DINAMICA DEL ESTABLECIMIENTO DE CACTACEAS: PATRONES GENERALES Y
CONSECUENCIAS DE LOS PROCESOS DE FACILITACION POR PLANTAS
NODRIZA EN DESIERTOS.

TESIS QUE PARA OBTENER EL GRADO DE DOCTOR EN ECOLOGIA PRESENTA

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CONTENIDO

RESUMEN

Los resultados de las investigaciones, contenidos en los seis capítulos que conforman esta tesis doctoral, tienen como tema central el establecimiento de especies vegetales en comunidades de zonas áridas y semiáridas. Específicamente, los estudios se centraron en el análisis detallado de lo que se ha denominado como fenómeno de asociación planta-nodriza, por el cual plántulas de diferentes especies se establecen bajo el dosel de árboles y arbustos perennes (plantas nodriza).

El marco teórico, los antecedentes y las hipótesis generales (capítulo 2), están basados en el hecho de que históricamente se ha conceptualizado que los desiertos son ecosistemas limitados por el agua. Posiblemente por esta razón, los estudios de la adaptación y la competencia han ocupado casi por completo la atención de los ecólogos por décadas, y por lo que las interacciones de índole positivo como el nodricismo han sido mínimamente integradas a la teoría ecológica de estos ambientes. Determinar la relevancia de esta interacción positiva en el establecimiento de nuevos individuos en las comunidades desérticas fue el objetivo general planteado.

Los patrones y la dinámica del establecimiento de especies de cactáceas en el Valle de Tehuacán, el centro de diversidad más importante de cactáceas columnares en América, es el tema que se analiza en los capítulos 3 al 5. Estas partes de la tesis están constituídas por tres artículos mandados a revistas con arbitraje internacional: dos aceptados en la revista Journal of Vegetation Science y uno actualmente en revisión en la revista Journal of Ecology. En el primero se presenta evidencia del fenómeno del

nodricismo en el Valle de Tehuacán para cinco especies de cactáceas. En este mismo reporte, se hace una caracterización del microambiente por debajo de diferentes especies. En el segundo, se analiza detalladamente la interacción entre la cactácea columnar Neobuxbaumia tetetzo y la nodriza Mimosa luisana. En este trabajo, se determina que existe una dinámica de reemplazamiento de las plantas nodrizas por las cactáceas que es debida a la competencia, evidenciando a su vez que la naturaleza de la interacción puede cambiar en el tiempo, empezando con un comensalismo y terminando en competencia o inclusive en un sistema análogo al de depredador-presa de Lotka-Volterra.

El tercer artículo, comprende un análisis experimental de las causas del nodricismo entre N. tetetzo y M. luisana. Los resultados indican que el microambiente producido por las plantas nodrizas, principalmente desde el punto de vista de la modificación del ambiente físico y de la protección de las plántulas contra la radiación y pérdida excesiva de agua, son las causas de la asociación interespecífica. La generalización de estos resultados experimentales a otros ecosistemas áridos, se obtuvo mediante el análisis de la distribución circular de especies de suculentas que habitan en los desiertos de Altar en Sonora y en el del Vizcaíno en Baja California, ambos localizados fuera de la faja intertropical. Ahí se encontró que la mayoría de los individuos pertenecientes a la diferentes especies se concentran en la parte norte de la planta-nodriza, la cual está sombreada durante todo el año.

En el último capítulo se hace una síntesis acerca de la importancia del proceso estudiado y lo que se considera son las consecuencias teóricas más importantes para el entendimiento de la dinámica de estos sistemas. En términos generales las comunidades de las zonas áridas y semiáridas deben ser conceptualizadas como mosaicos con estados de ocupación del espacio en donde coinciden diferentes especies vegetales, animales y microorganismos. Se concluye que el nodricismo promete ser un tema central en las investigaciones ecológicas de los desiertos por sus importantes implicaciones teóricas a nivel de individuo, población y comunidad.

SUMMARY

The research presented in the six chapters of this doctoral thesis has as a central theme the establishment of species in arid and semiarid plant communities. Specifically, the study concentrated on the analysis of the nurse-plant association phenomenon, which is caracterized by the seedling establishment of different species beneath the canopies of perennial trees and shrubs (acting as nurse-plants) in arid lands.

The general approach to the problem and the main hypotheses (chapter 2) are based on the fact that deserts have historically been considered as water-limited ecosystems. Possibly for this reason, studies on adaptation and competition have occupied the attention of the ecologists for several decades. At the same time, positive interactions like the nurse-plant phenomenon have not been considered as equally important in the arid-land ecological theory. The assessment of the importance of positive biotic interactions in the establishment of new individuals in the community was the central objective of this work.

The establishment pattern and dynamics of cactus species in the Tehuacán Valley, a center of diversity for giant columnar cacti in America, are considered in the chapters 3, 4 and 5. These chapters are formed by three papers that have been sent for their publication to international magazines: two have already been accepted by the Journal of Vegetation Science, and the other has been submitted to the Journal of Ecology. In the first paper, evidence that five species of cacti recruit themselves beneath the canopies of nurse-plants, and a characterization of

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the microenvironment beneath trees and shrubs acting as nurse-plants, are presented.

In the second paper, the interaction between the columnar cactus Neobuxbaumia tetetzo and the nurse-plant Mimosa luisana is analyzed. In this paper, a replacement pattern due to competition is detected, in which the columnar cactus excludes the nurse-plant. The results also indicate that the nature of the interaction may change in time, starting with comensalism and finishing with competition, or even in a cycle analogous to a Lotka-Volterra predator-prey system.

The third paper presents the experimental analysis of the underlying mechanisms associated to the establishment of N. tetetzo beneath the canopy of M. luisana individuals. The results show that the amelioration of the physical environment, mainly the protection of the seedlings from direct solar radiation and excessive transpiration, is the main determinant of the nurse-plant effect. The generality of these results was tested by analyzing the circular distribution of saplings of succulents with respect to the nurse-plants in the Deserts of Altar in Sonora and the Vizcaíno in Baja California, which are situated outside the tropical belt. Most of the individuals showed a non-random circular distribution, concentrating towards the north which is shaded all the year.

The last chapter a synthesis is made on the relevance of the nurse-plant association phenomenon and of its theoretical consequences for the understanding of the dynamics of deserts. In general terms, arid environments should be conceptualized as mosaics with different patches in which plants, animals and

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microorganisms coexist. It is concluded that the nurse-plant
phenomenon promises to develop as a central theme in the
ecological investigations in arid and semiarid regions, given its
theoretical implications on individual, population and community
levels.

INTRODUCCION

¿ Cuáles son los factores que determinan la dinámica de los eventos ecológicos en los desiertos ? Esta ha sido la pregunta central, y la base de una intensa polémica desde el inicio del presente siglo. En los trabajos pioneros realizados por Shreve (1929, 1931, 1942) se señala al agua como el factor de mayor significancia en estos sistemas biológicos. Noy-Meir (1973), que sintetiza los aspectos más importantes acerca de la ecología de las zonas áridas, considera también a los desiertos como "ecosistemas limitados por el agua". Señala, en este sentido, una serie de aspectos relevantes tales como los bajos niveles de precipitación y su impredecibilidad, expresada tanto en su variabilidad temporal (entre años y estaciones) y espacial a niveles regional y local. De acuerdo con esta conceptualización, factores como la temperatura y la radiación son importantes, dado su impacto en el balance hídrico de los organismos y del suelo, en particular su capacidad de almacenamiento de agua y la accesibilidad de ésta para las plantas y los animales. Sin embargo, cómo y qué tipo de interacciones surgen entre las poblaciones, ya sea de la misma o de diferentes especies, a través de la competencia o inclusive de la cooperación, han sido preguntas muy postergadas en la literatura ecológica de las zonas áridas, aún cuando su ocurrencia ya había sido señalada en diferentes estudios (Muller 1953; Agnew & Haines 1960; Beatley 1969; Waisel 1971).

De la misma manera, la alta diversidad de las formas de vida en los desiertos que ha sido interpretada por diversos autores como la expresión de diferentes soluciones al problema del uso

del agua, el recurso más limitante (Solbrig et al. 1977), fue la base para aseverar sobre la dificultad o incluso la imposibilidad de la existencia de competencia interespecífica (Shreve 1942, Went 1942), pero favoreciendo la coexistencia y la riqueza específica de las comunidades desérticas (Noy-Meier 1980).

Es claro, que aceptar que los procesos ecológicos de estas comunidades están determinados por el factor agua, lleva a la conclusión que con el estudio exclusivo de la autoecología de las especies, estaríamos en condiciones de entender el funcionamiento de estos ecosistemas. Sin embargo, a partir de la década de los sesentas la demostración de la existencia de competencia fue el tema central de un gran número de investigaciones, y no es hasta el trabajo de Fonteyn & Mahall (1978) cuando es demostrada de manera directa. Tal y como ha sido señalado en varios de estos estudios la competencia ocurre en las regiones áridas y semiáridas, destacándose su importancia en la estructuración de las comunidades (Fowler 1986). Sin lugar a dudas, el estudio de la adaptación y el paradigma de la competencia han ocupado el interés de las investigaciones en desiertos durante los últimos 30 años, y quizá por tal motivo otras interacciones principalmente las de índole positivo, han quedado relegadas por mucho tiempo.

El presente trabajo, muestra evidencia que permite señalar que el paradigma del factor agua debe ser reconsiderado, ya que se documenta que especies vegetales de los desiertos presentan interacciones que inician con el establecimiento de algunas bajo el dosel de otras. Este comensalismo (Barbour et al. 1980), de

hecho es considerado a partir de la realización de este trabajo, como el fenómeno más importante y significativo dentro del campo de las interacciones entre plantas de los desiertos. En términos generales, árboles y arbustos modifican el microambiente por debajo de su dosel y actúan como plantas nodriza, facilitando el establecimiento de plantas anuales y perennes generando mosaicos de ocupación del espacio. Estos parches, representan los escenarios donde se dan las interacciones entre las especies.

Este fenómeno fue reportado desde el siglo pasado para la asociación entre el saguaro (Carnegiea gigantea) y el palo verde (Cercidium mycrophyllum) en el desierto Sonorense (Engelman 1859). Aun cuando dicha interacción fue estudiada por Shreve (1931) y reportada para otras especies anuales y perennes (Tabla 1), no es sino hasta que McAuliffe (1984a, 1988) y Fowler (1986) la consideran importante en el entendimiento de procesos ecológicos en los desiertos. De éstos, quizá uno de los más significativos es el del establecimiento de nuevos individuos en la comunidad, ya que al ocurrir bajo condiciones impredecibles de precipitación, altos niveles de radiación solar, temperaturas en el suelo de hasta 70° C, así como bajo el impacto de la actividad de granívoros y herbívoros (Chew & Chew 1970; Inouye, Byers & Brown 1980), puede afectar sensiblemente la dinámica de las poblaciones y quizá la estructura y la diversidad de las comunidades.

