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## Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*

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**Abstract.** Pattern analysis and association analysis showed that recruitment of the giant columnar cactus *Neobuxbaumia tetetzo* in the semi-arid valley of Zapotitlán is largely limited to areas beneath the canopies of perennial shrubs, acting as nurse plants. Chi-square and Haberman tests revealed that young cacti were more frequently found beneath canopies of leguminous shrubs, especially *Mimosa luisana*, than were older cacti. Segregation analysis indicated a positive association (= negative segregation) of young cacti and *M. luisana* canopies, but older cacti were randomly distributed with respect to *M. luisana*. This, and the height class distributions of cacti associated with *M. luisana* or not, suggested the replacement of *M. luisana* by *N. tetetzo*. *Mimosa luisana* plants in association with *N. tetetzo* had greater amounts of dead basal area than *M. luisana* lacking associated *N. tetetzo*. This suggested competition from *N. tetetzo* promotes the replacement process.

The roots of *N. tetetzo* are  $\leq 30$  cm deep. Interception of soil water before penetration to deeper roots of *M. luisana* may be the mode of competition between the two species.

**Keywords:** Competition; Facilitation; Giant columnar cactus.

### Introduction

The successful establishment of succulents in the Sonoran Desert is largely limited to areas beneath the canopy of 'nurse' plants (Turner et al. 1966; Steenbergh & Lowe 1977; McAuliffe 1984a,b). This pattern of establishment may arise through protection of young cacti by other plant canopies from solar radiation, excessive water loss, frost (Nobel 1980; Jordan & Nobel 1981), mechanical injury and predation. Steenbergh & Lowe (1977) have suggested that dispersal by animals can also contribute to the observed distribution patterns.

The establishment of succulents beneath other plants may eventually affect the original 'nurse plant'. McAuliffe (1984a) found that establishment of *C. gigantea* is facilitated by *C. microphyllum* which in the long term is competitively excluded by the former. Yeaton (1978) has documented a cyclical relationship in the Chihuahuan

Desert between the Creosote bush (*Larrea tridentata*) and Cholla cactus (*Opuntia leptocaulis*) suggesting that the latter eventually replaces the former.

The nurse effect is known from many arid and semi-arid regions (see also Valiente-Banuet et al. 1991, where evidence of the nurse effect is shown for five cacti). In the present study we analyze the spatial relationships of *tetetzo*, *Neobuxbaumia tetetzo*, a giant columnar cactus. Since root competition for water may be involved in the replacement pattern (McAuliffe 1984a; Yeaton 1978; Yeaton & Romero-Manzanarez 1986) we looked for competitive effects of the *N. tetetzo* and analyzed the structural surface (i. e. the root surface without regard to ephemeral rain roots) and areal extent of roots.

### Material and Methods

The study was carried out in Zapotitlán de las Salinas, C Mexico (18° 20' N, 97° 28' W), a valley in the rain shadow of the Eastern Sierra Madre. Average rainfall is 380 mm; soils are rocky and shallow, derived mainly from sedimentary and metamorphic rocks. The vegetation can be characterized as arid tropical scrub with physiognomic dominance of giant columnar cacti (Rzedowski 1978; Zavala-Hurtado 1982; Valiente-Banuet et al. 1991).

#### *Analysis of spatial relationships*

Vegetation composition, patterns of distribution and association between species were determined in a 20 m  $\times$  30 m quadrat in a *Neobuxbaumia tetetzo* stand in March-April 1987. All perennial plants in the plot were marked and the nearest neighbour to each one was recorded. For every individual of *N. tetetzo* height and presence or absence of a shrub canopy above it were recorded. The number of *N. tetetzo* individuals under each perennial species was counted and the null hypothesis was tested ( $\chi^2$ ) that the number of *N. tetetzo* individuals beneath each species is a function of the total area covered by canopies

of that shrub species. The standardized residuals were used to test the significance of each cell (Haberman test, see Greig-Smith 1983). The residuals are approximately normally distributed with zero mean and unit variance, so that any adjusted variable  $> 2$  (5% point of the normal distribution) is regarded as a significant deviation.

