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MORFOLOGIA FUNCIONAL DE *Cephalocereus columna-trajani* (CACTACEAE) EN UNA COMUNIDAD SEMIARIDA DEL TROPICO MEXICANO

TESIS

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PRESENTA

JOSE ALEJANDRO ZAVALA HURTADO

DIRECTOR DE TESIS: DR. EXEQUIEL MARIA EZCURRA REAL DE AZUA

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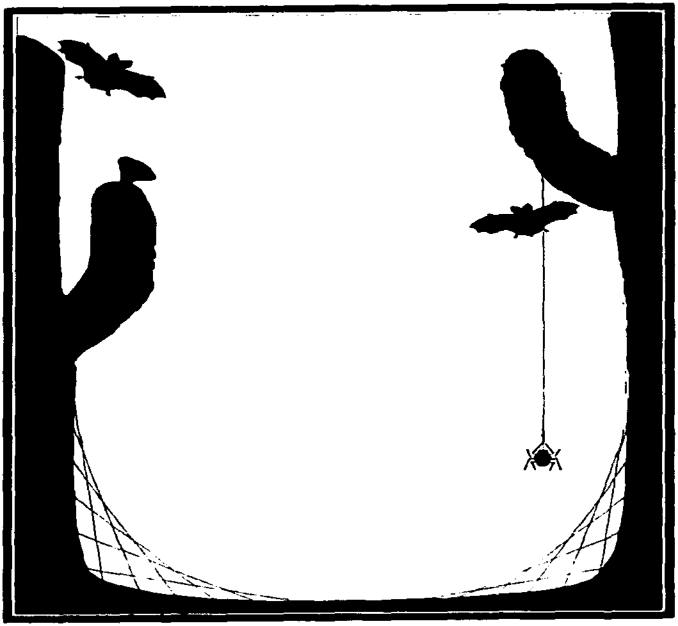

...entonces, ¿ por qué estas inmensidades áridas se han aferrado tan fuertemente a mi memoria?

(Charles Darwin)

Contenido

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Resumen. **(MORFOLOGÍA FUNCIONAL DE** ***Cephalocereus columna-trajani*** **(CACTACEAE) EN UNA COMUNIDAD SEMIÁRIDA DEL TRÓPICO MEXICANO).** En esta tesis se aborda un planteamiento morfométrico para el estudio de aspectos de la biología de la cactácea columnar gigante *Cephalocereus columna-trajani* (Karwinski ex. Pfeiffer) Schumann y su entorno comunitario. La Tesis consta de tres artículos en los que se abordan igual número de aspectos del tema referido. *C. columna-trajani* presenta un pseudocefalio que normalmente está orientado hacia el noroeste y el tallo se inclina en la misma dirección. Este pseudocefalio es una estructura lanosa de la cual emergen las flores de esta cactácea y la orientación observada parece tener como función el minimizar la radiación solar incidente sobre las flores, con lo que se evita una evaporación excesiva. Por otra parte, esta orientación también serviría para maximizar la superficie fotosintética expuesta por esta planta. En el segundo capítulo de esta Tesis se presenta un muestreo de campo en el que se describe estadísticamente la orientación del pseudocefalio bajo diferentes condiciones (en sitios con obstrucciones topográficas en distintas laderas y sin obstrucciones). Además se analiza el valor adaptativo de la orientación e inclinación del tallo mediante experimentos de simulación por computadora en los que se estudia el régimen de radiación en cactos con diferentes orientaciones, inclinación del tallo y posición del pseudocefalio. El tercer capítulo presenta un trabajo en el que se estiman la tasa de crecimiento y la edad de individuos de una población de *C. columna-trajani*. Con base en relaciones alométricas se analizan las consecuencias ecológicas del proceso de reparación somática de esta especie luego de recibir un daño que implica la pérdida del meristemo apical. Se encontró que los individuos reparados crecen más rápidamente y presentan una producción de flores más alta que aquellos que no sufrieron daño. Finalmente, se propone un modelo para estimar la edad a la que los individuos reparados sufrieron el daño, encontrándose que aparentemente no sobreviven individuos dañados cuando no han rebasado los dos metros de altura ni aquellos que sobrepasan los 6 metros. Esto parece indicar que el gasto en reparación está directamente relacionado con las expectativas de reproducción futura. En el último capítulo se presenta una clasificación de formas de vida del valle de Zapotitlán basada en 30 características morfológicas de 107 especies de plantas perennes del lugar. La clasificación de formas de vida se realizó mediante un análisis de conglomerados y fue validada con un análisis discriminante múltiple y mediante su comparación con un modelo nulo de clasificación aleatoria. Las formas de vida identificadas representan estrategias adaptativas mediante las cuales las plantas enfrentan las presiones de selección que impone el peculiar ambiente del desierto. De los resultados obtenidos en esta Tesis se concluye que *Cephalocereus columna-trajani* presenta características morfológicas peculiares de las que se puede inferir una clara relación con su desempeño ecológico y por tanto es un sujeto idóneo para abordar estudios de diferentes aspectos de morfología funcional. Es promisorio que estos estudios ayuden a resolver problemas biológicos fundamentales mediante el análisis de la conducta de las plantas y sus consecuencias ecológicas y evolutivas.