Se ha propuesto que las plantas nodriza proveen protección contra la radiación y el daño producido por las heladas (Shreve 1931; Turner et al. 1966; Steenbergh & Lowe 1976; Nobel 1980; Nobel & Geller 1987) así como contra el daño mecánico incluida la

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depredación (Niering et al. 1963; Steenbergh & Lowe 1977, 1983; McAuliffe 1984b; Jaksic & Fuentes 1980; Parker 1982). Los patrones de asociación también han sido atribuídos a una dispersión no aleatoria por los animales (Steenbergh & Lowe 1977) o por el viento (Went 1942), así como el hecho de que el suelo por debajo de los arbustos de las zonas áridas y semiáridas tienen mayores concentraciones de nitrógeno que las zonas abiertas adyacentes (García-Moya & McKell 1970; Wallace & Romney 1972; Nishita & Haug 1973; West & Klemmedson 1978; entre otros) creando islas de fertilidad y quizá de importancia causal en las asociaciones interespecíficas. Recientemente el nitrógeno ha sido considerado como un factor limitante importante en las zonas áridas (West & Klemmedson 1978; West 1981; Reynolds 1986). También las plantas de las zonas áridas y semiáridas pueden colectar agua a partir de las lluvias ligeras, depositándola en la base (Glover & Gwynne 1962), y favoreciendo las asociaciones entre especies en estos ambientes.

Todas estas ideas forman el contexto teórico, y los antecedentes de las hipótesis que se exploran en el presente trabajo, el cual inicialmente, se abocó a la búsqueda de evidencia bibliográfica que permitiera asegurar que el fenómeno del nodricismo fuera universal a las zonas áridas y semiáridas del mundo, (Tabla 1). A su vez, determinar el porcentaje de especies dentro de una comunidad que comparten el patrón, daría nuevas evidencias de su importancia. En México, el establecimiento predecible de especies por debajo de arbustos, ha sido reportado para Idria columnaris por Humphrey (1974), para la

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jojoba, Simmondsia chinensis por Murrieta & Espericueta (1977) y Molina (1980), así como para nopaleras del desierto Chihuahuense por Yeaton & Romero-Manzanares (1986). Unicamente en este último se aportan datos estructurales de la vegetación a partir de los cuales se dedujeron patrones del establecimiento de las especies, mientras que los demás señalan el establecimiento de las especies de manera anecdótica. Con base en lo anterior, determinar la ocurrencia del fenómeno en ambientes áridos mexicanos constituyó otro de los aspectos abarcados en esta tesis. Particularmente, las preguntas centrales para esta fase de la investigación estaban relacionadas con la identidad de las plantas "nodriza", las subordinadas, el grado de dependencia de estas últimas sobre las primeras, las causas que determinan estas asociaciones interespecíficas así como su impacto sobre la dinámica de poblaciones y consecuentemente como posible proceso estructurador en las comunidades. Esta etapa se desarrolló con el estudio de los patrones y la dinámica del establecimiento de especies de cactáceas en el Valle de Tehuacán, entre abril de 1987 y Octubre de 1990. La zona de estudio, localizada dentro de la provincia fitogeográfica del Valle de Tehuacán-Cuicatlán (Rzedowski 1978), es considerada como el centro de más alta diversidad de cactáceas columnares a nivel mundial (Briones et al. 1989). Su flora se calcula en aproximadamente 2620 especies, lo cual equivale a más del 1% de la flora del mundo con un elevado grado de endemismo (Dávila et al. 1990 y Smith 1965), rasgo que comparte con otras zonas áridas de México (Rzedowski 1962). A nivel de la vegetación, las comunidades vegetales más ampliamente distribuídas y en donde se trabajó, son la Tetechera, en la cual

la especie dominante es la cactácea columnar Neobuxbaumia tetetzo, y el Cardonal dominado también por otra cactácea columnar, Cephalocereus hoppenstedtii.

Los resultados de estas investigaciones se presentan en tres artículos, dos de los cuales ya han sido aceptados en la revista Journal of Vegetation Science, y el tercero que ha sido sometido a arbitraje en la revista Journal of Ecology.

En el primero se presenta evidencia del proceso para cinco especies de cactáceas del Valle de Zapotitlán de las Salinas. Se determina la identidad de las especies nodriza, y se caracteriza el microambiente por debajo de su copa.

En el segundo artículo, se analiza detalladamente la interacción de la cactácea columnar Neobuxbaumia tetetzo, con la especie nodriza Mimosa luisana. Se presenta evidencia que N. tetetzo reemplaza competitivamente a la especie nodriza. A su vez, analizando las relaciones alométricas entre las raíces y el tallo principal de la cactácea, con respecto al sistema radicular de la nodriza, se buscó información relacionada con la ocupación de las raíces en el suelo, que apoyara la hipótesis que la competencia por agua es el mecanismo asociado al reemplazamiento.

Las causas que determinan la asociación entre N. tetetzo y M. luisana por medio de un análisis experimental bajo condiciones de campo es el tema tratado en el tercer artículo.

En el último capítulo se hace una síntesis sobre las perspectivas y alcances del fenómeno del nodricismo para el entendimiento de la dinámica de los ecosistemas desérticos.

TABLA 1.- ESPECIES REPORTADAS EN LA LITERATURA CUYO PATRON DE
ESTABLECIMIENTO OCURRE POR DEBAJO DE ARBUSTOS. SE ANOTA LA
ESPECIE, LA FORMA DE VIDA, LA FUENTE Y LA LOCALIDAD DE ESTUDIO.

REPORTES CON PLANTAS ANUALES

FUENTE	ESPECIE(S)	LOCALIDAD
Jepson (1925)	varias	D. California, E.U.
Shreve (1931, 1934, 1942)	varias	D. Sonorense, E.U.
Osborn et al. (1932)	varias	D. Australiano.
Went (1942)	varias	D. California, Colorado y Mojave.
Muller (1953)	Malacothrix sp., Rafinesquia sp., Phacelia sp, Chenictis sp.	D. California, E.U.
Muller & Muller (1956)	varias	D. California, E.U.
Agnew & Haines (1960)	varias	D. Irak.
Evans & Young (1970)	varias (malezas)	D. Sonorense, E.U.
Halvorson & Patten (1975)	varias	D. Sonorense, E.U.
Jaksic & Fuentes (1980)	varias	D. Chileno.
Shmida & Whittaker (1981)	varias	D. California, E.U.
Yavitt & Smith (1983)	gramíneas	Pastizales de Arizona.

REPORTES CON PLANTAS PERENNES

FUENTE	ESPECIE(S)	LOCALIDAD
Engelmann (1859)	Carnegiea gigantea	D. Sonorense, E.U.
Compton (1929)	Suculentas	D. de Karoo, Sudáfrica.
Shreve (1931,1934, 1942)	varias	D. Sonorense, E.U.
Jaeger (1961)	Carnegieae gigantea y otras cactáceas.	D. Sonorense, E.U.
Glover & Gwynne (1962)	Justicia spp., Achyranthes sp., Hypoestes sp.	D. Este de Africa, Kenia.

McDonough (1963)	Carnegiea gigantea	D. Sonorense, E.U.
Niering et al. (1963)	Carnegiea gigantea	D. Sonorense, E.U.
Hastings & Turner (1965)	Carnegiea gigantea	D. Sonorense, E.U.
Greig-Smith & Chadwick (1965)	Acacia tortilis	D. Nilo, Sudán
Turner et al. (1966)	Carnegiea gigantea	D. Sonorense, E.U.
Turner et al. (1969)	Carnegiea gigantea	D. Sonorense, E.U.
Sadr-Uddin & Qadir(1970)	Euphorbia caducifolia	D. Distrito de Karachi, Pakistán.
Humphrey (1974)	Idria columnaris	D. Sonorense, México.
Steengergh & Lowe (1976, 1983)	Carnegiea gigantea	D. Sonorense, E.U.
Murrieta & Espericueta (1977)	Simmondsia chinensis	D. Sonorense, México.
Sherbrooke (1978)	Simmondsia chinensis	D. Sonorense, E.U.
Yeaton (1978)	Opuntia leptocaulis	D. Chihuahuense, E.U.
Molina (1980)	Simmondsia chinensis	D. Sonorense, México.
Jordan & Nobel (1979)	Agave desertii	D. Sonorense, E.U.
Mares et al. (1977)	Amaranthus fimbriatus, A. palmeri, Tidestromia lanuginosa, Kallstroemia californica, K. grandiflora, Euphorbia spp., E. hyssopifolia, Ipomoea sp., Ambrosia confertoflora.	D. Sonorense, E.U
	Boerhaavia coccinea, Solanum sp., Verbesina encelioides, Bidens subalternus.	D. del Monte, Argentina.
Vandermeer (1980)	Carnegiea gigantea	D. Sonorense, E.U.
Parker (1982)	Gutierrezia microcephala	D. Chihuahuense, E.U.
McAuliffe (1984a, 1984b, 1988)	Mammillaria microcarpa, Echinocereus englemannii	D. Sonorense, E.U.

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	Carnegieae gigantea,	
	Larrea tridentata	
	Fouquieria splendens,	
	Jatropha cardiophylla,	
	Krameria sp,	
	Cercidium microphyllum,	
	Opuntia acanthocarpa,	
	Opuntia phaeacantha,	
	Ferocactus wislizenii,	
	Echinocereus fasciculatus,	
	Opuntia leptocaulis,	
Hutto *et al*. (1986)	*Carnegiea gigantea*	D. Sonorense, E.U.
Yeaton & Romero-Manzanares (1986)	*Opuntia* spp.	D. Chihuahuense, México.
Smith & Goodman (1986)	6 especies.	Savanas Sudafricanas.
McAuliffe & Janzen(1986)	*Carnegiea gigantea*	D. Sonorense, E.U.
Fowler (1986)	varios	D. Sonorense, E.U.
Jordan & Nobel (1989)	*Carnegiea gigantea*	D. Sonorense, E.U.
Yeaton & Esler (1990)	varios	D. Karoo, Sudáfrica.

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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 valley Zapotitlán de las Salinas, central Mexico, harbours a high diversity of cacti. Pattern analysis indicated that the establishment of two columnar cacti, *Neobuxbaumia tetetzo* and *Cephalocereus hoppenstedtii*, and 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 too strong 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*; *Mammillaria 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 1990) 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 1990).

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 valley Zapotitlán de las Salinas (18° 20' N, 97° 28' W; states of Puebla and Oaxaca), 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 xerilo', 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; Rzedowski 1973), 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 to 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.
Cephalocereus hoppenstedtii	76	33.8 ± 3.4	51.7 ± 4.7
Neobuxbaumia tetetzo	16	30.2 ± 5.5	51.7 ± 4.7
Mammillaria colina	30	28.7 ± 2.2	51.7 ± 4.7
M. casoi	11	32.2 ± 5.0	51.7 ± 4.7
Coryphanta pallida	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 analysis, three were found with a number of associated

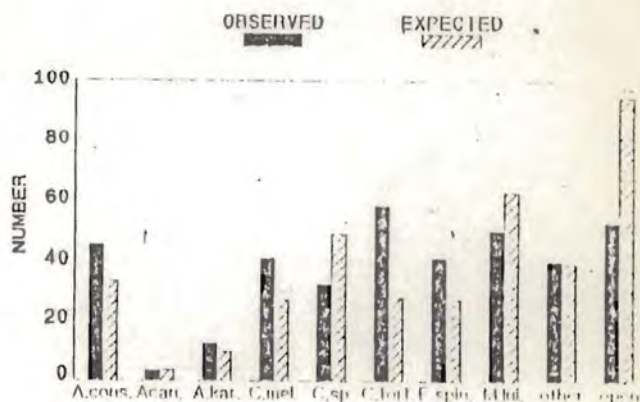**Fig. 1.** Observed and expected numbers of cacti associated with perennial plants: $\chi^2 = 80.94$, $P = 0.005$. A. cons. = *Acacia constricta*; Acan. = *Acanthaceae* 1; A. kar. = *Agave karwinskii*; C. mel. = *Caesalpinia melanadenia*; C. sp. = *Caesalpinia* sp.; C. tort. = *Castela tortuosa*; E. 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	C. hoppenstedtii			M. colina			M. casoi			C. pallida			N. tetetzo		
	Obs.	Exp.	Test	Obs.	Exp.	Test	Obs.	Exp.	Test	Obs.	Exp.	Test	Obs.	Exp.	Test
Acacia constricta	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
Acanthaceae	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
Agave karwinskii	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
Caesalpinia melanadenia	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
Caesalpinia sp.	6	5.4	0.27	13	28.3	− 3.00	0	3.3	− 1.80	10	10.3	0.00	3	1.7	1.0
Castela tortuosa	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
Eupatoriwn spinosarum	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
Mimosa luisana	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

cacti higher than expected by chance (χ^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*, *Mammillaria 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* (Fig. 6).

