canopies, which indicates that the requirements of seedlings can be different from those of the adult stage. We propose that *M. dioica*, *M. mazatlanensis*, *E. sciurus* var. *floresii* and *S. thurberi* var. *thurberi* occupy shaded spaces because they do not survive direct solar radiation, rather than for reasons of herbivory. In the desert shrubland of Mazocahui island, there are no visible signs of herbivory on cacti. Low herbivory pressure could allow a high percentage of cacti in open spaces. Stones >8 cm diameter cover nearly 50% of the ground, providing runoff water and protecting seedlings of cacti without interfering with the solar radiation needed by adult plants. The soil-surface temperature in open areas is significantly higher than under shrubs. The maximum temperature of 56°C on bare ground is 19°C higher than under *H. brasiletto* and 22°C higher than under *E. californica* (Fig. 2). This temperature is close to the inhibition level (57°C) in cortical cells of *F. acanthodes* roots, caused by tonoplast degradation (Jordan & Nobel, 1984). However, the radiation load could be attenuated by stones covering the roots and shading the stem base; furthermore stones reduce evaporation. We corroborated that most individuals (except the cylindropuntias) are within 1 cm of the nearest stone, and *E. sciurus* roots are seen immediately below the stone where water accumulates from runoff.

The cylindropuntias *O. echinocarpa* Engelmann & Bigelow, *O. acanthocarpa* Engelmann & Bigelow and *O. ramosissima* Engelmann occur in association with different nurse plants of the Mojave Desert, among them *Hilaria rigida* (Thurb.) Benth. ex Scribn. and several spiny shrubs (Cody, 1993). These chollas can germinate in shrubland openings, but they are scarce because of heavy herbivory. Cases in which cylindropuntia does not co-exist with potential nurse plants are due to competition (Yeaton & Cody, 1976; Yeaton *et al.*, 1977). In all cases, competition is determined by overlapping of root systems. In Mazocahui island, *O. burrageana* and *O. fulgida* occupy open spaces of the shrubland where they can avoid competition with shrubs. An hypothesis is that herbivory pressures are lower on the island than in the Mojave Desert, where cylindropuntia is nursed against herbivores. There are no surface stones in the microsites occupied by this group; its great heat convection capacity and ability to propagate from detached stems (observed in *O. fulgida*) could explain its establishment in open spaces.

It is unlikely that low dew and fog contributions such as $3{\cdot}07\,\mathrm{g}\,95\,\mathrm{cm}^{-2}$ (equivalent to 0·32 mm rainfall) could increase water potential for cacti before evaporating in the morning. According to Hadley (1972), there is a consensus that the beneficial effects of dew and fog should be ascribed to the presence of liquid water on photosynthetic surfaces, which reduces transpiration and creates a moister environment for growth. Gas exchange of cacti takes place at night when the dew point is reached. The shrubs may also intercept light rains; a creosote bush shrubland with 30% cover can intercept up to 3·6 mm rainfall on its foliage (Tromble, 1988). In accordance with these data, the globose cacti of the island were seen under isolated shrub canopies in open shrubland, but not in dense shrubland. The water supplied by dew and fog and light rains should be considered with respect to discontinuous seed hydration, a common process in deserts that could be enhanced in open spaces of the island. Assuming that germination of cacti occurs mainly in the summer and seedlings cope with ensuing drought for at least 8 months from November to June, the 'seed hydration memory' (*sensu* Dubrovsky, 1996) would improve establishment, favoring early germination in the summer; seeds treated with discontinuous hydration reduce the mean germination time, seedlings accumulate more biomass and show higher survivorship than those from non-treated seeds.

In conclusion, the coastal desert of Topolobampo has more benign conditions than interior deserts along gradients of physical stress and herbivory. We hypothesize that structural and successional characteristics in the plant community mirror such environmental differences. The distribution of the platyopuntias in Mazocahui island is associated with shrubs, which correlate with less extreme soil-surface temperatures, prolonged moisture, and high fertility. There was no evidence of replacement of shrubs by cacti. The cyclones that affect the Sinaloa coast exert control over the community structure, inducing co-existence. The distribution of *E. sciurus* var. *floresii*, *M. dioica*, *M. mazatlanensis* and *S. thurberi* var. *thurberi* differ from the observed pattern in cacti of interior deserts. The abundant stones in the open shrubland can replace shading by shrubs without interfering with the radiation required by adult plants. Stone also improve the water availability for cacti. The colonization of open spaces without surface stones by cylindropuntias could be the result of morphological adaptations and propagation with low competition. The occupation of open spaces could be facilitated by low pressure of herbivory.

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References

Agresti, A. (1990). *Categorical Data Analysis*. U.S.A.: John Wiley & Sons. 558 pp.

Arriaga, L., Maya, Y., Díaz, S. & Cancino, J. (1993). Association between cacti and nurse perennials in a heterogeneous tropical dry forest in northwestern México. *Journal of Vegetation Science*, **4**: 349–356.