In order to detect replacement of *N. tetetzo* by the dominant associated shrub, *Mimosa luisana* (*Leguminosae*, a plotless technique proposed by Pielou (1961) was used to test segregation among individuals of these two species. Nearest neighbour data for these two species were arranged in different size categories of the cactus: 0-20 cm; 20-40 cm; 40-60 cm; 60-80 cm and  $> 80$  cm. The data for each size category were compiled in a  $2 \times 2$  contingency table.  $\chi^2$  tests were carried out under the null hypothesis of independent dispersion of both species. Segregation was estimated using Pielou's index:

$$S = 1 - [n(b+c) / (a+b)(b+d) + (c+d)(a+c)] \quad (1)$$

where  $a$  = no. of times the nearest neighbour of a cactus is another cactus;  $b$  = no. of times the nearest neighbour of a cactus is *Mimosa*;  $c$  = no. of times the nearest neighbour of *Mimosa* is a cactus;  $d$  = no. of times the nearest neighbour of *Mimosa* is another *Mimosa*, and  $n$  = sample size.  $S$  is zero if both species are independently distributed and +1 if they are completely segregated. For  $S = -1$  there is a negative segregation, i.e. the nearest neighbour always belongs to the other species.

In order to describe vertical relations between *M. luisana* and *N. tetetzo*, 131 *Mimosa* shrubs (57 with and 74 without *N. tetetzo* occurring beneath their canopies) were analysed. *M. luisana* was considered associated with a *N. tetetzo* if the cactus was located beneath the shrub canopy. Like many desert shrubs, *M. luisana* has a polypodial growth form with a short and buried central stem. Diameters of living and dead main branches of the shrub were measured at ca. 15 cm, and the basal area, BA, of the main branches was determined for both live and dead branches as  $BA = \pi/4 \cdot \sum d_i^2$ , where  $d_i$  is the diameter of branch  $i$ . The proportion of dead BA was expressed as the ratio between dead BA and total BA.

Proportions of BA of dead trunks per plant for *M. luisana* individuals associated with *N. tetetzo* versus non-associated individuals were compared in a two-way analysis of variance with arc-sine transformation.

#### Measurements on roots of *Neobuxbaumia tetetzo*

Root systems of eight *N. tetetzo* individuals ranging from 0.01 to 5.43 m high were excavated. The length and proximal and distal diameters of each excavated root segment were used to calculate surface area of root segments as truncated cones. To estimate the ground surface area explored by the roots, the average length of

the main root branches, used as the radius of a circle, was computed. Only first order branches were used, and the ground cover values were regressed against plant height.

#### Soil nitrogen status

Nitrogen content of 15 paired samples of soil beneath and outside the canopy of *M. luisana* was determined by a modified micro-Kjeldahl technique.

## Results

#### Spatial relationships

In the 20 m  $\times$  30 m plot, 476 individuals of 24 species of flowering plants were recorded. *Neobuxbaumia tetetzo* and *Mimosa luisana* were the most abundant species with 44.5 % and 13.7 % of the total number of individuals respectively. The observed abundance of *N. tetetzo* beneath the canopies of some legumes and other shrubs such as *Cordia cylindrostachya* Jacq. and *Verbesina* sp. is higher than expected (Table 1). This means that the distribution of the cactus is coarse-grained with respect to some species in the plot. The height distributions of *N. tetetzo* growing beneath and between perennial plants respectively are different (Fig. 1). Most of the smaller individuals are associated, while larger cacti are mostly non-associated. Individuals of *N. tetetzo*  $< 40$  cm are negatively segregated, while taller individuals are distributed independently from the nurse plant (Table 2).

#### Effects on nurse plants

The competitive effect of *N. tetetzo* on its nurse should be reflected in the vigour of the latter. The two-way analysis of variance indicates that there is a significant difference in the percentages of dead basal area between associated and non-associated shrubs ( $F$ -ratio = 12.5,  $P < 0.0001$ ). There is also a significant effect ( $F$ -ratio = 43.3,  $P < 0.0001$ ) of the size classes manifested in a higher dead basal area percentage in the bigger individuals (Fig. 2). Finally, a significant effect of the interaction of these factors was found ( $F$ -ratio = 3.1,  $P = 0.005$ ).