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).
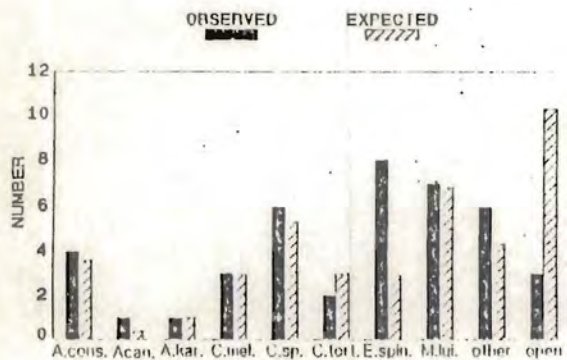

Fig. 2. Observed and expected numbers of *Cephalocereus hoppenstedtii* individuals, associated with perennial plants. χ^2 = 16.8, P < 0.005.

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
C. hoppenstedtii	16	6	9	17	7.18	NS
N. tetetzo	19	10	14	9	4.77	NS
M. casoi	9	10	4	9	2.75	NS
M. colina	20	24	14	18	2.73	NS
C. pallida	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*.
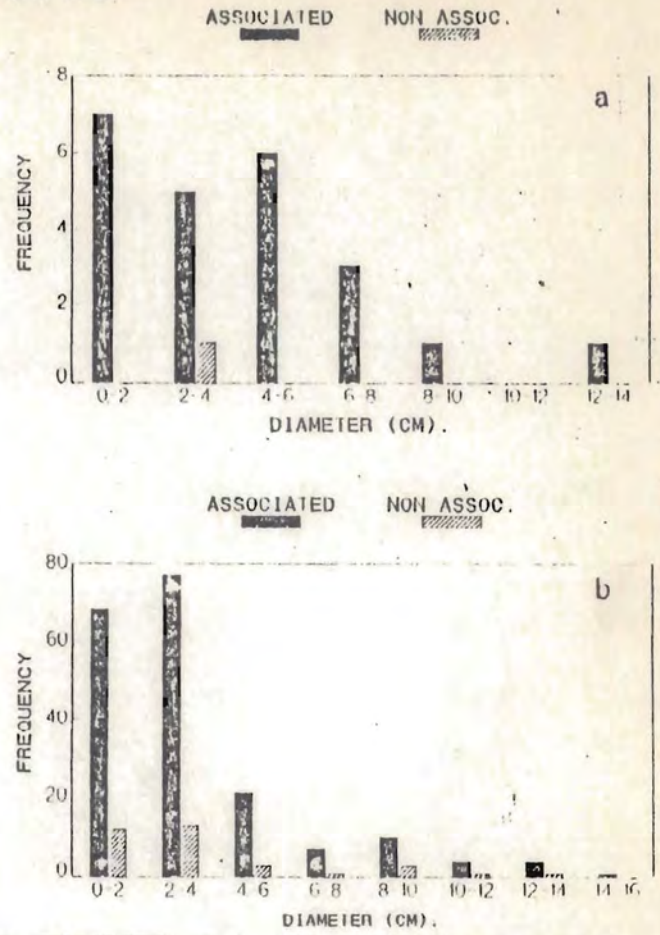
Fig. 4. Diameter distribution of individuals of globose cacti associated and not associated with perennial plants: (a) *Mammillaria casoi*, (b) *Mammillaria colina*.

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).

Fig. 6. Temperatures on the soil surface beneath the canopy of *Mimosa luisana*, *Prosopis laevigata* and *Cercidium praecox*, and in open space for a 24-hour period (July 16, 1988).

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 benea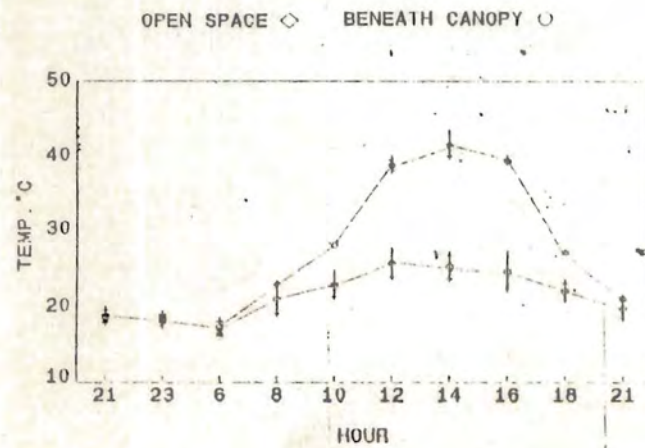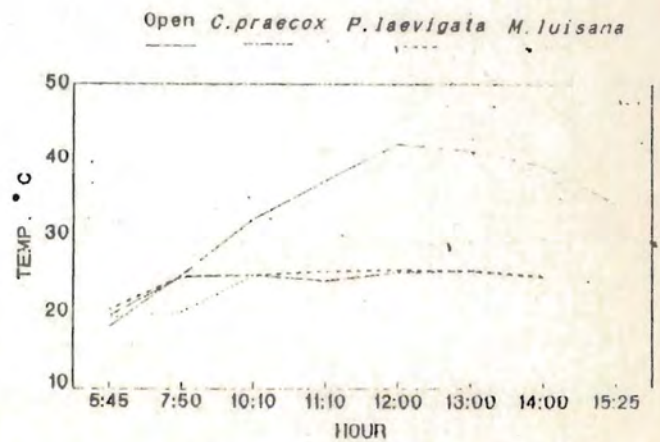th the canopy of perennial plants (e.g. McAuliffe 1984a, 1984b; Yeaton & Romero-Manzanares 1986; Yeaton 1978). The considerable difference in midday temperature found between open space and beneath shrubs (also reported by Fowler 1986 and McAuliffe 1988), suggests that the protection against radiation 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 suggest 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 a 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 during 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.

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 dynamical 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 (cf. Steenbergh & Lowe 1983).

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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 result together with analysis of height class distributions for cacti associated and not associated with *M. luisana* respectively, indicated the replacement of *M. luisana* by *N. tetetzo*. *Mimosa luisana* plants having *N. tetetzo* associated with them had greater amounts of dead basal area than *M. luisana* lacking associated *N. tetetzo*. This indicated the possible importance of competition from *N. tetetzo* in driving the replacement process.

The root system of *N. tetetzo* is shallow, reaching not more than 30 cm depth. Interception of soil water by roots of *N. tetetzo* before penetration to deeper roots of *M. luisana* may be the mode of competition between the two species.

Keywords: Competition; Facilitation; Giant columnar cactus; Replacement pattern.

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 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. References are included in a parallel study (Valiente-Banuet et al. 1990) in which evidence of the nurse effect is shown for five cacti. In the present study we analyze the spatial relationships of tetecho, *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 the valley Zapotitlán de las Salinas in central Mexico (18° 20' N, 97° 28' W), situated 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. 1990).

Analysis of spatial relationships

Vegetation composition, patterns of distribution and association between species were determined in a 20 m x 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 *N. tetetzo* individual, height and the presence
or absence of a shrub canopy above it were recorded.
The number of *N. tetetzo* individuals under each peren-
nial species was counted and a chi-square test was
carried out to test the null hypothesis 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 distribu-
tion) is regarded as a significant deviation.

In order to detect a replacement between *N. tetetzo*
and the dominant associated shrub, *Mimosa luisana*
Brandegee, *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 × 2 contingency table.
Chi-square tests were carried out under the null hypoth-
esis of independent dispersion of both species. Segrega-
tion was estimated using Pielou's index:

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

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 = π /4. Σ 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-sin 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
together with proximal and distal diameters of each
excavated root segment were used to calculate surface
area of root segments as truncated cones. In order to
estimate the ground surface area explored by the roots,
the average length of the main root branches was com-
puted and used as the radius of a circle. 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 be-
neath and outside the canopy of *M. luisana* was deter-
mined by a modified micro-Kjeldahl technique.

Results

Spatial relationships

In the 20 m × 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 individu-
als 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 dis-
tributed 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,
$P < 0.0001$). Also there is 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 individu-
als (Fig. 2). Finally, a significant effect of the interaction
of these factors was found (F-ratio = 3.1, $P = 0.005$).

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 |*dij*| > 2 are significantly different (5 % of the normal distribution). CC% = Canopy cover %.

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

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 ± 0.002 % and 0.19 ± 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

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-square	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

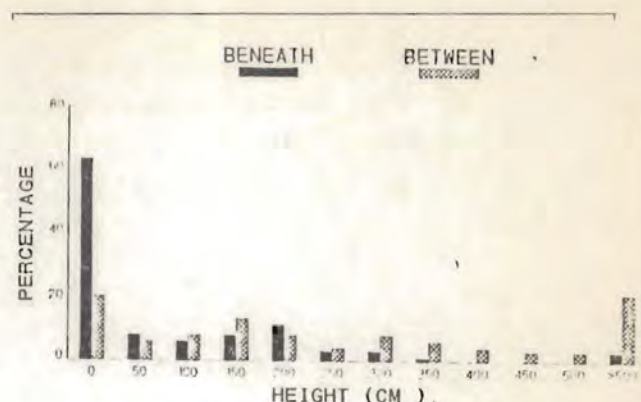** $p < 0.001$; * $p < 0.05$; NS not significant, $p > 0.05$.

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

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 dynamical 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 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 rhizospheral 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

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 (cm²); SA = structural area (cm²); OV = occupied volume (cm³).

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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Fig. 2.

