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Journal of Vegetation Science, Vol. 2, No. 1. (Feb., 1991), pp. 15-20.

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Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico

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Abstract. The Zapotitlán de las Salinas valley, central Mexico, harbours a high diversity of cacti. Pattern analysis indicated that the establishment of two columnar cacti, *Neobuxbaumia tetetzo* and *Cephalocereus hoppenstedtii*, and of three small globose cacti, *Coryphanta pallida*, *Mammillaria colina* and *M. casoi*, is aggregated and associated with perennial nurse shrubs. Some nurse species, *Castela tortuosa*, *Caesalpinia melanadenia* and *Eupatorium spinosarum* have a higher number of cacti beneath their canopies than would be expected by chance. A replacement pattern was found between the columnar cacti and their nurses, an aspect which was not found with the globose cacti.

Following the assumption that protection against excessive radiation is the main factor determining the nurse effect, the azimuth orientation of the cacti with respect to their nurses was evaluated. Only *Coryphanta pallida* presented a non-random distribution with a tendency towards the North and West. The difference in maximum temperature between the soil surface under the different nurse species and of open spaces, which is reached at midday, was 16 °C. No significant differences were found in beneath-canopy temperatures for the three nurse species considered. Soil nitrogen levels were significantly lower beneath the different nurse plants than in open spaces. This result suggests that soil fertility is not an important factor in the nurse-plant phenomenon in Zapotitlán.

Keywords: *Cactaceae*; *Cephalocereus hoppenstedtii*; *Coryphanta pallida*; *Mammillaria casoi*; *M. colina*; *Neobuxbaumia tetetzo*; Nurse phenomenon; Replacement pattern; Zapotitlán Valley.

Nomenclature: Zavala-Hurtado (1982).

Introduction

Arid and semi-arid vegetation of different parts of the world is formed by mosaics of perennial plants beneath which the recruitment and establishment of several species, including cacti, occurs in a non-random fashion. This 'nurse plant' phenomenon has been described for the Sonoran and Chihuahuan Deserts, for desert regions

of Iraq and other dry regions of the world with annual and perennial plants recruiting themselves beneath canopies of perennials (e.g. Went 1942; Muller & Muller 1953; Agnew & Haines 1960; Halvorson & Patten 1975). The case of the giant cactus *Carnegiea gigantea* and the tree *Cercidium microphyllum* in the Sonoran Desert has been described ever since the last century (Hutto, McAuliffe & Hogan 1986). Another case involves the Cholla cactus *Opuntia leptocaulis* under Creosote bush *Larrea tridentata* (Yeaton 1978). Replacement patterns have been established for both species pairs, with the cacti recruiting beneath the perennial shrubs, which later become excluded through competition or induced senility (Yeaton 1978; Vandermeer 1980).

In a parallel paper (Valiente-Banuet, Vite & Zavala-Hurtado 1991) the case of the giant columnar cactus *tetecho*, *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana* is presented.

The universality of the process for different arid and semi-arid zones, the number of species in the community that have this kind of establishment pattern, and the causes that underlie the process, have not been studied in depth. Some hypotheses have considered the relevance of the microhabitat beneath the canopies including soil conditions modified by the shrubs (which are discussed in the companion paper, Valiente-Banuet, Vite & Zavala-Hurtado 1991).

The present study was made in a semi-arid environment in central Mexico where giant columnar cacti are the dominant physiognomic component of the vegetation. The main aim of the study was to determine the occurrence of the nurse phenomenon for two giant columnar cacti and three small globose cacti. Nurse relationships were detected by observing the spatial patterns of the cacti with respect to perennial shrubs in the community, and by characterizing the microhabitat beneath the shrubs in terms of temperature and soil fertility.

Material and Methods

The study site

The study was carried out in the Zapotitlán de las Salinas valley (18° 20' N, 97° 28' W; state of Puebla), a local basin in the semi-arid Tehuacán - Cuicatlán region (Rzedowski 1973), situated in the rain shadow of the Eastern Sierra Madre. Average rainfall in the Zapotitlán Valley is 380 mm and annual mean temperature is 21 °C (García 1973). The soils are rocky and shallow, and are derived mainly from sedimentary and metamorphic rocks. The vegetation has been classified as 'matorral xerofilo', arid tropical scrub (Rzedowski 1978; Zavala-Hurtado 1982). The flora has neotropical affinities; ca. 630 genera and 1400 species of seed plants occur, including nearly 30% endemics (Smith 1965; Villaseñor, Dávila & Chiang in press), with 12 endemic species of cacti out of a total of 53 (Meyrán 1980).