Abstract. **(FUNCTIONAL MORPHOLOGY OF *Cephalocereus columna-trajani* (CACTACEAE) IN A SEMIARID COMMUNITY OF THE MEXICAN TROPIC).** This Thesis follows a morphometric approach for the study of biological aspects of the giant columnar cactus *Cephalocereus columna-trajani* (Karwinski ex. Pfeiffer) Schumann and its community scenario. The dissertation is divided in three papers where an equal number of topics in the above-mentioned theme are covered. *C. columna-trajani* bears a pseudocephalium showing a consistently North-western orientation and a stem tilting towards the same direction. This pseudocephalium is a hairy structure from which flowers raise. The observed orientation seems to act minimising incident Solar radiation on flowers, so avoiding an excessive evaporation. On the other hand, this orientation maximises as well photosynthetic surface exposed to direct Solar radiation. Chapter II of this Thesis presents a field survey where pseudocephalium orientation under varying conditions (in sites with topographic obstructions in different slopes and without obstructions) is described statistically. Additionally, adaptive value of stem tilting and orientation is analysed using computer simulation experiments studying radiation regimes on cacti with varying stem tilting and pseudocephalium orientation. Chapter III is a paper where growth rate and age of individuals in a population of *C. columna-trajani* are estimated. Based on allometric relationships, ecological consequences of somatic repair after the loss of apical meristem caused by a damage are analysed. Repaired individuals grow faster and produce more flowers than those without damage. Finally, in this Chapter a model for the estimation of age when damage occurred is proposed, finding that individuals below 2 m when damaged and those above 6 m do not survive. This seems to indicate that repair expense is directly related to future reproduction expectancy. In last Chapter I present a Zapotitlán's plant life-forms classification based on 30 morphological characteristics of 107 perennial plant species. Life-forms classification was performed by means of a cluster analysis and was validated with a multiple discriminant analysis applied on the resulting classification and on a null model of random classification. Life-forms represent adaptive strategies allowing plants to cope the selection pressures imposed by the peculiar desert environment. A conclusion of this Thesis is that *Cephalocereus columna-trajani* shows peculiar morphological characteristics clearly related with its ecological performance and so, it is a suitable subject on which different aspects of functional morphology can be approached. It is promising that these studies could assist in the solution of relevant biological problems from the plant behaviour analysis altogether with its ecological and evolutionary consequences.

I. INTRODUCCION.

I. Introducción

Morfología funcional de plantas

"This is the most interesting department of Natural History and may be said to be its very soul"
Charles Darwin, The Origin of Species (1859, en White 1984)

Las formas vegetales son muy diversas e interesantes en cuanto a su significado para la biología. La morfología vegetal puede ser vista como uno de los principales factores que influencian la sobrevivencia y, por tanto, es una de las piedras angulares de la ecología de poblaciones de plantas (Bell 1984). La morfología funcional es el estudio de la forma de las plantas vista como una manera de enfrentar a su medio ambiente, incluyendo las ventajas y restricciones que aquella impone para el desempeño ecológico de éstas.

Históricamente la ecología se ha ocupado del problema de interpretar las variaciones en la morfología de las plantas ; sin embargo, éste no es un problema resuelto. Darwin se interesó en la morfología vegetal relacionándola con su función. Esto se aprecia en su serie de libros sobre plantas insectívoras, morfología floral y plantas trepadoras (1875, 1884 y 1885 respectivamente, en Bell 1984).

Durante su crecimiento, una planta responde a su entorno y su forma refleja, al menos parcialmente, las circunstancias en que ha crecido. De hecho, se puede decir que el crecimiento y forma de las plantas son componentes de su conducta: i.e., representan la respuesta vegetal a las presiones de su medio ambiente (Waller 1984).

Las plantas pueden ser vistas como ensamblajes de metámeras (Harper y White 1974), cada una de las cuales consiste de una sección de tallo (internodo) con su hoja u hojas y sus meristemos laterales asociados El crecimiento vegetal resulta de la producción reiterada de metámeras por los meristemos formando módulos. Como la reiteración resulta de la diferenciación de los meristemos, una morfología vegetal particular es el producto de "decisiones" de desarrollo acerca del número y tipos de módulos y, por tanto, de ramas producidas (Watson y Casper 1984).

La capacidad reproductiva de las plantas puede estar influenciada tanto por caracteres inherentes a su historia de vida como por aspectos de su morfología como son el tamaño, disponibilidad de meristemos y relaciones alométricas entre las estructuras reproductivas y vegetativas. Por ejemplo, la arquitectura de la copa de la planta en conjunto con caracteres fisiológicos pueden contribuir significativamente a la capacidad de la planta para asimilar carbono, competir efectivamente y, por tanto, para ser productiva. Asi, la morfología de la planta puede tener implicaciones importantes para su adecuación por su capacidad de influir en las cantidades de recursos disponibles para la reproducción y el mantenimiento (Kohorn 1994).

Como sucede con la conducta animal, la forma de las plantas tiene que ver, entre otras cosas, con su capacidad de dispersión, protección contra depredadores y otros enemigos naturales y, fundamentalmente, con la adquisición de recursos (luz, agua, nutrientes, agentes polinizadores y dispersores).

Desde los grandes exploradores del Siglo XIX (Humboldt 1805, Grisebach 1838, en Acot 1990), los botánicos han intentado interpretar la diversidad de formas vegetales en el planeta. Tal vez los primeros intentos sistemáticos de relacionar la forma vegetal con el clima son las clasificaciones de formas de vida de du Rietz y Raunkiaer (1931 y 1934, respectivamente, en Boutin y Keddy 1993). Esta relación forma-clima deriva en una explicación adaptacionista de casi cualquier característica de las plantas, en términos de algún componente de la adecuación (maximización de producción primaria, escape de herbívoros, producción de semillas, etc.).

Aunque casi nadie pone en duda que la morfología de las plantas tiene muchas implicaciones en cuanto a su conducta en un ambiente dado, no se debe perder de vista que determinadas características morfológicas pueden ser simplemente relictos del pasado o productos secundarios de la selección de alguna otra característica (Harper 1982).

La adaptación ha sido un tópico de discusión durante mucho tiempo. Entre otras cosas, se ha dicho que es una idea no falsificable y conduce a la atomización de los organismos en componentes independientes e ignora alternativas no adaptativas (Losos y Miles 1994).

Según Gould y Vrba (1982, en Losos y Miles 1994), adaptación es "*cualquier característica que promueve la adecuación y que fue construida por selección natural sobre su función actual*". Hay características que promueven la adecuación pero surgen por otra razón (como una adaptación para alguna otra cosa o por razones no adaptativas; Losos y Miles 1994).

La interpretación de la correlación fenotipo-medio ambiente como resultado de la evolución de adaptaciones a un medio particular -opuesta a la selección de ambientes por fenotipos que surgen de mecanismos no adaptativos- se ha basado parcialmente en el fenómeno de convergencia. La convergencia de forma y función en ambientes similares de antecesores diferentes implica selección por factores ambientales, aunque no puede excluirse la selección de hábitat. La convergencia puede inferirse a partir de la similitud de organismos no relacionados en el mismo lugar (Ricklefs y Miles 1994). Por ejemplo, la ocurrencia de semejanzas estructurales entre plantas del desierto, independientemente de sus relaciones filogenéticas y distribución geográfica, es bien conocida y hay una preponderancia de ciertas formas de crecimiento en las floras del desierto que son raras en otros tipos de ecosistemas (Solbrig *et al.* 1977, Cody 1989).