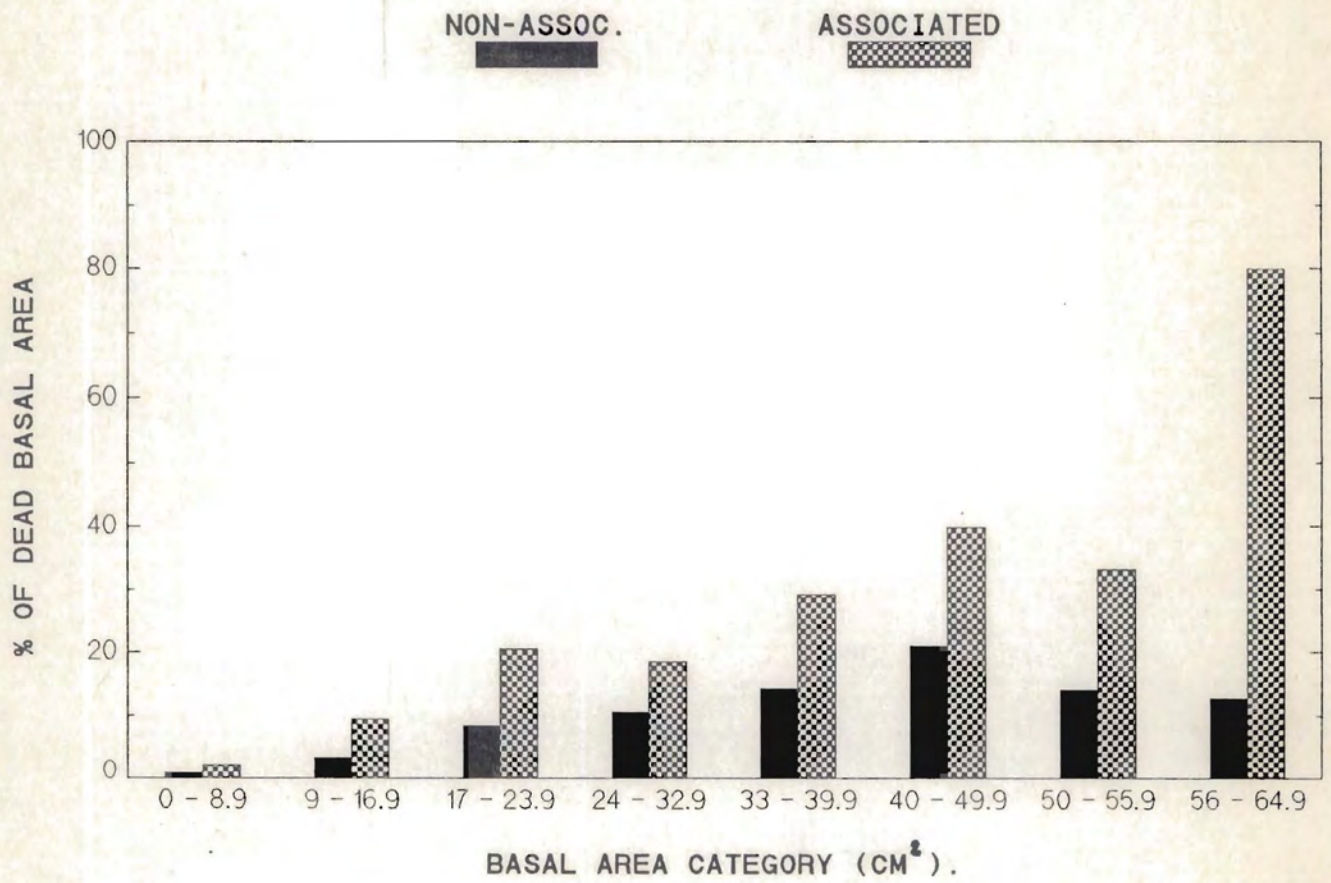SHADE AS A CAUSE OF THE ASSOCIATION BETWEEN THE CACTUS

NEOBUXBAUMIA TETETZO AND THE NURSE-PLANT MIMOSA LUISANA IN

THE TEHUACAN VALLEY, MEXICO.

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Suggested running head: Shade as a cause of interspecific
association.

First author will check the proofs.

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SUMMARY

1.- The establishment phase of <u>Neobuxbumia tetetzo</u>, a giant
columnar cactus dominant in the Tehuacán Valley in central-
southern Mexico, occurs mostly beneath the canopies of trees and
shrubs which act as nurse-plants. This pattern cannot be
attributed to preferential seed dispersion, as <u>Neobuxbaumia</u>
fruits open while still on the plant, dropping ca. 1000 seeds
per fruit which fall randomly around the parent plant.

2.- An experimental field analysis of germination and
survivorship of cohorts under different environmental conditions
was done in order to determine the underlying mechanisms
associated to the establishment of <u>N</u>. <u>tetetzo</u> beneath the
canopies of <u>Mimosa luisana</u>, a legume which is the most abundant
shrub in the community.

3.- The experimental treatments followed a factorial design,
with three levels of radiation (open space, artificial
homogeneous shade and the shade produced by <u>Mimosa luisana</u>), two
levels of predation (exclusion and non-exclusion of predators),
and four topographic aspects (North, East, South and West).

4.- Seed germination was lowest in open spaces. In all
treatments exclusion from predators significantly increased
seedling establishment. Only the shaded treatments had live
individuals at the end of the experiment. The results suggest
that the nurse-plant effect between <u>Neobuxbaumia tetetzo</u> and
<u>Mimosa luisana</u> is chiefly the result of differential survival in
shaded microsites with less direct solar radiation, and
consequently with lower daytime temperatures and lower

evaporative demand.

5.- In order to determine the generality of these results, field samplings were conducted in two Mexican deserts located outside the tropical belt: the Vizcaíno Desert in Baja California and the Gran Desierto in Sonora. As in these deserts direct solar radiation has a southern azimuth all year round, a non-random circular distribution of the saplings of succulent species with respect to the nurse-plants would be expected, with establishments concentrating mostly towards the shaded north. Five of the six succulent species analyzed showed a significant trend to establish north of the nurse-plants.

6.- The results of this study support the idea that direct solar radiation, temperature and evaporative demand are the main factors related to the nurse-plant effect. The amelioration of the physical environment produced by the nurse-plants is of primary importance as a driving force in the patch-structurated population dynamics of many desert plants, affecting the structure and diversity of many desert and semidesert communities.

INTRODUCTION

In deserts the establishment phase of perennial plants occurs under unpredictable conditions of precipitation, high predation rates, and in soils with high temperatures and low water content. A knowledge of the dynamics of early seedling growth is important for an understanding of the dynamics of populations and the structure of desert communities. In many arid zones, the recruitment of several species occurs under perennial "nurse" plants, which modify the environment beneath their canopies (Jepson 1925; Halvorson & Patten 1975; Turner et al. 1966; McAuliffe 1988; among others).

Many explanations have been given for this phenomenon. The facilitation process may occur because the acumulation of seeds beneath perennial plants may be higher than in openings. This non-random dispersion of seeds has been attributed to transport by animals (Yeaton 1978; Hutto, McAuliffe & Hogan 1986; Olin, Alcorn & Alcorn 1989), wind (Went 1942) or water (Agnew & Haines 1960). Following germination, greater predation of individuals that are not hidden by the nurse-plants (Niering et al. 1963; McAuliffe 1984b; 1986; 1988; Sherbrooke 1977; Jaksic & Fuentes 1980; Parker 1982; etc), the facilitation of seedling establishment by reduced direct solar radiation and lower soil temperatures beneath the nurse-plant (Turner 1966; 1981; Steenbergh & Lowe 1977; McGinnies 1981; Nobel 1980, Franco & Nobel 1989), the protection of seedlings during freezing periods (Steenbergh & Lowe 1977, 1983; Nobel 1980) and higher nutrient levels of the soil beneath canopies (García-Moya & McKell 1970, Franco & Nobel 1989, McAuliffe 1988) may enhance the survival of

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seedlings under perennial shrubs. Finally, seed germination may be increased by the accumulation of fine windblown material that modifies soil structure beneath perennial plants (Wallace & Romney 1980).

In the Tehuacán Valley in central-southern Mexico, the establishment phase of Neobuxbaumia tetetzo (Weber) Backeberg, a giant columnar cactus dominant of an extensive vegetation type locally called Tetechera, occurs mostly beneath the canopies of trees and shrubs (Valiente-Banuet, Vite & Zavala-Hurtado, in press). This association is characterized by a replacement pattern in which open spaces are colonized by shrubs apparently capable to establish themselves under harsh physical conditions. Later, these shrubs facilitate the establishment of cactus seedlings beneath their canopies. As the cacti grow the nurse plants die and the older cacti are usually seen growing alone. This replacement pattern has been associated to competition between N. tetetzo and the most common shrub in the community, Mimosa luisana Brandeg. (Valiente-Banuet et al. a in press). Similarly, Yeaton (1978), McAuliffe (1984a) and Yeaton & Romero-Manzanares (1986) have reported similar recruitment and replacement processes for other shrub-cactus systems.

In this work, an experimental analysis of the germination and survivorship of cohorts in the field under different conditions is described. This analysis allowed the elucidation of the underlying mechanisms associated with the establishment of Neobuxbaumia tetetzo beneath the canopies of Mimosa luisana. The factors analyzed were radiation, herbivory, soil type and

aspect of the slope.

MATERIALS AND METHODS

The study site

The study was conducted at the semiarid Valley of
Zapotitlán (18°20′ N, 97°28′ W), a local basin of the Tehuacán
Valley in the state of Puebla, Mexico. This region owes its
aridity to the rain shadow produced by the Eastern Sierra Madre
(Smith 1965). It has an average rainfall of 380 mm, an annual
mean temperature of 21°C, and very rare freezing events (García
1973). Soils are rocky, derived from sedimentary and
metamorphic rocks. The main vegetation type is an arid tropical
scrub ("matorral xerófilo", Rzedowski 1978) in which giant
columnar cacti constitute dominant elements of the vegetation.
More specifically, the study was made on a hill located inside
the Botanical Garden of the Secretary of Urban Development and
Ecology (SEDUE), which is situated approximately 30 km South of
the city of Tehuacán. This is a mountainous zone in which
Neobuxbaumia tetetzo, a branched columnar cactus that reaches
12 m in height, is the dominant species with densities of more
than 1200 adults/ha (adults are arbitrarily defined as
individuals higher than one metre). The flowering and fruiting
seasons occurs from mid May until end of June, just before the
rainy season. First reproduction occurs when the plant is
around two metres high. The fruits open on the plant and
although some of the seeds are removed by birds, most of the
seeds (1-2 mm in diameter) fall to the ground forming a uniform
black carpet. Under laboratory conditions, the seeds have 99 %

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germination. Seedlings recruit themselves beneath the canopy of several species of shrubs. The most frequent of these nurse plants is the deciduous legume Mimosa luisana (Valiente-Banuet, Vite & Zavala-Hurtado, in press).

Experimental design

Within the hill located inside the botanical garden, four 20 m X 20 m quadrats were located, each on a slope with a different aspect (North, East, South, West). The experimental treatments followed a factorial experimental design, with three levels of radiation (open space, artificial homogeneous shade and the shade produced by Mimosa luisana), two levels of predation (exclusion and non-exclusion of predators, not distinguishing between vertebrates and invertebrates), and the four different aspects (N, E, S, W). Thus, for each aspect the treatments were open space, artificial shade and beneath nurse-plants each with excluded and non-excluded conditions. For each treatment 180 seeds were sown in a square plot 30 cm by side. The seeds were located on the soil surface, previously cleaned of other seeds. Care was taken to minimise disturbance of soil structure. Because artificial shades were established in openings, soil conditions in this treatment differed initially from those beneath perennial plants. The experiment was set up on 15 July 1988.