Barth, R.C. & Klemmedson, J.L. (1978). Shrub–induced spatial patterns of dry matter, nitrogen, and organic carbon. *Soil Science Society of America Journal*, **42**: 804–809.

Bertness, M.D. & Callaway, R. M. (1994). Positive interactions in communities. *Trends in Ecology and Evolution*, **9**: 191–193.

Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R. & Ingraham, A.O. (1999). Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology*, **80**: 2711–2726.

Briones, O., Montaña, C. & Ezcurra, E. (1996). Competition between three Chihuahuan Desert species: evidences from plant size–distance relations and root distribution. *Journal of Vegetation Science*, **7**: 453–460.

Búrquez, A. & Quintana, M.A. (1994). Islands of diversity: ironwood ecology and the richness of perennials in a Sonoran Desert biological reserve. In: Nabhan, G.P. & Carr, J.L. (Eds), *Ironwood: an Ecological and Cultural Keystone of the Sonoran Desert*, pp. 9–27. Washington, D.C.: Conservation International. 92 pp.

Cajuste, L. (1977). *Química de suelos con un enfoque agrícola*. Chapingo, México: Colegio de Postgraduados, 278 pp.

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

Cody, M.L. (1993). Do cholla cacti (*Opuntia* spp., subgenus cylindropuntia) use or need nurse plants in the Mojave Desert? *Journal of Arid Environments*, **24**: 139–154.

Cross, A.F. & Schlesinger, W.H. (1999). Plant regulation of soil nutrient distribution in the northern Chihuahuan Desert. *Plant Ecology*, **145**: 11–25.

Danin, A. (1999). Desert rocks as plant refugia in the Near East. *The Botanical Review*, **65**: 93–170.

Dubrovsky, J.G. (1996). Seed hydration memory in Sonoran Desert cacti and its ecological implication. *American Journal of Botany*, **83**: 624–632.

Flores–Flores, J.L. & Yeaton, H.R.I. (2000). La importancia de la competencia en la organización de las comunidades vegetales en el Altiplano Mexicano. *Interciencia*, **25**: 1–8.

Fowler, N. (1986). The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, **17**: 89–110.

Franco, A.C. & Nobel, P.S. (1989). Effect of nurse plants on the micro-habitat and growth of cacti. *Journal of Ecology*, **77**: 870–886.

García, E. (1973). *Modificaciones al sistema de clasificación climática de Köppen (para adaptarlo a las condiciones particulares de la República Mexicana)*. México, D.F.: Instituto de Geografía, UNAM, 245 pp.

García-Moya, E. & McKell, C.M. (1970). Contribution of shrubs to the nitrogen economy of a desert–wash plant community. *Ecology*, **51**: 81–88.

Gibbons, J.D. (1985). *Nonparametric Statistical Inference*. New York, U.S.A.: Marcel Dekker, Inc., 408 pp.

Gibbs, J.G. & Patten, D.T. (1970). Plant temperatures and heat flux in a Sonoran Desert ecosystem. *Oecologia* (Berlin), **5**: 165–184.

Hacker, S.D. & Gaines, S.D. (1997). Some implications of direct positive interactions for community species diversity. *Ecology*, **78**: 1990–2003.

Hadley, N.F. (1972). Desert species and adaptation. *American Scientist*, **60**: 338–347.

Jordan, P.W. & Nobel, P.S. (1984). Thermal and water relations of roots of desert succulents. *Annals of Botany*, **54**: 705–717.

Leirana-Alcocer, J. & Parra-Tabla, V. (1999). Factors affecting the distribution, abundance and seedling survival of *M. gaumeri*, an endemic cacti of coastal Yucatán, México. *Journal of Arid Environments*, **41**: 421–428.

Mandujano, M. del C., Montaña, C., Méndez, I. & Golubov, J. (1998). The relative contributions of sexual reproduction and clonal propagation in *Opuntia rastrera* from two habitats in the Chihuahuan Desert. *Journal of Ecology*, **86**: 911–921.

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

McAuliffe, J.R. (1984*b*). Prey refugia and the distributions of two Sonoran Desert cacti. *Oecologia* (Berlin), **65**: 82–85.

McAuliffe, J.R. (1988). Markovian dynamics of simple and complex desert plant communities. *American Naturalist*, **131**: 459–490.

Niering, W.A., Whittaker, R.H. & Lowe, C.H. (1963). The saguaro: a population in relation to environment. *Science*, **142**: 15–23.

Nobel, P.S. (1978). Surface temperatures of cacti—influences of environmental and morphological factors. *Ecology*, **59**: 986–996.

Nobel, P.S. (1988). *Environmental Biology of Agaves and Cacti*. New York, U.S.A.: Cambridge University Press. 270 pp.

Nobel, P.S. (1989). Temperature, water availability, and nutrient levels at various soil depths—consequences for shallow-rooted desert succulents, including nurse plant effects. *American Journal of Botany*, **76**: 1486–1492.

Nobel, P.S. & Hartsock, T.L. (1986). Influence of nitrogen and other nutrients on the growth of *Agave deserti*. *Journal of Plant Nutrition*, **9**: 1273–1288.

Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**: 25–51.

Olsen, S.R. & Dean, L.A. (1965). Phosphorus. *Agronomy*, **9**: 1035–1049.

Patten, D.T. (1978). Productivity and production efficiency of an upper Sonoran Desert ephemeral community. *American Journal of Botany*, **65**: 891–895.

Phleger, F.B. & Ayala-Castañares, A. (1969). *Marine Geology of Topolobampo Lagoons*, *Sinaloa*, *México*, pp. 101–136. México, D.F.: Memorias del Simposium Internacional sobre Lagunas Costeras, UNAM–UNESCO. 686 pp.

Rzedowski, J. (1978). *Vegetación de México*. México, D.F.: LIMUSA, 432 pp.

Schemenauer, R. S. & Cereceda, P. (1991). Fog–water collection in arid coastal locations. *Ambio*, **20**: 303–308.

Smith, S.D., Didden-Zopfy, B. & Nobel, P.S. (1984). High-temperature response of North American cacti. *Ecology*, **65**: 643–651.

Smith, S.D., Patten, D.T. & Monson, R.K. (1987). Effects of artificially imposed shade on a Sonoran Desert Ecosystem: microclimate and vegetation. *Journal of Arid Environments*, **13**: 65–85.

Sokal, R.R. & Rohlf, F.J. (1981). *Biometría*. Madrid, Spain: H. Blume Ediciones. 831 pp.

Steenbergh, W.F. & Lowe, C.H. (1969). Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. *Ecology*, **50**: 825–834.

Suzán, H., Nabhan, G.P. & Patten, D.T. (1996). The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. *Journal of Vegetation Science*, **7**: 635–644.

Tewksbury, J.J. & Lloyd, J.D. (2001). Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia*, (Berlin), **127**: 425–434.

Tewksbury, J.J. & Petrovich, C.A. (1994). The influence of ironwood as a habitat modifier species: a case study on the Sonoran Desert Coast of the Sea of Cortez. In: Nabhan, G.P. &

Carr, J.L. (eds.), *Ironwood: an Ecological and Cultural Keystone of the Sonoran Desert*, pp. 29–54. Washington, D.C.: Conservation International. 92 pp.

Tielbörger, K. & Kadmon, R. (2000). Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, **81**: 1544–1553.

Tromble, J.M. (1988). Water interception by two arid lands shrubs. *Journal of Arid Environments*, **15**: 65–70.

Turner, R.M., Alcorn, S.M. & Olin, G. (1969). Mortality of transplanted saguaro seedlings. *Ecology*, **50**: 835–844.

Turner, R.M., Alcorn, S.M., Olin, G. & Booth, J.A. (1966). The influence of shade, soil, and water on saguaro seedling establishment. *Botanical Gazette*, **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 Tehuacán Valley, México. *Journal of Ecology*, **79**: 961–971.

Valiente-Banuet, A., Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Núñez, H., Barnard, G. & Vázquez, E. (1991*a*). Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central México. *Journal of Vegetation Science*, **2**: 15–20.

Valiente-Banuet, A., Vite, F. & Zavala–Hurtado, J.A. (1991*b*). Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*. *Journal of Vegetation Science*, **2**: 11–14.

Vandermeer, J. (1980). Saguaros and nurse trees: a new hypothesis to account for population fluctuations. *The Southwestern Naturalist*, **25**: 357–360.

Vetaas, O.R. (1992). Gradients in field-layer vegetation on an arid misty mountain plateau in the Sudan. *Journal of Vegetation Science*, **3**: 527–534.

Virginia, R.A. & Jarrell, W.M. (1983). Soil properties in a mesquite–dominated Sonoran Desert ecosystem. *Soil Science of America Journal*, **47**: 138–144.

Vogelmann, H.W. (1973). Fog precipitation in the cloud forest of eastern México. *BioScience*, **23**: 96–100.

Yeaton, R.I. (1978). A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan Desert. *Journal of Ecology*, **66**: 651–656.

Yeaton, R.I. & Cody, M.L. (1976). Competition in plant communities: the Northern Mojave Desert. *Journal of Ecology*, **64**: 689–696.

Yeaton, R.I. & Esler, K.J. (1990). The dynamics of a succulent Karoo vegetation. A study of species association and recruitment. *Vegetatio*, **88**: 103–113.

Yeaton, R.I. & Romero-Manzanares, A. (1986). Organization of vegetation mosaics in the *Acacia schaffneri–Opuntia streptacantha* association, southern Chihuahuan Desert, México. *Journal of Ecology*, **74**: 211–217.

Yeaton, R.I., Travis, J. & Gillinsky, E. (1977). Competition and spacing in plant communities; the Arizona upland association. *Journal of Ecology*, **65**: 587–595.

Yeaton, R.I., Layendecker, E., Sly, K.S. & Eckert, R. (1983). Micro-habitat differences between *Opuntia parryi* and *O. littoralis* (Cactaceae) in the mixed chaparral inland coastal sage association. *The Southwestern Naturalist*, **28**: 215–220.