Plasticidad fenotípica

Las plantas normalmente no responden al ambiente moviendo sus cuerpos, sino variando su fisiología y crecimiento (Waller 1984).

Cuando hay heterogeneidad ambiental dentro del ámbito de tolerancia de una especie, es poco probable que un solo fenotipo maximice la adecuación en todas las situaciones posibles. En tal caso, un cambio en el fenotipo en función del ambiente (plasticidad fenotípica) puede conferir mayor tolerancia al medio. La plasticidad fenotípica es, por tanto, una solución al problema de adaptación a ambientes heterogéneos (Via *et al.* 1995).

La plasticidad fenotípica es la capacidad de un individuo para alterar su fisiología y/o morfología en respuesta a cambios de condiciones ambientales. Algunos ejemplos de plasticidad fenotípica son la producción de hojas de sol y sombra, respuestas a la herbivoría tales como la compensación fotosintética, cambios en la disposición de las hojas y en altura (Schlichting 1986). Aunque se puede suponer que la plasticidad fenotípica es, en muchos casos, adaptativa, la demostración de esto en la practica es muy difícil. Algunos problemas son la identificación de poblaciones que difieren en sus respuestas plásticas, la selección de un conjunto apropiado de condiciones ambientales para examinar la plasticidad y la selección de medidas de la adecuación de la planta que permitan un examen apropiado del significado adaptativo de las respuestas plásticas Nobel (1980) dice que los cambios morfológicos en microclimas diferentes deben verse sólo como correlaciones mientras las bases fisiológicas no sean establecidas claramente.

A pesar de la flexibilidad de las plantas para enfrentar ambientes heterogéneos, ellas están limitadas en su crecimiento y forma por su genoma, así como por restricciones mecánicas. Así por ejemplo, los tallos aéreos se enfrentan a la fuerza de gravedad y al viento. Esto significa que una planta debe asignar una fracción creciente de su biomasa total al soporte a medida que crece en altura.

Individuos, poblaciones y comunidades

La ecología vegetal incluye el estudio de procesos que operan a diferentes niveles de escala y complejidad y que van desde las plantas individuales hasta interacciones entre y dentro de poblaciones y en comunidades. A pesar de este ámbito de escala y complejidad, estos procesos están estrechamente relacionados y muchos procesos estudiados a nivel de poblaciones o de comunidad se pueden considerar como una consecuencia directa del crecimiento de plantas individuales (Clark 1990). Wainwright (1994) discute las vias por las que la variación fenotípica (morfológica) influye en la adecuación individual y en la ecología de poblaciones y comunidades. El diseño del organismo (el fenotipo) limita la capacidad del individuo para llevar a cabo sus actividades cotidianas. Esta capacidad interactúa con el medio ambiente para restringir y moldear los patrones de uso de recursos. El uso de recursos es el factor interno que determina dos componentes de la adecuación: reproducción y sobrevivencia. Además, los patrones de uso de recursos juegan un papel central en la determinación de patrones de la ecología del individuo. Los patrones individuales interactúan para producir estructura en la dinámica de poblaciones y comunidades.

Wainwright (1994) sostiene que la morfologia funcional provee la posibilidad para explicar las relaciones causales entre el fenotipo y la función y, por lo tanto, puede jugar un papel muy importante en el planteamiento de explicaciones mecánicas para preguntas ecológicas clásicas como las referentes al autoaclareo en poblaciones de plantas (Weller 1987) o la regulación de la diversidad en comunidades vegetales (Chesson y Pantastico-Caldas 1994).

Schoener (1986) defiende una jerarquía ecológica donde los patrones y procesos observados a un nivel tienen bases mecánicas en los niveles inferiores. Este autor enfatiza una jerarquía de ecología del individuo, ecología de poblaciones y ecología de comunidades Así, para entender patrones al nivel de la comunidad se requiere de la identificación de mecanismos que determinan patrones al nivel de la ecología del individuo. De esta manera, la utilidad de la morfología ecológica para el entendimiento de los mecanismos que forjan los patrones a los niveles poblacionales y comunitarios dependerá en parte del éxito que se tenga en el trabajo al nivel de los individuos.

Objeto de estudio

En esta tesis se presentan tres trabajos que representan un igual número de maneras de abordar la pregunta general sobre las implicaciones funcionales de características morfológicas en plantas. Estos trabajos siguen un enfoque esencialmente morfométrico, esto es, la caracterización de formas biológicamente relevantes de manera que puedan ser manejadas cuantitativamente (*sensu* Oxnard 1978).

El objeto de estudio es la cactácea columnar gigante *Cephalocereus columna-trajani* (Karwinski ex. Pfeiffer) Schumann y su entorno comunitario. Esta cactácea es endémica de la región semiárida poblano-oaxaqueña y es particularmente abundante en el valle de Zapotitlán, donde es el elemento fisonómicamente dominante de la unidad de vegetación denominada **cardonal** (Zavala Hurtado 1982).

C. columna-trajani es conocida localmente como **cardón blanco** o **viejito**. Los individuos de esta especie son plantas columnares que alcanzan hasta 10 m de altura y ramifican sólo cuando sufren lesiones severas. El tallo es verde grisáceo claro y se encuentra inclinado consistentemente hacia una dirección NNW. En esta misma dirección, al alcanzar la madurez, se produce un pseudocefalio longitudinal lateral, que es una estructura lanosa de la cual emergen las flores.

El **cardonal**, además del **viejito**, se caracteriza por la presencia principal de *Mimosa luisana*, *Mascagnia seleriana*, *Echinopteryx eglandulosa*, *Agave kerchovei*, *Pedilanthus aphylus*, *Euphorbia antisiphyllitica*, *Bursera arida*, *Lippia graveolens* y *Calliandropsis nervosus*. Esta unidad de vegetación domina el paisaje de los cerros que conforman la sierra de Miahuatepec, en el límite oriental del valle de Zapotitlán. Se encuentra en terrenos muy accidentados con una pendiente media de 10.7°. La superficie del suelo es muy pedregosa y éste es poco profundo y con una relativamente alta cantidad de materia orgánica, fósforo, sodio y magnesio. La textura es moderadamente fina, del tipo migajón arcilloso-limoso (Zavala-Hurtado 1982).