Rodents and birds were excluded by covering completely the experimental units with a 12 mm wire mesh with the bottom edges buried in the soil to a depth of 10 cm. Ants were excluded with an insecticide powder (Clordane) which was applied every three

days during the first week and every eight days after, until the seedlings were big enough to resist uprooting by ants. Shaded plots were established using green 1.5 mm nylon nets that were overlapped until light intensity was within one standard deviation of the mean intensity beneath the canopies of Mimosa luisana.

Nurse-shaded plots were always established in the base of Mimosa luisana individuals of similar size, North of the main stem. The 24 treatment combinations were replicated three times, giving a total of 72 experimental units.

Data analysis

Establishment of seedlings

Success in germination and initial establishment for the different treatments was measured as the number of live seedlings present in each plot one week after sowing (in moist soil, N. tetetzo germinates in approx. 48 h). Differences were evaluated through a contingency table analysis made with a log-linear model (McCullagh & Nelder 1983). The null hypothesis assumed an equal number of seedlings establishing in all the treatments. Departures from this null model were examined for statistical significance.

Comparison of survivorship curves for the different treatments

For the comparison of the survivorship curves among treatments log-linear models were fitted considering time as a continuous variable and predation, aspect and shadow as statistical factors (i.e. categoric variables). The models were fitted with the GLIM statistical package (Healy 1988) and the

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goodness-of-fit was evaluated with a X^2 test using the $\underline{G}$ statistic.

The model was based on the following assumptions. Consider a species with constant mortality ($\underline{d}$). In a cohort, by definition, it holds that

$$\frac{1}{N}\cdot\frac{dN}{dt} = -d \qquad , \quad (1)$$

Integrating eqn.(1), it can be seen that $\underline{N}_{\underline{t}} = \underline{N}_0 \exp(-\underline{d}.\underline{t})$, which can be also written as

$$N_t = \exp(a - d.t) \qquad , \quad (2)$$

where $\underline{a} = \ln \underline{N}_0$ and $\underline{N}_{\underline{t}}$ is the number of survivors at time $\underline{t}$. Eqn. 2 is a log-linear model, which can be fitted through the corresponding statistical procedure (McCullagh & Nelder 1983). This model describes a type II survivorship curve (constant mortality rate, Pearl 1928).

If, on the other hand, mortality is not constant in time, eqn. (1) can be now written as

$$\frac{1}{N}\cdot\frac{dN}{dt} = -d + b.t \qquad , \quad (3)$$

where $\underline{d}$ is the initial mortality rate at $\underline{t}=0$, and $\underline{b}$ is a parameter describing how this initial rate is increased (if $\underline{b}<0$) or decreased (if $\underline{b}>0$) with time. Integrating eqn.(3), the analog of eqn.(2) for the case of varying mortality rates can be obtained,

$$N_t = \exp(a - d.t + c.t^2) \qquad , \ (4)$$

where $\underline{d}$ is the initial mortality rate, and the quadratic parameter $\underline{c}=\underline{b}/2$ is a measure of the shape of the curve. All other symbols are the same those as in eqn.(2). This equation describes a log-linear model where the quadratic parameter $\underline{c}$ is a measure of the intensity with which mortality rates vary in time. If $\underline{c}<0$, the initial mortality tends to increase with time, and the model describes a type I survivorship curve. If $\underline{c}>0$, the initial mortality tends to decrease with time and the model describes a type III survivorship curve. If $\underline{c}$ does not differ significantly from zero, then the mortality rate tends to be constant in time and the best model is the one described in eqn.(2). Thus, fitting eqn.(4) to the data by means of a log-linear fitting procedure allows testing hypotheses on the shape of the survivorship curve.

RESULTS

Germination and establishment

The total number germinated seeds per treatment is presented in Table 1. Germination occurred within the first eight days after the experiment started, since the first rains fell two days after the experiment was initiated. Although all factors and interactions were significant, radiation and predation alone explained more than twenty percent of the deviance each, and sixty percent when pooled (Table 2). The other terms never explained individually more than five percent, and 16.6% pooled together. In all cases, exclusion from

predators significantly increased the number of established seedlings. The lower number of seedlings in the non-excluded treatments was associated mainly with the seed removing activity of granivores, although it was seen that ants were also capable of uprooting small seedlings during their first days. Seed predators observed during the experiment were birds (Toxostoma curvirostre, Columba livia, Zenaida asiatica, Z. macroura, Columbina inca, C. passerina), and harvester ants (Pogonomyrmex spp. and other unidentified species). The number of established seedlings in the non-excluded treatments did not differ between open spaces and beneath nurse-plants (P>0.05). Under artificial shade, however, predation was lower in the South and North aspects. Without the effect of predators, exposure to direct solar radiation significantly decreased the establishment of seedlings. Furthermore, under excluded conditions no significant differences were found between the artificial shade and the nurse-plant treatments. In open spaces, seedling establishment was significantly lower in the sites with west exposure.

Comparison of survivorship curves

The fitted model to the survivorship curves explained 89.1% of the deviance (Table 3). Expectedly, time alone explains 47.6% of the total deviance (survivorship frequencies are, by definition, a monotonically decreasing function of time), and time as a quadratic component explained 14.1% of the deviance. Of the other statistical factors included in the model, the most important effect was the interaction between shade and time,

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which explained 11.1% of the deviance. All other factors
(including all possible interaction terms) explained 16.3% of
the deviance, but no term expained individually more than 3% .

Initial mortalities and the quadratic coefficients of the
survivorship curves are presented in Table 4. All the quadratic
coefficients are positive and significantly different from zero,
which indicates that all survivorship curves are type III, in
which initial mortality is very high and tends to decrease with
time (Fig. 1). In all cases, initial mortality rates were
significantly higher in open spaces than in shaded conditions.
Additionally, these initial rates increased substantially in
most of the non-excluded treatments, which shows that predation
is very important once the seeds are on the soil. This trend,
however, was not so clear in the artificial shade plots.

Only the shaded treatments had live individuals at the end
of the experiment (Fig. 1 and Table 5). These treatments showed
initial mortality rates and quadratic coefficients significantly
lower than in open spaces. In the excluded and shaded
treatments, survivorship curves were not significantly different
between the artificial and nurse-plant shades in any of the four
aspects. The curves, however, were different in the non-
excluded conditions, and the pattern varied according to the
aspect of the plot. In the North, South and West aspects
survivorship was higher under artificial shade, but in the East
aspect it was higher under the nurse plants. This pattern
possibly arises from the patchy foraging behaviour of predators
already mentioned.

The number of live individuals at the end of the experiment

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and two years after initiation are shown in Table 5. Although substantial mortality was registered during the second year, it seems to be largely independent of the exclusion from herbivores (no tests were made on this table for lack of sufficiently high frequencies).

DISCUSSION

Several studies have analyzed the establishment of succulents under field conditions. For example, Steenbergh & Lowe (1969, 1977) reported that for the giant columnar cactus Carnegiea gigantea a large proportion of the seed crop is consumed by birds while the fruits are on the plant and another large proportion is removed by birds, mammals and insects (mainly harvester ants) when the seeds are on the ground. This implicates that a very small percentage of seeds ($< 10^{-3}$) remains on the ground until suitable conditions for germination occur during the summer. According to our observations with Neobuxbaumia tetetzo, the most important effect of the seed removers seems to occur once the seeds are on the ground, probably because the fruits of N. tetetzo have a colorless fleshy pulp which contrasts with the bright red fleshy pulp of Carnegiea gigantea, which serves as a visual attractant for frugivorous birds. The thousands of seeds of N. tetetzo that fall uniformly to the ground are removed intensively by ground-foraging birds and also by harvester ants. This harvester activity occurs similarly in open spaces and under nurse plants, indicating that differential mortality of seeds by preferential predation in some patches is not occurring in the study site.

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The lower predation rates found in some artificial shaded treatments when compared with beneath nurse-plant plots, are probably due to the plastic mesh which altered in some way the behaviour or the search pattern of predators. We do not know at present what is the demographic fate of the seeds removed by the different granivores. Our observations indicate that most of the seeds removed by ants die, but the fate of those consumed by birds is still unknown. In the case of Carnegiea gigantea, birds may disperse the seeds under the canopies of shrubs and trees, thus further contributing to the nurse-plant effect (Steenbergh & Lowe 1977; Hutto, McAuliffe & Hogan 1986; Olin, Alcorn & Alcorn 1989).

The importance of soil moisture for the germination of seeds under field conditions has been associated with variation in microrelief and to the presence of safe microsites (Harper et al. 1965). The lowest number of seeds that germinated in this study occurred in openings in which solar radiation heats the surface, hence decreasing soil moisture to levels beneath that required for germination. This hypothesis is further supported by the fact that in openings most of the seeds germinated when they were close to stones or under them, and very few managed to germinate in completely open spaces. Larmuth & Harvey (1978) found that the presence of stones is of vital importance for germination and survival of seedlings in S.E. Morocco, because of their role as dew collectors. In the Tehuacán valley, stones clearly help to maintain humidity for a short time, but their role in long-term survival does not seem relevant. The

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successful establishment of seedlings in rocky habitats has also been mentioned by Steenbergh & Lowe (1969, 1977).

The best conditions for germination were in shaded sites where evaporative demand is lower and, consequently, where soil moisture is more adequate. According to Steenbergh & Lowe (1977), moisture availability is sufficiently prolonged in shaded sites to permit germination. Additionally, lower transpiration of desert plants and lower water output have been reported for shaded conditions in wadis by Abd El Rahman & Batanouny (1965a, b) when compared with open spaces. Also, in comparing the microclimate beneath shrubs and in open spaces, Shreve (1931) concluded that vegetational differences between these patches were associated with differences in solar radiation, which modify soil temperatures and rates of transpiration. In the Zapotitlán Valley, soil temperatures beneath and between perennial plants reached a maximum difference of 16°C in the summer (Valiente-Banuet et al. in press).

Microclimatic differences between open and shaded conditions were reflected in the survivorship curves observed. Only the shaded treatments had live individuals at the end (350 days) and also two years after initiation of the experiment. All the unshaded seedlings were dead in less than a hundred days, a result also reported for Carnegiea gigantea (Turner et al. 1966) and for Agave deserti (Jordan & Nobel 1979). In both of these studies seedlings died even with watering, a result that shows the lethal effect of high temperature for succulent plants with CAM photosynthetic pathway.

In shaded, predator-excluded treatments, no differences between the artificial shade and the nurse-plant effect were found. As the artificial shade plots were located on sites that were previously open spaces, these similar survivorship patterns suggest that the differences in soil properties reported for both kind of patches (Valiente-Banuet, Vite & Zavala-Hurtado, in press) were not important for seedling survival. However, higher nutrient levels encountered beneath nurse-plants have been shown to modify the rates of growth of cacti (Turner et al. 1966; Franco & Nobel 1989), and also of certain non-succulent plants (Halvorson & Patten 1975). The relationship between nurse plants and nutrient levels, and its effect on the survivorship and growth of cacti, should be analyzed in more detail because faster growth rates may increase the probability of seedling survival, by allowing a more rapid "escape" from the critical stages of early growth. Related to this, Jordan & Nobel (1981) have reported that the volume of water stored is critical for determining the length of drought succulents can survive.