Methods

A 20 m × 30 m sampling plot was located on a southern slope harbouring a mixed community dominated by columnar cacti and drought-deciduous shrubs. Most measurements and samplings were done in March 1988, towards the middle of the dry season. The mean distance of the individuals of each of five species of cacti to the nearest shrub was measured and compared with an expected random distribution obtained by placing thirty random points within the sampling plot and measuring their distance to the nearest shrub. The cacti are two giant columnar cacti *Cephalocereus hoppenstedtii* and *Neobuxbaumia tetetzo*, and three small globose species: *Mammillaria colina*, *M. casoi* and *Coryphanta pallida*.

The frequency of cacti under each perennial species was determined and a chi-square test was carried out to test the null hypothesis that the number of cacti beneath each species is proportional to the total area covered by the canopy of that shrub species. The standardized residuals were used to test the significance of each cell (Haberman in Greig-Smith 1983). The standardized residuals are normally distributed with zero mean and unit variance, so that any value greater than 2 (the approximate 5 % point of the normal distribution) was regarded as a significant deviation.

To detect the existence of a replacement pattern, height frequency histograms were constructed for the columnar cacti, classified into two categories: associated and non-associated with a shrub. For the globose cacti, histograms were made for diameter classes. Additionally, for each cactus species the azimuth of individuals growing beneath the canopy of shrubs, with respect to the shrub main stem, was recorded along a transect.

Table 1. Observed (Obs.) and expected (Exp.) mean distances (cm) ± standard error from cacti to the nearest perennial plant in the cactus- shrub community of Zapotitlán Valley. All differences are significant at $P \leq 0.001$.

Species	N	Obs.	Exp.
<i>Cephalocereus hoppenstedtii</i>	76	33.8 ± 3.4	51.7 ± 4.7
<i>Neobuxbaumia tetetzo</i>	16	30.2 ± 5.5	51.7 ± 4.7
<i>Mammillaria colina</i>	30	28.7 ± 2.2	51.7 ± 4.7
<i>M. casoi</i>	11	32.2 ± 5.0	51.7 ± 4.7
<i>Coryphanta pallida</i>	29	37.5 ± 3.5	51.7 ± 4.7

The temperatures beneath the canopy of *Mimosa luisana* ($n = 5$) and in open space ($n = 2$) were registered over a whole day, July 23, 1988. Additionally, temperatures beneath the canopy of *Cercidium praecox*, *Mimosa luisana*, *Prosopis laevigata*, and in open space were registered during 15 h on July 16, 1988.

Thirty soil samples, 0 - 10 cm, were taken at random in the sampling plot, 15 from beneath the canopy of six different shrubs and 15 in open space. The nitrogen concentration was determined using a Technicon (334-74 WB) autoanalyzer and the differences were tested with an analysis of variance (ANOVA; Zar 1974).

Results

All five cactus species are found significantly nearer to shrubs than would be expected by chance ($P < 0.001$), implying an aggregated pattern with respect to the shrubs (Table 1). Out of the 29 species of shrubs included in the

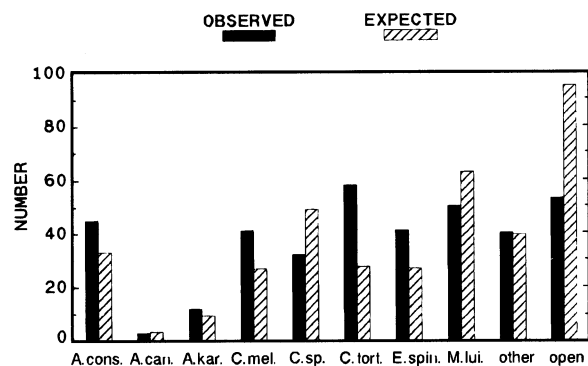


Fig. 1. Observed and expected numbers of cacti associated with perennial plants: $\chi^2 = 80.94$, $P = 0.005$. A. cons. = *Acacia constricta*; Acan. = *Acanthaceae* 1; A. kar. = *Agave karwinskii*; C. mel. = *Caesalpinia melanadenia*; C. sp. = *Caesalpinia* sp.; C. tort. = *Castela tortuosa*; E. spin. = *Eupatorium spinosarum*; M. lui. = *Mimosa luisana*; Other = other species; Open = open space.