Area de estudio

El valle de Zapotitlán es una cuenca local que conforma el límite suroeste del valle de Tehuacán, en el Estado de Puebla. Esta zona (18° 20' N, 97° 28' O) forma parte de la región semiárida Poblano-oaxaqueña (Vite *et al.* 1992), situada en la sombra de lluvia de la Sierra Madre Oriental. El clima es semiárido del tipo $BS_0hw''(w)(e)(g)$ (García 1981). La precipitación promedio anual es de 380 mm y la temperatura media anual de 21°C. Los suelos son litosoles calcáreos rocosos y poco profundos y derivan primordialmente de rocas sedimentarias y metamórficas. La vegetación corresponde al **matorral xerófilo** (Rzedowski 1978) y su flora tiene afinidades neotropicales. El valle de Tehuacán posee una de las floras más diversas de ecosistemas semiáridos en el hemisferio occidental con cerca de 630 géneros y 1400 especies de fanerógamas de las cuales alrededor del 30% son endémicas (Smith 1965; Villaseñor, Dávila y Chiang 1991). Este nivel de endemismo es poco usual para una región contenida en un gran continente y se acerca al grado de endemismo encontrado en algunas islas oceánicas (Smith 1965). Dentro de esta flora destacan las cactáceas con 53 especies, de las cuales 12 son endémicas (Meyrán 1973). Finalmente, esta es la región con mayor diversidad de cactáceas columnares en el mundo.

Objetivos y sinopsis del contenido

El objetivo general de este trabajo es contribuir al conocimiento de la ecología de *Cephalocereus columna-trajani* en el valle semiárido de Zapotitlán, Puebla. Esta contribución se basa en un enfoque morfométrico que implica el análisis de diversos aspectos de las interacciones de individuos y poblaciones de esta especie con su medio ambiente. Estos aspectos abarcan los niveles individual, y comunitario y quedan comprendidos dentro de los siguientes objetivos particulares:

i) Al nivel individual, se pretende analizar el valor funcional de la inclinación del tallo y orientación del pseudocefalio en términos de intercepción de radiación solar directa para individuos de *Cephalocereus columna-trajani* en el valle de Zapotitlán.

ii) También en el nivel individual, se pretende evaluar las consecuencias, en términos de tasas de crecimiento y producción de flores, de la reparación somática en individuos de una población de *Cephalocereus columna-trajani* en el valle de Zapotitlán.

iii) Finalmente, en el nivel comunitario, se intenta generar una clasificación de formas de vida vegetales en las comunidades que habita *Cephalocereus columna-trajani* en el valle de Zapotitlán con base en caracteristicas morfológicas con implicaciones funcionales.

Estos objetivos fueron abordados mediante tres trabajos independientes que conforman el cuerpo de esta tesis:

En el Capitulo II se presenta un análisis funcional de la morfología de *C. columna-trajani*. En este trabajo, que fue enviado a la revista *Ecology*, se analizan los conflictos funcionales que implica la presencia de una superficie no fotosintética (el pseudocefalio) y la inclinación del tallo. El estudio involucra (a) observaciones de campo con base en las cuales se describen cuantitativamente los patrones de orientación del pseudocefalio e inclinación del tallo, así como la morfología promedio de los individuos muestreados de *C. columna-trajani* y (b) simulaciones por computadora en las que se compara la eficiencia de captación de radiación solar directa de cactus con diferentes morfologías (pseudocefalio orientado en diferentes direcciones, en cactus erectos e inclinados).

El artículo presentado en el Capítulo III fue publicado en el *Journal of Arid Environments* (Zavala-Hurtado y Díaz-Solís 1995). En este estudio se aborda la pregunta: ¿cuáles son los costos del proceso de reparación somática después de un daño que ocasiona la fractura del tallo con la consiguiente pérdida del meristemo apical, en términos de sobrevivencia, crecimiento y reproducción en *Cephalocereus columna-trajani*? A partir de una estratificación de la población en individuos no dañados e individuos reparados, se realizó un análisis comparativo entre ambas subpoblaciones en lo referente a sus tasas de crecimiento, edad de la primera reproducción y producción de flores. Finalmente, a partir de una relación alométrica simple entre el diámetro del tallo y la altura (relacionada con la edad) se hizo una estimación de la altura que tenían los individuos dañados cuando sufrieron la fractura del tallo ; a partir de esta estimación, se calculó la probabilidad de una reparación exitosa (sobrevivencia después del daño) dependiendo de la altura del cactus al momento de ser dañado.

Finalmente, el Capitulo IV está constituido por un articulo publicado en la *Revista de Biología Tropical* (Zavala-Hurtado *et al.* 1996). Este es un trabajo a nivel comunitario basado en la suposición de que las características morfológicas de las plantas representan estrategias conductuales para enfrentar las presiones ambientales particulares del desierto. En dicho articulo se describe una clasificación multivariada de las formas de vida de plantas perennes en el valle de Zapotitlán basada en características morfológicas relacionadas con la eficiencia fotosintética, la conservación y almacenamiento de agua y la regulación térmica. Además, en una escala local (1 km^2), se exploró la relación entre los patrones espaciales de los ensamblajes de formas de vida y algunas variables ambientales (geomorfologia, humedad y pH del suelo) mediante un análisis multivariado de ordenación. Finalmente, se presentan las curvas de respuesta de formas de vida selectas a lo largo de los gradientes ambientales interpretados con base en el análisis de ordenación.

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II. STEM TILTING AND PSEUDOCEPHALIUM ORIENTATION IN *Cephalocereus columna-trajani* (CACTACEAE): A FUNCTIONAL INTERPRETATION.

Here comes the Sun,
here comes the Sun,
and I say :
it's all right.

(George Harrison)

Stem tilting and pseudocephalium orientation in *Cephalocereus columna-trajani* (Cactaceae): a functional interpretation[§].