Our germination and survivorship results indicate that radiation and its associated factors, temperature and evaporation, determine the interspecific association between Mimosa luisana and Neobuxbaumia tetetzo. The same observation also has been pointed out by Turner et al. (1966) and Franco & Nobel (1989) for the columnar cactus Carnegiea gigantea and by Halvorson & Patten (1975) for non-succulent plants. In short, our experimental results suggest that excessive radiation,

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evaporation and temperature in open spaces, and the resulting
mortality, are the main cause of the nurse-plant effect.

In order to test this hypothesis, field samplings in the
Vizcaíno desert in Baja California, Mexico (27°33'N, 113°12'W),
and in the Gran Desierto in Sonora, Mexico (32°01'N, 113°31'W)
were done. Given that both deserts extend north of the
intertropical belt (Turner & Brown 1982), direct solar radiation
shows a Southern azimuth all year round, as opposed to the
Tehuacán site, which is within the tropics and where summer
radiation comes from the north. If the radiation hypothesis of
the nurse plant effect were true, a non-random circular
distribution of saplings with respect to the nurse plant would
be expected in the Vizcaíno and Gran Desierto sites, with a
preferential establishment towards the north of nurse-shrubs.
Thus, as a means to falsify our hypothesis, we analyzed the the
azimuthal frequency of saplings with respect to the nurse shrub
of six succulent plants: five cactus species (Carnegiea gigantea
(Engelman) Britton & Rose, Ferocactus wislizenii (Engelman)
Britton & Rose, Opuntia acanthocarpa Engelman & Bigelow, an
unidentified species of Cylindropuntia and Pachycereus pringlei
(Watson) Britton & Rose), and one euphorb (Pedilanthus
macrocarpus Benth.). With the exception of Ferocactus
wislizenii, all other species showed a significantly non-random
distribution with preferential establishment towards the north
(Fig. 2). These results support the idea that the amelioration
of the physical environment, in terms of radiation evaporative
demand and temperature, are the main factors related to the
nurse-plant effect. These observations also indicate that

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besides the different qualities of nurse-plants, it is possible that slight gradients at very small scale are present beneath the canopies within each patch. This aspect has been suggested also by Shmida & Whittaker (1981) for annuals growing associated to perennial plants and Franco & Nobel (1989) found that Carnegiea gigantea seedlings were more associated with the base than to the edges of the nurse-plants. This, of course, does not exclude other factors possibly reinforcing this effect, such as seed dispersion. In the case of Ferocactus wislizenii, the individuals avoid direct solar radiation and excessive heat load by growing with an inclination towards the South, an aspect that has been reported for Copiapoa spp., a Chilean barrel cactus (Ehleringer et al. 1980). This capacity to actively regulate direct radiation possibly explains its lack of a significant azimuth with respect to the nurse plant.

In conclusion, the nurse plant effect in arid and semiarid regions is chiefly the result of differential survival in shaded microsites with less direct solar radiation, and consequently, with lower daytime temperatures and lower evaporative demand. Differences in soil fertility under nurse plants are of secondary importance, at least in our study area. Lacking in this study is determination of the importance of nurse-plants as water collectors delivering water at the base of the plant, as suggested by Glover & Gwynne (1962), and also the possible importance of the "hydraulic lift" in which water absorbed by deep roots, is deposited in upper soil layers (Caldwell & Richards 1989).

The importance of the nurse-plant protection lies in a moister and thermally buffered microsite for seedling establishment and survival. This can be a crucial factor for CAM seedlings, which have closed stomata during the day and are unable to thermoregulate by transpiration when the heat load is maximum, and also for some non-succulent plants whose transpiration rates are more pronounced in openings (Shreve 1934, 1942, Went 1942, Osborn et al. 1932, Shmida & Whittaker 1981, among others). Although the relevance of radiation as an underlying mechanism should be assessed for other subordinated species, we can conclude that this factor is of primary importance as a driving force in the patch-structured population dynamics of many desert plants establishing under shrubs. We believe that the decreased radiation under nurse-plants, together with other factors such as seed dispersal and the unpredictability of rains, are primarily responsible for the structure and diversity of many desert and semidesert communities.

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FIGURE CAPTIONS

1.- Survivorship curves of cohorts located under different experimental treatments along 350 days (July of 1988-June 1989). Wide lines indicate predator-excluded treatments and thin lines non-excluded treatments. _____ beneath nurse-plants;

_ _ _ _ under artificial shadow and ...... in open space.

2.- Circular distribution of saplings of succulents with respect to perennial shrubs in the Gran Desierto and the Vizcaíno desert. Azimuthal categories were determined by dividing the circumference in four (North is between 315° and 45°, East between 46° and 135° and so on). X^2 values were obtained by comparing the observed distribution with an expected uniform distribution.

		OPEN SPACE	ARTIFICIAL SHADE	Mimosa SHADE
NORTH	EXCLUDED	31	163	125
	NON-EXCL.	0	99	6
SOUTH	EXCLUDED	48	147	182
	NON-EXCL.	3	71	9
EAST	EXCLUDED	48	138	138
	NON-EXCL.	10	7	20
WEST	EXCLUDED	12	111	133
	NON-EXCL.	7	5	5

Table 1.- Total number of seeds of Neobuxbaumia tetetzo germinated in the different experimental treatments.

SOURCE	x^2	D.F.	r^2
PREDATION	772.5	1	0.38
RADIATION	444.3	2	0.22
ASPECT	55.1	3	0.027
PREDATION*RADIATION	73.2	2	0.036
PREDATION*SLOPE	57.0	3	0.028
PREDATION*SLOPE	57.4	6	0.028
PRED*RADIATION*ASPECT	96.4	6	0.047
MODEL	1555.9	23	0.766
RESIDUAL	456.8	48	
TOTAL	2012.7		

Table 2.- Analysis of the deviance for the number of germinated
seeds at the begining of the experiment (after 8 days of
seeding). All factors and interactions are significant
(P<0.005).

SOURCE	x^2	D.F.	r^2
TIME	31750	1	0.476
TIME^2	9401	1	0.1409
RADIATION	1942	2	0.0291
PREDATION	1522	1	0.0228
ASPECT	246	3	0.0037
TIME*RADIATION	7371	2	0.1105
OTHER EFFECTS	7209	63	0.1081
MODEL	59441	73	0.8910
RESIDUAL	7265	408	
TOTAL	66706		

Table 3.- Analysis of deviance for the survivorship curves.
All factors and interactions are significant (P<0.005).
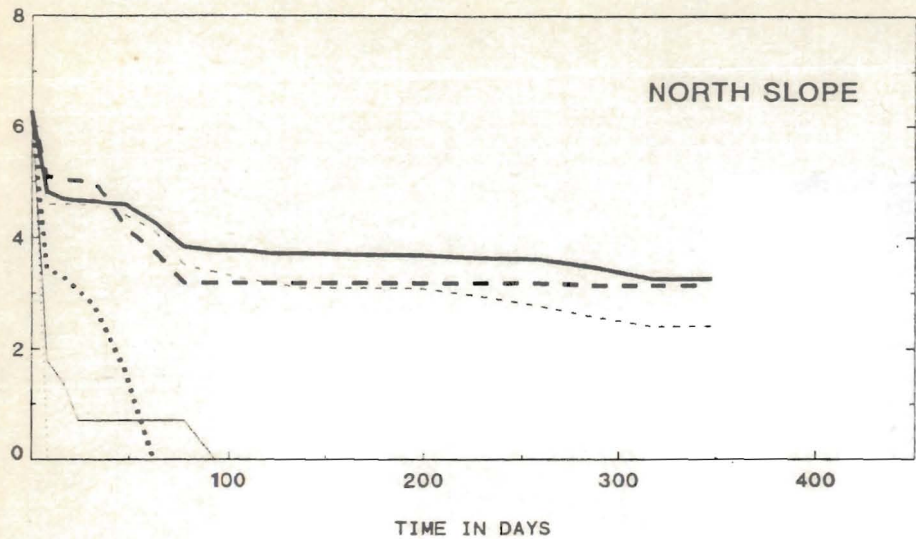Other effects indicate all the interactions.

		LINEAR PARAMETER			NON-LINEAR PARAMETER		
		OPEN SPACE	ARTIFICIAL SHADE	MIMOSA SHADE	OPEN SPACE	ARTIFICIAL SHADE	MIMOSA SHADE
NORTH	Excluded	-0.1595	-0.0330	-0.0231	0.000395	0.000077	0.000052
	Non-Excl.	-1.0000	-0.0305	-0.2752	0.002881	0.000066	0.000727
SOUTH	Excluded	-0.2149	-0.0307	-0.0399	0.000544	0.000067	0.000082
	Non-Excl.	-0.5448	-0.0261	-0.1276	0.001468	0.000061	0.000330
EAST	Excluded	-0.1298	-0.0624	-0.0342	0.000312	0.000143	0.000074
	Non-Excl.	-0.2621	-0.1733	-0.0718	0.000683	0.000460	0.000185
WEST	Excluded	-0.2658	-0.0252	-0.0271	0.000693	0.000053	0.000056
	Non-Excl.	-0.2504	-0.1050	-0.1942	0.000656	0.000277	0.000520

TABLE 4.- Initial mortality rates (linear parameters) and non-linear
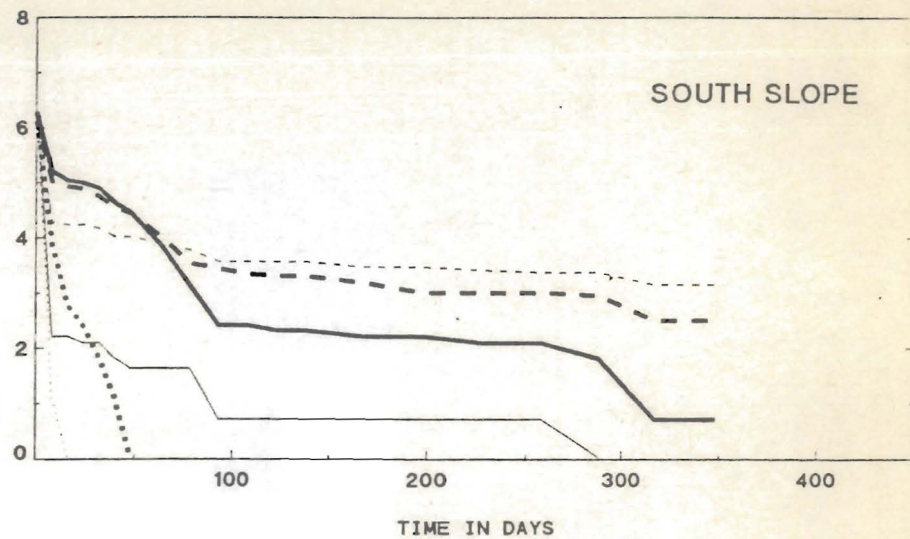parameters of the survivorship curves in the different treatments.