#### Allometric relationships of *Neobuxbaumia tetetzo* roots

The relationship between structural area of roots ( $Y$ ) and height of cacti ( $X$ ) can be described with a power (or linear log-log) function:  $\ln Y = -0.45 + 1.74 \ln X$ ;  $r = 0.99$ ;  $p < 0.001$ . A similar relationship is found between height ( $X$ ) and surface area covered by the roots ( $Y$ ) (Table 3):  $\ln Y = 1.23 + 1.83 \ln X$ ;  $r = 0.97$ ;  $p < 0.001$ .

#### Soil nitrogen pattern

Average nitrogen contents inside and outside the canopy of *M. luisana* were  $0.22 \pm 0.002$  % and  $0.19 \pm$

**Table 1.** Haberman One Cell Significance test for observed (Obs.) and expected (Exp.) numbers of *N. tetetzo* < 80 cm beneath the canopy of perennial plants and in open space. Values of  $|d_{ij}| > 2$  are significantly different (5 % of the normal distribution). CC% = Canopy cover %.

Species	CC%	Obs.	Exp.	$d_{ij}$
<i>Mimosa luisana</i> Brand.	46.8	59	55.3	0.91
Open space	11.9	15	43.2	-5.63
<i>Caesalpinia melanadenia</i> (Rose) Standley	9.5	12	1.1	10.97
<i>Cordia cylindrostachya</i> Roem. et Schult.	9.5	12	0.6	15.50
<i>Prosopis laevigata</i> (Willd.) Johnst.	4.8	6	2.7	2.08
<i>Cercidium praecox</i> (Ruiz & Pavón) Harm	3.2	4	11.6	-2.38
<i>Verbesina</i> sp.	3.2	4	0.5	5.04
<i>Acacia constricta</i> Benth.	3.1	4	2.0	1.44
<i>Hechtia podantha</i> Mez.	2.4	3	5.0	-0.92
Others (16 spp.)	5.6	7	3.7	1.75

0.001 %, respectively. This difference is slightly significant ( $P = 0.06$ ) as evaluated by an ANOVA using arc-sine correction.

**Discussion**

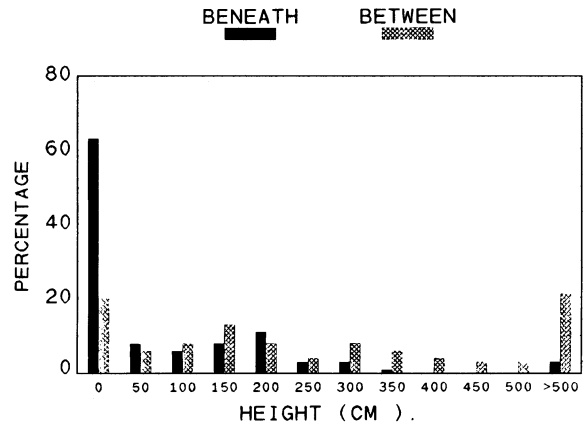
According to the spatial relationship analysis presented, there is clear evidence of the occurrence of the nurse plant phenomenon in the Tehuacán Valley, with a more benign climate than the Sonoran desert. The occurrence of predictable recruitment patterns of plants beneath the canopies of other plants suggests that common underlying mechanisms may be operating, including (a) seed dispersion by animals, wind or water beneath canopies; (b) post-germination mortality of seedlings in open spaces restricting them to areas beneath plant canopies; and (c) amelioration of physical conditions and modification of soil nutrient levels beneath plant canopies (McAuliffe 1988). Thus, vegetation with cacti and nurse plants can be regarded as a dynamic mosaic with simultaneous coexistence of all possible stages (McAuliffe 1988).

Our edaphic results indicate that there is a slight difference in the nitrogen concentration beneath the canopies of *M. luisana*. This aspect should be explored further as higher concentrations of soil nitrogen beneath

**Table 2.** Segregation analysis of *Neobuxbaumia tetetzo* and *M. luisana* for different height categories of the cacti, according to Pielou (1961).