José Alejandro Zavala-Hurtado(1), Fernando Vite(1) & Exequiel Ezcurra(2)

(1)*Departamento de Biología, Universidad Autónoma Metropolitana-Iztapalapa, Apartado Postal 55-535, 09340-México, D.F.; México*
(2)*Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, 04510-México, D.F.; México*

Abstract. This paper analyzes the functional implications of stem tilting and pseudocephalium orientation in the giant columnar cactus *Cephalocereus columna-trajani*. This species shows a consistent northern orientation of its pseudocephalium (a non-photosynthetic hairy structure where flowers are produced) and stem tilting in the same direction. Analysis of pseudocephalium orientation was made on field data gathered from subpopulations of *C. columna-trajani* from slopes with different exposures. Additionally, from morphometric characteristics measured in the field, a model cactus was constructed with the purpose of simulating radiation interception by different morphologies. Variations of this model cactus allowed the simulation of irradiance on erect and tilted cacti, as well as on plants with varying pseudocephalium orientation. Results of irradiance interception by different morphologies were related to actual data of growth rates, flowering period and rainfall and temperature patterns on the study zone. Sampled individuals of *C. columna-trajani* showed a significant NNW pseudocephalium orientation (angular mean = 339°±22°). Simulations showed that tilted cacti with pseudocephalii facing northwards increase yearly interception of direct solar radiation by the whole plant compared to erect cacti with or without a pseudocephalium (2% and 7% increase respectively), and with tilted cacti with the pseudocephalium facing away from the North (9 to 10% increase). Additionally, the observed morphology decreases radiation interception during the hottest and driest period of the year. From our results, pseudocephalium orientation and stem tilting in *C. columna-trajani* appears to be a morphological adaptation that allows the fine-tuning of a columnar morphology to its thermal and radiation environment. However, the cost of tilting in this giant columnar cactus is that branching (which increases photosynthetic area and reproductive output) appears to be almost impossible without serious risk of stem breakage.

[§] **Enviado a:** *Ecology*

Key Words: Adaptation; semiarid lands; functional morphology; growth rate; irradiance; PAR; pseudocephalium; tilting; thermal regulation; Zapotitlán, Mexico.

Introduction

Cephalocereus columna-trajani (Karwinski ex Pfeiffer) Schumann is a giant, usually unbranched, columnar cactus which forms dense populations on hills of the semiarid region of Puebla and Oaxaca in intertropical Mexico (Bravo-Hollis 1978). This spectacular plant (Fig. 1), known locally as cardón, reaches a height of 10-12 m and characterizes a vegetation unit named cardonal in the xerophytic scrub of the Valley of Zapotitlán (Zavala-Hurtado 1982).

An eye-catching feature of these populations is the marked stem tilting of the upper shoot of the cactus, which bends northwards with a similar orientation in almost all plants. In the concave side of the bent stem, and also facing approximately North, a pseudocephalium is found in all adult plants (Fig. 1; Greenwood 1964). The pseudocephalium is a cluster of densely pubescent, flower-bearing areoles that are formed along the sides or at the top of a cactus stem, not including the shoot apex (Gibson and Nobel 1986). *C. columna-trajani* individuals initiate the production of the pseudocephalium when they attain an average height of 3.35 m and become reproductive (Zavala-Hurtado & Diaz-Solís 1995). The developing flower buds are embedded, and hence protected, in the previously-formed pseudocephalium hairs. To our knowledge, this unique morphological adaptation is not found in other columnar cacti.

The surface of the pseudocephalium is not photosynthetic. On the one hand, the woolly cover impedes the arrival of light to the epidermis. On the other, the tissue surface under the hairy mat of the pseudocephalium is suberose and does not contain chloroplasts. Thus, this cactus species may lose a significant proportion (9 to 10%) of its potentially photosynthetic tissues with the development of the pseudocephalium. Because of their stem-succulent nature and their extremely low surface-volume relationship, giant columnar cacti maintain a large proportion of non-photosynthetic parenchyma, which lives at the expense of the relatively scarce chlorenchyma that is only found in the epidermis of the stem. Thus, on a whole-plant basis the compensation level for net photosynthesis is high (Nobel 1988), and the functionality of the stem epidermis as a light-capturing structure is extremely important. In this context, the evolution of a morphological trait such as the pseudocephalium, that has evolved at the cost of losing a significant amount of the photosynthetic epidermis, needs to be explored in terms of its functional morphology.

In this paper, we advance the hypothesis that pseudocephalium orientation and stem tilting in *Cephalocereus columna-trajani* actually has functional advantages in terms of radiation interception compared with unbranched erect cacti with no pseudocephalium and tilted cacti with pseudocephalium orientations different from the observed one. Additionally, we hypothesized that the northwestern orientation of the pseudocephalium and stem tilting protect the flowers from direct solar radiation. This hypothesis is explored by means of: (a) a statistical description of the orientation of the pseudocephalium in *Cephalocereus columna-trajani* in plain terrain, and in north, south, east, and west slopes; (b) simulations of irradiance received by a model cactus with the pseudocephalium at different azimuths, and with and without tilting of the trunk, and (c) analysis of radiation interception curves in terms of their relationship with growth rate, flowering, rainfall and temperature curves.

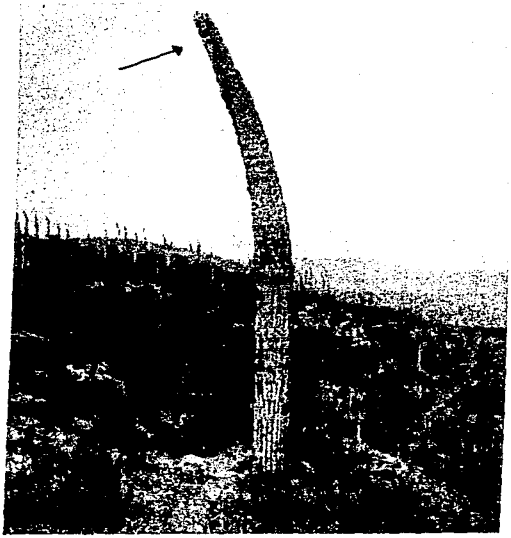

Fig. 1. Individual plant of *Cephalocereus columna-trajani* in Zapotitlán, Mexico; the photograph was taken from the West of the plant. The stem is tilted towards the NNW (as is the rest of the population visible in the background). The black arrow shows the pseudocephalium.