		OPEN SPACE	ARTIFICIAL SHADE		Mimosa SHADE	
NORTH	EXCLUDED	0	23	(4)	26	(1)
	NON-EXCL.	0	11	(1)	1	(1)
SOUTH	EXCLUDED	0	11	(3)	2	(2)
	NON-EXCL.	0	23	(7)	0	(0)
EAST	EXCLUDED	0	1	(0)	4	(1)
	NON-EXCL.	0	1	(0)	6	(1)
WEST	EXCLUDED	0	10	(7)	8	(2)
	NON-EXCL.	0	4	(2)	1	(1)

Table 5.- Number of live individuals of Neobuxbaumia tetetzo
at the end of the experiment (350 days). Values in
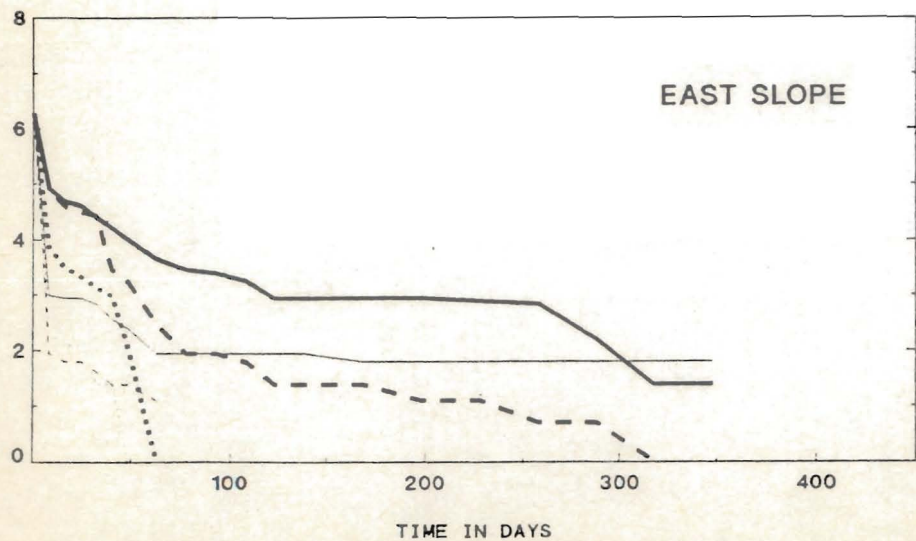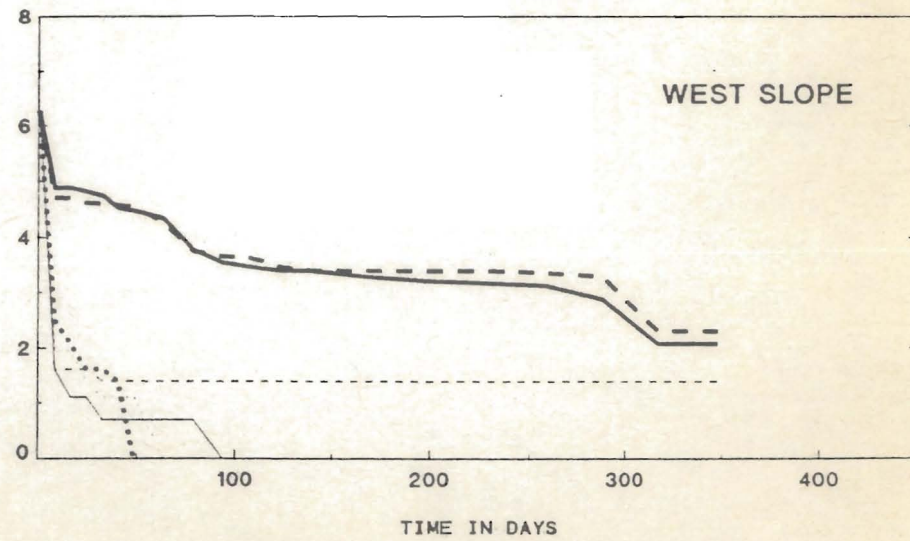parentheses indicate live individuals after two years.

(n = 95)

$x^2 = 127.6$ $p < 0.005$

(n = 67)

$x^2 = 4.46$ $p > 0.05$

Opuntia acanthocarpa

(n = 53)

$x^2 = 20.6$ $p < 0.005$

Opuntia sp.

(n = 113)

$x^2 = 62.8$ $p < 0.005$

Pachycereus pringlei

(n = 147)

$x^2 = 79.0$ $p < 0.005$

Pedilanthus macrocarpus

(n = 112)

$x^2 = 65.2$ $p < 0.005$

ORIENTATION WITH RESPECT TO THE NURSE PLANT
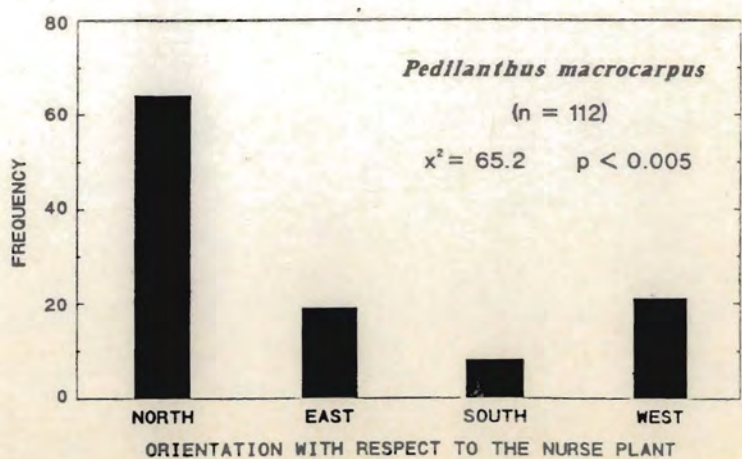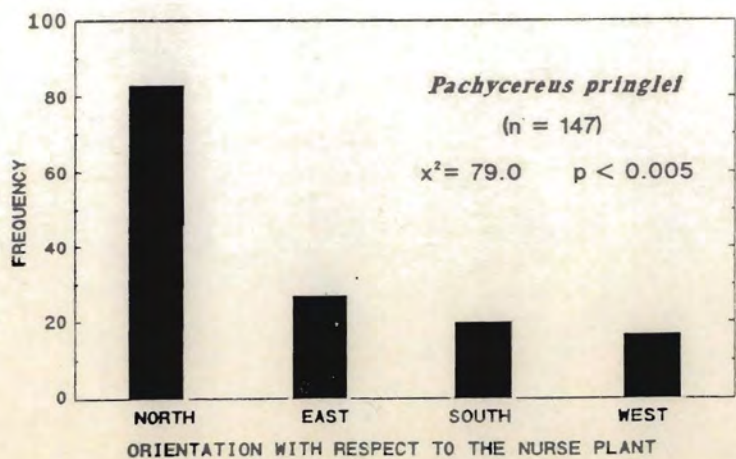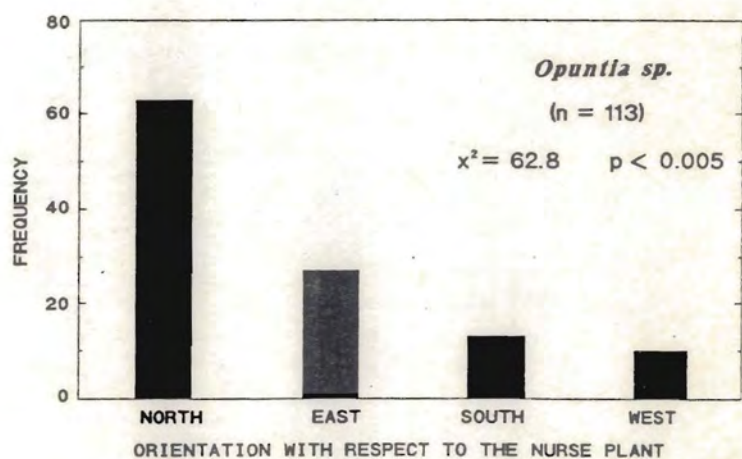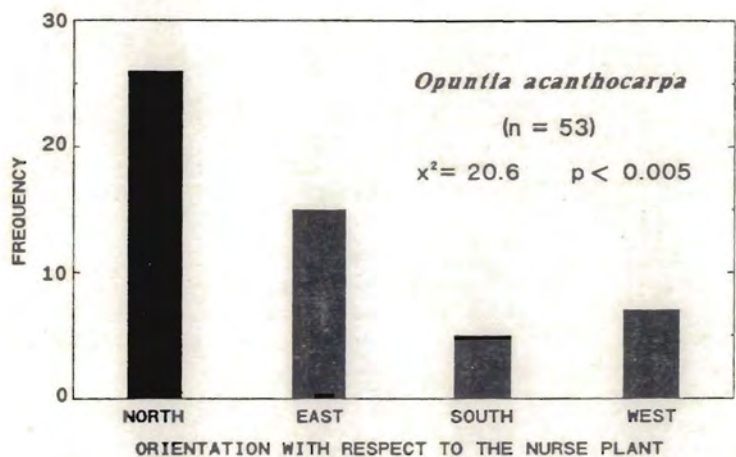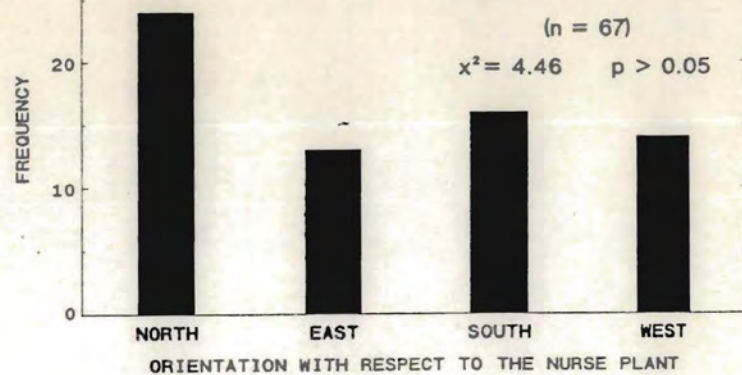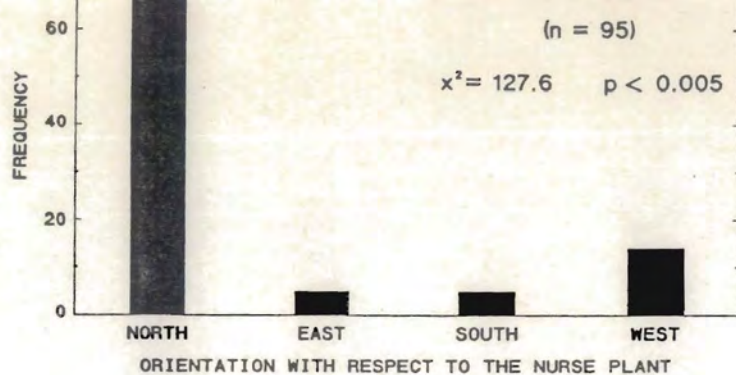
CONCLUSIONES GENERALES

La aceptación de la hipótesis que la disponibilidad de agua controla los procesos ecológicos en las zonas áridas y semiáridas, llevaría a la conclusión que el estudio detallado de la autoecología de las especies es la base para entender el funcionamiento de estos sistemas. La evidencia recabada en esta tesis indica que esta hipótesis autoecológica (Noy-Meir 1980) es incompleta.