Table 2. Observed (Obs.) and expected (Exp.) number of cacti under the canopy of shrubs; standardized residuals values are shown (Test). Absolute values > 2 are significant at 5 % of the normal distribution.

Species	<i>C. hoppenstedtii</i>			<i>M. colina</i>			<i>M. casoi</i>			<i>C. pallida</i>			<i>N. tetetzo</i>		
	Obs.	Exp.	Test	Obs.	Exp.	Test	Obs.	Exp.	Test	Obs.	Exp.	Test	Obs.	Exp.	Test
<i>Acacia constricta</i>	4	3.6	0.19	25	19.2	1.40	1	2.2	-0.80	12	7.0	1.94	3	1.1	1.73
<i>Acanthaceae</i>	1	0.4	1.00	2	2.0	0.00	0	0.2	-0.40	0	0.7	-0.80	0	0.1	-0.30
<i>Agave karwinskii</i>	1	1.0	0.00	7	5.5	0.60	2	0.6	1.72	1	2.0	-0.70	1	0.3	1.17
<i>Caesalpinia melanadenia</i>	3	3.0	0.00	30	15.9	3.70	3	1.8	0.86	4	5.8	-0.70	1	0.9	0.04
<i>Caesalpinia sp.</i>	6	5.4	0.27	13	28.3	-3.00	0	3.3	-1.80	10	10.3	0.00	3	1.7	1.00
<i>Castela tortuosa</i>	2	3.0	-0.50	36	15.9	5.40	9	1.8	5.40	11	5.8	2.20	0	0.9	-0.90
<i>Eupatorium spinosarum</i>	8	2.9	3.00	22	15.5	1.70	3	1.8	0.90	8	5.6	1.00	0	0.9	-0.90
<i>Mimosa luisana</i>	7	6.9	0.04	34	36.3	-0.40	4	4.2	0.00	5	13.3	-2.30	0	2.2	-1.40
Others	6	4.4	-1.10	24	23.2	-3.80	2	2.7	-1.80	4	7.7	-0.40	4	1.4	1.30
Open space	3	10.3	-2.30	24	54.9	-4.60	1	6.3	-2.10	24	20.0	0.95	1	3.3	-1.20

analysis, three were found with a number of associated cacti higher than expected by chance ($\chi^2 = 80.94$, d.f. = 9, $P = 0.005$; Fig. 1).

Comparison of observed and expected numbers of cactus individuals growing beneath shrubs shows that *Mammillaria colina*, *M. casoi* and *Coryphanta pallida* were significantly associated with *Castela tortuosa*, and that *M. colina* was also significantly associated with *Caesalpinia melanadenia* (Table 2). Of the two species of columnar cacti only *Cephalocereus hoppenstedtii* was significantly associated with one perennial species, *Eupatorium spinosarum* (Fig. 2). For each cactus species, the open spaces had a significantly lower number of individuals than would be expected by chance.

Most of the smaller individuals of the columnar cacti *C. hoppenstedtii* and *N. tetetzo* were significantly associated to shrubs, but this situation is reversed when they reach heights of 2 - 3 m (Fig. 3). This pattern did not

occur with globose cacti, which usually live in association with shrubs during most of their life (Fig. 4).

The azimuth orientation of cacti with respect to the nearest main stem of a shrub is randomly distributed (Table 3). Only *Coryphanta pallida* presented a non-random distribution with a tendency towards the North and West.

The mean daily temperature fluctuation is only small beneath shrubs, with a maximum at 12 h, as shown for *Mimosa luisana* (Fig. 5). Temperature fluctuation in the open is much bigger with a maximum, reached at 14 h, ca. 16 °C higher than under the shrub. No significant differences were found with other shrub species: *Cercidium praecox* and *Prosopis laevigata*.

The mean nitrogen concentration of the soil samples beneath shrubs was significantly lower than the nitrogen concentration in open space (1271 ± 78 and 1755 ± 102 ppm respectively; $F = 13.11$, $P = 0.001$).

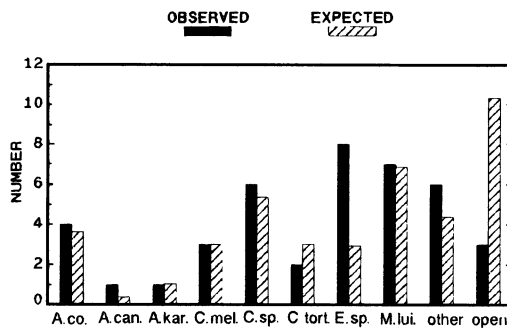


Fig. 2. Observed and expected numbers of *Cephalocereus hoppenstedtii* individuals, associated with perennial plants. $\chi^2 = 16.8$, $P < 0.005$.