Methods

Study site.- Field data were gathered from a cardonal in a hill at the semiarid Valley of Zapotitlán (18° 20' N, 97° 28' W, 1550 m elevation), a local basin of the Tehuacán Valley in the Pueblan-Oaxacan Region in the Mexican State of Puebla (Vite et al. 1992). Climate in this zone is semiarid with summer rains. Annual mean temperature is 18-22°C and precipitation is around 400 mm/year. The soils are shallow, stony, and halomorphic (Byers 1967). Semiarid conditions are imposed by the rain shadow of the Sierra Madre Oriental which intercepts humid winds from the Gulf of Mexico. The vegetation has been classified as a xerophytic scrub (matorral xerófilo; Rzedowski 1978).

Orientation of the pseudocephalii in the field

Five samples of 50 individuals of *C. columna-trajani* each were drawn from five different conditions: eastern, western, northern, and southern slopes and an unobstructed plain. Azimuth of pseudocephalium for each individual was measured using a Brunton compass corrected for true north. Angular mean and circular deviation of pseudocephalium azimuth for each sample were calculated using circular statistics (Zar 1974).

Modeling plant morphology

The irradiance received by a *Cephalocereus columna-trajani* individual was estimated from that computed for a three-dimensional figure made-up of 209 intercepting planes, or facets, each with specific dimensions, azimuth, tilting angle, and suppressed photosynthetic area due to the pseudocephalium. The data for the construction of the geometric model cactus were gathered from ten randomly-selected adult individuals with a mean height of 5.63 m (min. 4.91 m; max. 6.82 m; *sd* = 0.63 m) growing in an unobstructed plain. We measured cactus heights to the nearest centimeter using a 10 m extendible pole gauge. Shoot diameter was measured to the nearest millimeter using a caliper. Measurements were taken every meter starting from the cactus base. Additionally, we recorded pseudocephalium length, and width every 0.5 m using a measuring tape. Tilting angle of the cactus shoot was measured for each of three two-meter-high segments from a vertical reference on printed photographs taken from a sample of 35 randomly-selected adult individuals growing in the same plain, with a mean height of 6.74 m (min. 5.80 m; max. 7.80 m; *sd* = 0.52 m; we used a larger sample for this measurement in order to obtain accurate regression estimations of tilting). With these data, a geometric model cactus was constructed as described in the Appendix.

The simulations were run for six theoretical morphologies: (a) erect plants without pseudocephalium (tilting angle = 0 and no. of facets covered by the pseudocephalium = 0 for all segments); (b) erect plants with NNW pseudocephalii (tilting angle = 0 for all segments); (c) tilted plants with NNW pseudocephalii; (d) tilted, East-oriented pseudocephalii (azimuth of facets rotated 111°); (e) tilted, West-oriented pseudocephalii (azimuth of facets rotated -69°); and (f) tilted, South-oriented pseudocephalii (azimuth of facets rotated -159°). Model cacti with no pseudocephalium have a photosynthetic surface of 5.70 m^2. In model cacti with a pseudocephalium the photosynthetic surface becomes reduced in 9.4% (although the total surface area is the same).

Simulation analyses

A computer program simulating direct solar radiation (Ezcurra et al. 1991) was supplied with data describing the azimuth, inclination and area of the 209 intercepting planes, plus the latitude and the date to be simulated. Using standard astronomical equations (Meeus 1988) the program calculates the apparent position of the sun from sunrise to sunset at 10-min intervals, and estimates the interception efficiency of each individual plane at each time.

Based on the fact that the pathway of the solar beam through the atmosphere becomes shorter as the sun approaches the zenith, the proportion of direct solar radiation that is dampened by the air mass was calculated as a function of the angular elevation of the sun above the celestial horizon (Ross, 1981) The estimations were done following Gates' (1980) method, which calculates direct solar radiation (W m^{-2}) intercepted by a given body with a known surface at a given hour of the day under a given air transmittance (which ranges between 0.5 and 0.8 in most desert areas). The simulations were run for three different dates: the equinox; the summer solstice, and the winter solstice, using an air transmittance value of 0.7 for each date. An extension of this program integrates the daily direct solar radiation (J m^{-2} d^{-1}), allowing the estimation for a whole year. Resulting figures of irradiance were multiplied by the photosynthetic area of the model cactus in order to estimate total irradiance received by the photosynthetic surface of the simulated plant.

As in most giant columnar cacti, the stem of *C. columna-trajani* is ribbed, and its total stem surface is around 5% larger than in the facet-projection we used for our simulations. The simulated radiation interception per unit photosynthetic surface may be referred either to the "true" (i.e. ribbed) surface, or to the un-ribbed geometric projection of the stem. For simplicity, we referred our results to the un-ribbed projection. If the results are referred to ribbed plants, then the intercepted radiation per unit area is proportionally less, but the relative differences between morphologies do not change.

The simulation data were supplemented with climatic information and with data on growth and flower production. Mean temperature and rainfall data (1990-1991) were provided by the climatological station of Zapotitlán Salinas (Servicio Meteorológico Nacional, Mexico). Average number of flowers per individual per month for 75 individuals of *C. columna-trajani* in 1990-1991 were drawn from our own unpublished data. Finally, mean monthly growth rates for the same two years were estimated from data of Zavala-Hurtado and Diaz-Solis (1995).

Results

Orientation of the pseudocephalii in the field

The five populations showed a significant mean direction (p < .001) according to a Raleigh test (Zar 1974). The mean azimuth and circular standard deviation of the pseudocephalium in plants from the unobstructed plain was 339° ± 21.8°. This orientation (hereafter called NNW) was considered as the typical natural orientation, and hence, the one to be evaluated in terms of efficiency in light interception.

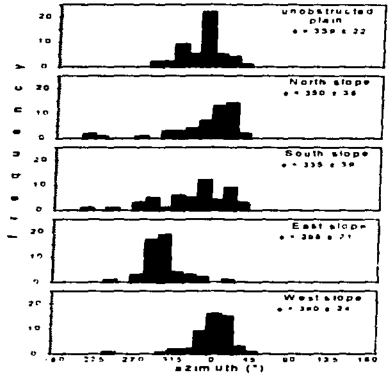

Fig. 2. Frequency distributions of pseudocephalium azimuth of fifty individuals of *Cephalocereus columna-trajani* from different slope-aspects in the valley of Zapotitlán, Mexico. Angular means (ϕ) and circular standard deviations of pseudocephalium azimuth are shown for each slope.