La dinámica de los procesos biológicos está fuertemente asociada a patrones de diferentes escalas que dependen de la abundancia del agua, de características geomorfológicas (ej. efecto de laderas) y de propiedades fisicoquímicas de los suelos (ej. textura y salinidad). No obstante, a escala microambiental una gran cantidad de especies interactúan a nivel de parches debido al establecimiento preferencial de individuos debajo del dosel de plantas perennes, cuya presencia genera microambientes más benignos. Los resultados de numerosos estudios realizados sobre este fenómeno, indican que éste es generalizable a una amplia variedad de desiertos del mundo y que involucra a una gran cantidad de taxa con diferentes formas de vida. En consecuencia, estos ambientes pueden ser considerados como mosaicos, con estados discretos de ocupación del espacio en donde coinciden diferentes especies vegetales, animales y microorganismos que utilizan dichos parches como áreas de refugio y forrajeo (Seely, De Vos y Louw 1977; Sartos, DePree y Whitford 1978; Charley y West 1977; Mares et al. 1977).

Las plantas nodriza, generan los ejes del nicho de otras. En el Valle de Tehuacán, 20 de las 33 especies que constituyen

una tetechera presentan patrones de establecimiento predecibles
por debajo de la copa de arbustos y árboles (Godínez, Guevara y
Valiente-Banuet, en preparación; Tabla 1). En el desierto
Sonorense, un número importante de especies de diferentes
comunidades con diferente grado de complejidad, muestran patrones
de colonización cualitativamente similares y predecibles
(McAuliffe 1988). En comunidades de California, el hecho de que
la riqueza de especies anuales incrementa conforma la cobertura
vegetal aumenta, tal y como fue reportado por Shmida y Whittaker
(1981), sugiere que los cambios microambientales producidos por
las plantas perennes, generan heterogeneidad, la cual junto con
la variabilidad en la disponibilidad de agua, son probablemente
la base de la coexistencia entre especies y la diversidad de las
comunidades. Los estudios realizados en el Valle de Tehuacán,
así como los de Hutto et al. (1986), indican que el número de
individuos de especies subordinadas encontradas bajo la copa de
diferentes especies, no sigue una distribución al azar, sino que
más bien se concentra en unas cuantas especies. Esto sugiere que
la calidad, vista como el grado de modificación microambiental e
incremento del intervalo de condiciones favorables debajo del
dosel de las nodrizas, puede variar entre éstas, aún cuando las
temperaturas (que podría ser un factor obvio) bajo el dosel de
tres especies en el Valle de Zapotitlán no difirieron. Lo
anterior enfatiza a su vez, la importancia de la dispersión para
explicar los resultados. De la misma manera, diferencias en la
distribución circular de plántulas alrededor de plantas nodrizas
sugiere que existen microgradientes que van de la base de la

planta hacia la periferia de la misma. Ambos niveles de variación señalados, pueden generar varianza en las dimensiones del nicho, tal y como ha sido sugerido por Shmida y Whittaker (1981). Casos similares son presentados por Mares et al. (1977) para especies de Prosopis en Norte y Sudamérica, los cuales además de tener una alta diversidad de herbáceas bajo sus doseles, mantienen también una fauna de invertebrados y vertebrados asociados.

La pedregosidad puede producir modificaciones microambientales parecidas a las generadas por las plantas nodrizas, dado que pueden proveer de agua a las plántulas por medio de la condensación de neblina (Larmuth y Harvey 1978), aspecto que debe ocurrir principalmente en los desiertos costeros.

En diferentes estudios incluyendo los realizados en este trabajo, se subraya que las plantas nodriza pueden modificar propiedades del ecosistema como son el ciclo de nutrientes aumentando los niveles de nitrógeno, el cual es considerado como un factor limitante importante, así como incrementar la productividad y quizá modificar también la hidrología a niveles locales. Estas modificaciones producidas por las plantas nodrizas claramente afectan propiedades del ecosistema, lo cual puede favorecer la integración de métodos y enfoques de la ecología de poblaciones y la de ecosistemas (Vitousek 1990).

En este sentido, la caracterización detallada en el espacio y el tiempo de los diferentes parches en una comunidad, con relación al flujo de nutrientes, gradientes de radiación solar de la base a la periferia del dosel, así como la posible capacidad

de las plantas para captar agua a partir de lluvias ligeras o inclusive de la humedad ambiental, son aspectos que requieren de un cuidadoso análisis experimental. Aunado a lo anterior, recientemente se ha demostrado que las raíces profundas de Artemisia tridentata, en zonas áridas de norteamérica, transportan agua de zonas profundas, depositándola en las capas del suelo más superficiales, lo cual puede ser utilizada por la misma planta o por otras especies asociadas. Este proceso ("hydraulic lift"; Caldwell y Richards 1989) requiere de un análisis cuidadoso a fin de determinar su relevancia en torno a la caracterización de los parches y en torno a la dinámica de las poblaciones que crecen bajo el dosel de otras.

Las causas de la asociación entre Neobuxbaumia tetetzo y Mimosa luisana, está relacionada a la sobrevivencia diferencial en los sitios sombreados, en donde la radiación, demanda evaporativa y/o temperatura son menores. El análisis de la distribución circular de estados juveniles de 4 suculentas en 2 desiertos extratropicales mostró concordancia con lo esperado, dando generalidad a los resultados. En términos generales, estas plantas con metabolismo ácido de las crasuláceas (CAM), tienen sus estomas cerrados durante el día por lo que son incapaces de termorregular por transpiración cuando la carga de calor es máxima.

Cada uno de los parches que constituyen las comunidades desérticas, conforman subsistemas locales en donde la competencia juega un papel importante en la dinámica de reemplazamiento entre las plantas subordinadas y las nodrizas. Los trabajos de Yeaton

(1978), Yeaton y Romero-Manzanares 1986, McAuliffe (1984) y

Valiente-Banuet et al. (en prensa), muestran patrones similares

de reemplazamiento de las especies subordinadas (cactáceas). Si

se aceptara que la sucesión puede implicar únicamente la

variación de la abundancia de las especies en el tiempo, entonces

estos patrones de reemplazamiento pueden concordar con el esquema

de sucesión autogénica de Connell y Slatyer (1977).

Independientemente de la connotación del término sucesión y su

dudosa aplicación a la ecología de las zonas áridas y semiáridas,

la dinámica de estos sistemas ha podido ser simulado por medio de

cadenas de Markov por McAuliffe (1988) y en un trabajo para la

vegetación del Karoo por Yeaton & Esler (1990).

Los patrones de reemplazamiento de las especies en los

parches, indican que la interacción empieza como comensalismo, y

con el tiempo pasa a ser una relación de competencia o inclusive

el análogo a un modelo depredador-presa (Vandermeer 1980).

El fenómeno de establecimiento de nuevos individuos en zonas

desérticas, es quizá el estado más crítico del ciclo de vida de

las plantas (Steenbergh y Lowe 1969). Este ocurre de manera

predecible por debajo del dosel de las plantas perennes que

incrementan la duración de los intervalos con condiciones

favorables para la germinación y el desarrollo de las plántulas.

En el caso de las cactáceas, como grupo mejor conocido, una de

las primeras consecuencias de lo anterior, es el marcado patrón

de agregación de las especies. La posible ocurrencia de

regulación en estas poblaciones debe ocurrir dentro de los

parches principalmente tal y como ha sido reportado por McAuliffe

y Janzen (1986; Díaz-Maeda (com pers). Este aspecto en la

actualidad, se encuentra completamente desconocido para otras formas de vida.

A partir de la evidencia encontrada, puede señalarse que el entendimiento de los factores que determinan el establecimiento de plantas capaces de hacerlo en espacios abiertos, podría hacerse bajo la hipótesis autoecológica (Noy-Meir 1980), por lo que la determinación de la predecibilidad de la lluvia es un tema fundamental en el entendimiento de la biología de estas especies. Para especies subordinadas, el establecimiento de nuevos individuos puede estar determinado por la llegada de diásporas a los diferentes parches, la dinámica acoplada de plantas nodriza-subordinadas, la calidad de las primeras, sus patrones de abundancia en la comunidad y éstas a su vez en relación con el ambiente físico. La variabilidad en los patrones de abundancia de agua pueden efectivamente afectar la dinámica de las poblaciones, pero su conjunción con la formación de un microambiente por las plantas nodriza es un tema de frontera no considerado hasta el momento.

El crecimiento de cactáceas bajo la sombra de otras especies, aun cuando puede reducir la captación de radiación fotosintéticamente activa (RFA) y por tanto del CO_2 fijado, no se ve claramente afectado. Franco y Nobel (1989) han sugerido que el déficit de RFA experimentado por cactáceas bajo sombra puede ser compensado por niveles altos de fertilidad encontrados en estos microambientes. Observaciones sobre la actividad fotosintética realizadas durante el desarrollo de este trabajo, sugieren que una explicación alternativa que requiere de

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investigación, es que las plántulas pueden modificar su metabolismo fotosintético bajo condiciones adecuadas de agua tal y como ha sido reportado para algunas cactáceas (Szarek y Ting 1975).

La información presentada en este trabajo permite señalar que la facilitación en las zonas áridas y semiáridas es un fenómeno central y general a estos ambientes, que afecta procesos ecológicos a escalas comunitarias, poblacionales e individuales. En mi opinión este proceso promete convertirse en un tema de estudio principal sobre la ecología de las zonas áridas y semiáridas de la presente década. Las hipótesis e ideas desarrolladas en este trabajo, por tanto pasarán a ser probadas en los próximos años.

TABLA 1. PATRONES DE DISTRIBUCION DE PLANTULAS CON RESPECTO A
PLANTAS PERENNES EN UNA TETECHERA EN EL VALLE DE
ZAPOTITLAN DE LAS SALINAS, PUE. (Tomado de Godínez,
Guevara y Valiente-Banuet, en preparación).

ESPECIE	PATRONES DE DISTRIBUCION
Agave karwinskii Zucc.	Asociado
Agave macroacantha Zucc.	Asociado
Agave marmorata Roezl	Asociado
Agave peacockii Croucher	Asociado
Beaucarnea gracilis Lem.	Asociado
Bouteloua media (Fourn.) Gould & Kapadia	Asociado
Cnidoscolus urens L.	Asociado
Coryphanta pallida Britt. & Rose	Asociado
Euphorbia antisyphillitica Zucc.	Asociado
Hechtia aff. podantha Mez.	Asociado
Loeselia coerulea (Cav.) Don.	Asociado
Mammillaria casoi Bravo	Asociado
Mammillaria collina Purpus	Asociado
Mimosa luisana Brandeg.	Asociado
Neobuxbaumia tetetzo (Weber.) Backeberg	Asociado
Pedilanthus aphyllus Boiss.	Asociado
Ruellia hirsuto-glandulosa (Oerst.) Hemsl.	Asociado
Sida abutifolia Miller	Asociado
Siphonoglossa ramosa Oerst.	Asociado
Tillandsia makoyana Baker	Asociado
Allionia incarnata L.	No Asociado
Ayenia fruticosa Rose	No Asociado
Cathestecum brevifolium Swall.	No Asociado
Sanvitalia fruticosa Hemsl.	No Asociado
Verbesina sp.	No Asociado
Acacia constricta Benth.	Desconocido
Caesalpinia melanadenia (Rose) Standl.	Desconocido
Cercidium praecox (Ruiz y Pavon) Harms.	Desconocido
Cordia curassavica (Jacq.) Roem. & Schult.	Desconocido
Ipomoea wolcottiana Rose	Desconocido
Portulaca mexicana P. Wils.	Desconocido
Prosopis laevigata (Willd.) Johnst.	Desconocido
Turnera diffusa Willd.	Desconocido

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