Table 3. Observed azimuth orientation of cacti with respect to the nearest perennial plant in the cactus - shrub community in Zapotitlán Valley and a test for deviation from a random azimuth orientation.

Species	N	S	E	W	χ^2	P
<i>C. hoppenstedtii</i>	16	6	9	17	7.18	NS
<i>N. tetetzo</i>	19	10	14	9	4.77	NS
<i>M. casoi</i>	9	10	4	9	2.75	NS
<i>M. colina</i>	20	24	14	18	2.73	NS
<i>C. pallida</i>	21	6	9	16	10.61	< 0.05

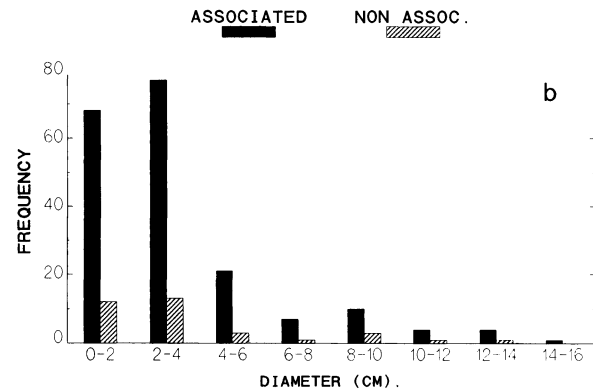
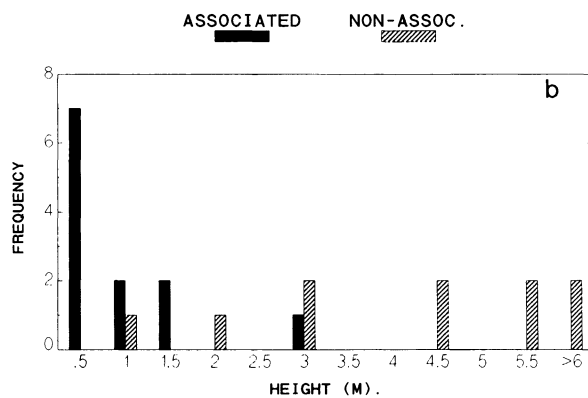
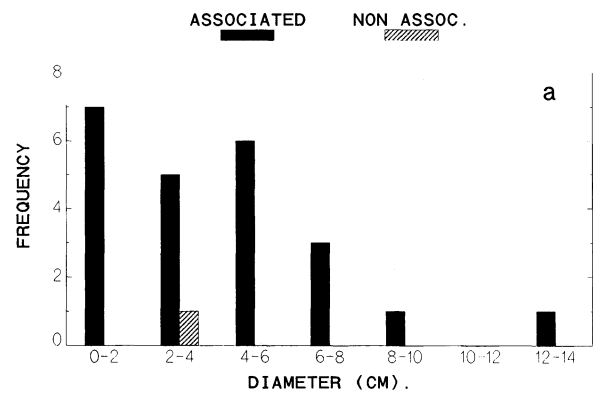
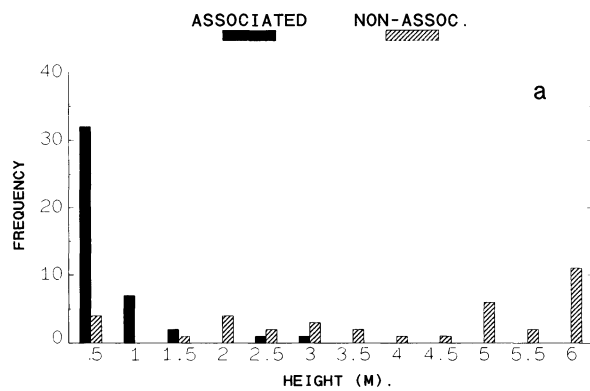


Fig. 3. Height distribution of individuals of columnar cacti associated and not associated with perennial plants: (a) *Cephalocereus hoppenstedtii*, (b) *Neobuxbaumia tetetzo*.

Fig. 4. Diameter distribution of individuals of globose cacti associated and not associated with perennial plants: (a) *Mammillaria casoi*, (b) *Mammillaria colina*.