Two-sample tests using the method of Watson and Williams (1956 in Zar 1974) revealed that there were non-significant differences ($p > .1$) in pseudocephalium orientation between cacti from the northern and southern slopes and the unobstructed plain. Cacti from the eastern slope showed significantly different ($p < .001$) pseudocephalium azimuth from cacti of all the other four sites. The same occurred with cacti from the western slope, which showed significantly different ($p < .001$) pseudocephalium azimuth from cacti of all the other sites, excepting the northern slope (Fig. 2).

Simulation analyses

In our model, an erect cactus with no pseudocephalium intercepts 11652 MJ y^{-1} of direct solar radiation (Table 1). The presence of a pseudocephalium in erect plants reduced light interception in values ranging from 11.6% when the structure faced east, to 3.1% in northern orientations. An erect cactus bearing a pseudocephalium with north-northwestern azimuth would reduce its light interception by 5.1%, compared with an erect cactus with no pseudocephalium.

Bending of the shoot in plants with a pseudocephalium increased dramatically light interception (Table 1). A tilted cactus with a north-facing pseudocephalium intercepts more (4.0%) light than an erect one without a pseudocephalium. In tilted cacti, minimum light-interception would occur for a plant with a pseudocephalium facing south. The average observed cactus morphology (tilted, with a NNW pseudocephalium) intercepts 1.7%

more light than that received by an erect individual with no pseudocephalium.

Table 1. Total annual direct solar radiation (MJ d^{-1}) intercepted by eleven simulated plants differing in location of pseudocephalium and tilting (see Appendix for details of model cacti). Percentages are relative to an erect cactus with no pseudocephalium.

	Erect	%	Tilted	%
No pseudocephalium	11652	100		
Pseudocephalium NNW	11062	94.9	11853	101.7
Pseudocephalium N	11285	96.9	12113	104.0
Pseudocephalium E	10303	88.4	10825	92.9
Pseudocephalium S	10324	88.6	10615	91.1
Pseudocephalium W	10303	88.4	10825	92.9

Looking at the yearly pattern of light interception (Fig. 3a), it can be seen that the average observed cactus morphology shows the highest light interception during fall and winter when relatively low temperatures prevail in the region (Fig. 3b). This estimated radiation-interception pattern contrasts with the theoretical patterns of erect cacti without pseudocephalium, and especially of south-tilted cacti, which would maximize light interception during the relatively hot summer months. Additionally, the less efficient east- and west-tilted cacti, would show lower interception values throughout the year. It also can be seen that tilting improves light interception from September to March in cacti with NNW-azimuths in relation to the interception pattern of cacti showing the same orientation of the pseudocephalium but no shoot bending.

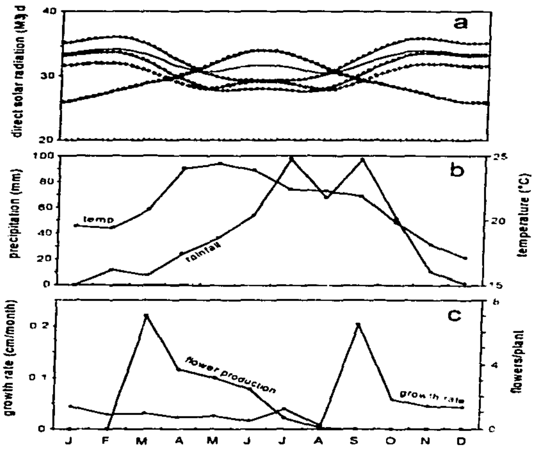

Fig. 3. (a) Simulated intercepted solar radiation by five different model cacti (continuous line: erect cactus with no pseudocephalium; open circles: erect cactus with pseudocephalium facing NNW; solid circles: tilted cactus with pseudocephalium facing NNW; line with triangles: tilted cactus with pseudocephalium facing E or W; and dashed line: tilted cactus with pseudocephalium facing S). (b) Average rainfall (solid circles) and mean monthly temperature (solid squares) from the Zapotitlán Salinas climatological station during 1990-91. (c) Mean growth rate (solid circles) and mean number of flowers produced per individual (solid squares) from a population of 75 *Cephalocereus columna-trajani* individuals during 1990-91.

Maximization of light interception during fall in the average cactus morphology (Fig. 3a) coincides with the peak in growth rate of *Cephalocereus columna-trajani* (Fig. 3c) and with the September rainfall period in the study site (Fig. 3b) for the analyzed years. Flower-blooming presents a peak in March (Fig. 3c), during a period of high incident radiation (Fig. 3a) and relatively low temperatures, before the onset of the rainy season (Fig. 3b).

The simulations of the daily patterns of light interception are presented only for the three most efficient morphologies: (a) erect plants with no pseudocephalium; (b) erect plants with a NNW-pseudocephalium; and (c) NNW-tilted plants with a pseudocephalium (Fig. 4). Simulations were performed for the equinox (Fig. 4a), the summer solstice (Fig. 4b), and the winter solstice (Fig. 4c).

Although the three types of cacti showed similar trends in their daily patterns of direct solar radiation interception, some relevant differences must be highlighted: (a) erect cacti with no pseudocephalium showed a symmetric pattern around noon; (b) cacti bearing a NNW-pseudocephalium (both erect and tilted) intercepted more radiation before noon in the summer solstice and in the equinox, compared to the radiation intercepted after midday; (c) tilted cacti with pseudocephalium showed the highest direct solar radiation interception of all morphologies during the equinox (33.7 MJ d^{-1}) and the winter solstice (34.1 MJ d^{-1}), and present an intermediate value during the summer solstice (29 5 MJ d^{-1}); (d) erect cacti with pseudocephalium showed the lowest radiation interception of all morphologies in the three simulations

(31.1 MJ d^{-1} on the equinox, 28.1 MJ d^{-1} on the summer solstice, and 32.2 MJ d^{-1} in the winter solstice); (e) erect cacti with no pseudocephalium showed intermediate values of radiation interception in the equinox and winter solstice (32.5 MJ d^{-1}, and 32.3 MJ d^{-1} respectively), and the maximum value of all morphologies during the summer solstice (31.8 MJ d^{-1}).