Height class (cm)	N	$\chi^2$	Segregation Coeff.	P
0 - 20	60	19.70	-0.38	**
20 - 40	26	3.96	-0.18	*
40 - 60	13	3.32	0.65	NS
60 - 80	12	3.27	-0.14	NS
> 80	61	0.593	0.14	NS

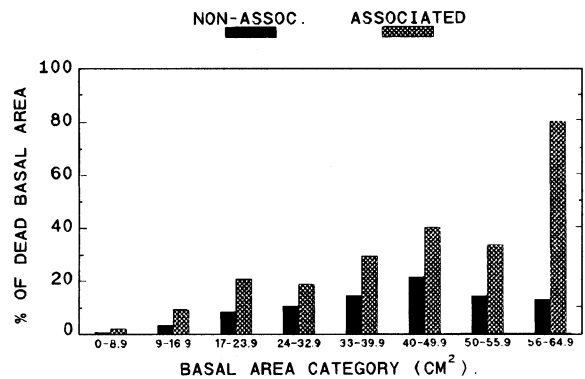
\*\*  $p < 0.001$ ; \*  $p < 0.05$ ; NS not significant,  $p > 0.05$ .



**Fig. 1.** Height distributions of *Neobuxbaumia tetetzo* individuals growing beneath and between perennial nurse plants.

shrubs in arid vegetation have also been reported for non-legumes (e.g. García-Moya & McKell 1970; Nishita & Haug 1973). This may be due to some kind of symbiotic activity, litter deposition from the plants, or rhizospheric free-living fixers (Farnsworth, Romney & Wallace 1978). The decomposition of surface litter in open desert space is due mostly to abiotic factors; here a relatively constant C:N ratio is maintained. Under nurse plants there is less UV radiation and more moisture; here, micro and meso-organisms are more active and the C:N ratio may be lower (Montaña et al. 1988). Nitrogen has been reported as a limiting factor in arid and semi-arid regions when moisture is available (West 1981). Annuals under nurse plants show a higher productivity than non-associated plants (Halvorson & Patten 1975; Turner et al. 1966).

The change in nurse plant interaction from initial commensalism to eventual competition was reported by Yeaton (1978), McAuliffe (1984a), and Yeaton & Romero-Manzanares (1986). The present study presents



**Fig. 2.** Percentage of dead basal area per size category of *Mimosa luisana* individuals associated and non-associated with a *Neobuxbaumia tetetzo* individual.

**Table 3.** Characteristics of the root system of *Neobuxbaumia tetetzo* ( $n = 8$ ). HP = height of the plant (cm); AL = average length of the root arms (cm); AD = average depth of the root arms (cm); IA = influence area (cm<sup>2</sup>); SA = structural area (cm<sup>2</sup>); OV = occupied volume (cm<sup>3</sup>).

HP	AL	AD	IA	SA	OV
1.0	1.35	0.79	5.75	0.79	4.58
5.4	1.94	1.00	11.78	3.63	11.78
6.5	9.13	3.28	262.06	21.08	838.61
12.8	7.60	3.19	181.46	56.40	579.10
35.0	47.00	2.37	6939.78	562.11	16438.95
66.0	54.00	12.50	9460.17	1815.70	118252.13
197.0	171.5	19.00	92401.31	6743.01	1755624.89
543.0	241.00	25.00	182466.84	21394.70	4561671.00

evidence of a replacement pattern between *N. tetetzo* and *M. luisana* which is due to competition between both species. From our results it is evident that the competitive effect of *N. tetetzo* individuals is higher in the bigger individuals of *M. luisana* than in the smaller ones. According to McAuliffe (1984a), competition for water is the most likely aspect associated with the interaction between *Carnegiea gigantea* and *Cercidium microphyllum*; this is probably the same for *N. tetetzo*. The root surface analysis in *N. tetetzo* suggests that part of the rainfall water could be successfully intercepted by the cactus before it can become available for the roots of the nurse plant. On the other hand, some of the roots of *Mimosa luisana* are rather shallow, which could be associated with the efficiency of water uptake by the root systems.

Our results suggest that nurse facilitation and competition govern coexistence patterns and structure of semi-arid communities with dominating cacti.

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