Discussion

All the cacti considered in the present study have a distribution pattern associated with five perennial species. This confirms previous studies on the establishment phase of succulents beneath the canopy of perennial plants (e.g. McAuliffe 1984a, 1984b; Yeaton & Romero-Manzanares 1986; Yeaton 1978). The considerable difference in midday temperature found between open space and beneath shrubs (also reported by Fowler 1986 and McAuliffe 1988), suggests that the protection against radiation by the nurse plant is an important factor in the pattern of recruitment. Franco & Nobel (1989), who found differences of more than 30 °C between outside and under the canopy of a nurse plant, pointed to the high deficit in the total daily PAR experienced by cacti growing in shade conditions. However, they add that the PAR deficit may be compensated by the higher soil fertility under the nurse shrubs. In our case, different nurse plants can provide the same shelter against high temperatures, but our nitrogen data do not show an increase in soil fertility beneath nurse plants. This

unexpected result contrasts with previous reports for temperate deserts (e.g. García-Moya & McKell 1970; Wallace & Romney 1972; Nishita & Haug 1973); this suggests that soil fertility under the nurse plant need not be an important causal factor in the cactus-nurse association.

While interpreting these results, one should take into consideration that cacti are succulents with CAM metabolism, which, during daytime, cannot regulate their temperature through transpiration. Thus protection of the seedling stage against radiation could be crucial in their survival, particularly in hot, semi-arid tropical environments such as Zapotitlán. Of the nurse plants with an associated number of cacti higher than expected by chance, *Castela tortuosa* is a typical xerophyte which maintains its leaves throughout the entire year, generating a permanent shelter against radiation. On the other hand, the nurse plants *Eupatorium spinosarum* and *Caesalpinia melanadenia* drop their leaves during the dry season.

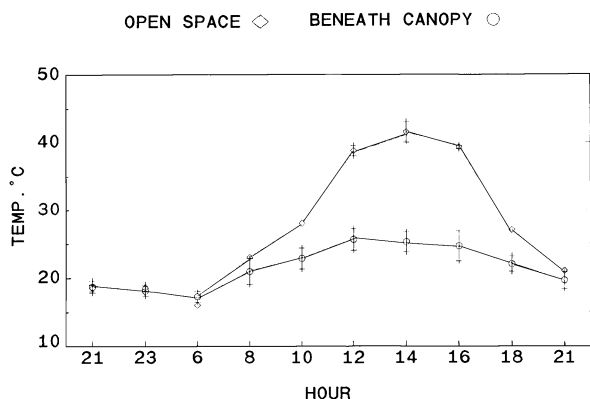


Fig. 5. Temperatures on the soil surface beneath the canopy of *Mimosa luisana* ($n = 5$) and in open space ($n = 2$) for a 24-hour period (July 23, 1988).

If radiation is an important factor here, a non-random microdistribution beneath the canopies of nurse plants may be expected with a preference for North slopes, which receive less annual radiation, and West slopes, which are generally cooler, while receiving radiation mainly in the afternoon. Of the five species studied, only *Coryphanta pallida* shows such a pattern. One explanation for the absence of an azimuth pattern could be that the Zapotitlán Valley, with its low latitude, receives direct solar radiation from the North in the summer. Thus a non-random azimuth pattern around nurse plants should be more pronounced in northern temperate deserts where direct solar radiation comes from the South all year.

The giant columnar cacti were associated with nurse plants only in their seedling and juvenile stages; adult columnar cacti tend to replace their nurse plants, which die when the cacti reach a height of 2 - 3 m. This creates a replacement pattern in which nurses are replaced by adult cacti, which in turn will leave open spaces suitable for recruitment by radiation-tolerant seedlings, when they eventually die. This pattern has been reported for other deserts and linked to competition for water (McAuliffe 1984a).

The nurse plant phenomenon in arid and semi-arid plant communities dominated by cacti, such as in the Zapotitlán Valley, can be considered essential for the development of a dynamic patch structure in these communities. This more dynamical approach to (semi-) arid plant communities has been emphasized by McAuliffe (1988). Although patch dynamics of desert communities is extremely slow, detection is possible through demographical and pattern studies of the intervening species.

Several mechanisms have been proposed to explain

these association patterns which include non-random dispersion, post-germination predation, and the protection against radiation and freezing effects by the nurse plants.

Acknowledgements. The authors thank Enrique Solís for the soil analyses. This study was supported by the Mexican Council for Science and Technology (CONACyT), grant no. P220CCOR880446.

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Received 12 February 1990;
Revision received 30 July 1990;
Accepted 23 September 1990.