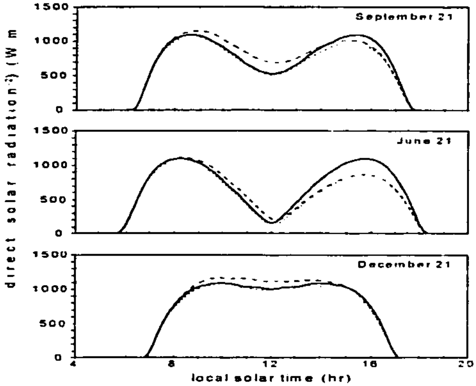

Fig. 4. Simulated daily interception of direct solar radiation (W m^{-2}) for cactus models of different morphology (continuous line [——]: erect cactus with no pseudocephalium; dotted line [· · · · · ·]: erect cactus with pseudocephalium facing NNW; and dashed line [- - - - - -]: tilted cactus with NNW-facing pseudocephalium). Graphs show intercepted radiation during (a) autumn equinox (the same simulation curve is obtained for March 21, the spring equinox); (b) summer solstice; and (c) winter solstice.

Discussion

Orientation in the flowering structures of columnar cacti is well-known. For example, in *Carnegiea gigantea* it has long been reported that flowers are primarily produced on the East-Southeast side of the top of the plant (MacDougall & Spaulding, 1910, cited in Nobel, 1981; Johnson, 1924), i.e. exactly on the opposite side from that for *C. columna-trajani*. For this northern species (*C. gigantea*), flower development seems to be enhanced by high surface temperatures achieved on the southern side of stem. Conversely, *Trichocereus chilensis* and *T. litoralis*, two species of columnar cacti from the southern hemisphere, produce flowers mainly in the warmer, northern side of the stem (Rundel, 1974).

Stem tilting, however, has only been studied in barrel cacti, a life-form with relatively short stems. Nobel (1988) argued that giant columnar cacti do not tilt because gravity would exert a considerable bending moment on their massive stems, causing their breakage. Indeed, from the many giant columnar species in the Tehuacán Valley, *C. columna-trajani* is the only one that exhibits stem tilting, and is also one of the only two species that do not usually branch. Additionally, stem breakage is a very frequent cause of physical injury on these plants (Zavala-Hurtado & Diaz-Solis 1995). Some barrel cactus species (e.g. *Ferocactus* spp. in North America and *Copiapoa* spp. in South America) expose their apical region (in which flowers are produced) to the South and North, respectively, (i.e. toward the equator) by means of a stem tilting. The northern azimuth and tilting in three species of *Copiapoa* was explained by Ehleringer et al. (1980) as a mean of increasing apical temperatures by enhancing meristematic activity during the winter and spring months. The equatorwards tilting of barrel cacti does not improve PAR interception and CO_2 uptake for the whole plant. On the contrary, the bending of the longitudinal stem axis towards the sun's trajectories in fact leads to less PAR annually incident on the stem (Nobel 1988). The functional advantages of tilting, hence, are possibly more related to temperature control than to a maximization of intercepted PAR.

The behavior of *C. columna-trajani* contrasts with previous reports on this problem in various aspects. First, *C. columna-trajani* is the only giant columnar species known to show a conspicuous stem tilting. Second, the species tilts away from the equator, and not towards it. Third, the flowers, which are embedded in the pseudocephalium, are also oriented away from the equator, in contrast with other columnar species that produce their flowers on the warmer side of the columnar stem facing the equator. And fourth, this cactus species is endemic to the intertropical zone, while all the previous reports of non-random orientation in columnar or barrel cacti are for subtropical plants growing either North of the Tropic of Cancer or South of the Tropic of Capricorn.

The importance of photosynthetically active radiation (PAR) as a limiting factor for cacti has been previously documented (Nobel 1980, 1981, 1982, Geller & Nobel 1986, 1987). PAR limitation occurs because of the opacity, rigidity, and vertical orientation of the photosynthetic surfaces of most cacti and of other CAM plants such as cactoid Euphorbiaceae. The capture of light in these desert succulents implies necessarily the risk of overheating their photosynthetic tissues. Many perennial desert plants - including succulent and non-succulent evergreen species - present their chlorenchyma vertically-oriented (e.g. Woodhouse et al. 1980, Nobel 1982, 1986, Cano-Santana et al. 1992, Ezcurra et al. 1991, 1992, Valverde et al. 1993). As a general rule, a vertically-oriented structure will intercept more light in the morning and afternoon, and less light at midday, when the sun is near the zenith. Thus, the vertical orientation helps to solve the compromise between capturing light and avoiding overheating during the warmer hours of the day. In the Tehuacán Valley, opuntioid, barrel, and columnar cacti establish under the shade of nurse plants, and their seedlings do not survive a dry season if they are exposed to direct solar radiation (Valiente-Banuet et al. 1991, Valiente-Banuet & Ezcurra 1991). Adult plants manage to survive direct exposure to the sun because of their vertical orientation. Felled individuals of *C. columna-trajani*, exposed horizontally to direct solar radiation, attain midday temperatures in their chlorenchyma above 55°C, while the normal erect plants are only slightly above air temperature, and around 35°C (unpublished data). In *Opuntia pilifera* the horizontal exposure of the usually vertical cladodes increases their midday temperature from 35°C to 47°C (Cano-Santana et al. 1992). Most cacti will show an abrupt increase in chlorophyll fluorescence (an indicator of decreasing electron flow in Photosystem I during photosynthesis) between 50 and 56°C. Furthermore, the electron transport involved in Photosystem II starts to decrease in cacti when the photosynthetic tissues reach temperatures between 40 and 50°C (Nobel 1988). Thus, even if the plant survives high midday temperatures, its photosynthetic system may lose much of its functional capacity if the chlorenchyma reaches temperatures above 45-50°C. The columnar life-form allows cacti to avoid the potentially harmful effects of high temperatures by maximizing PAR interception in the early morning and late afternoon. The strategy, however, has a cost, as PAR interception becomes suboptimal. For example, while horizontal cladodes of *Opuntia pilifera* in Zapotitlán intercept in one day as much as 41 mol photons per m^2 of cladode area, vertical cladodes facing East and West will intercept 23 mol m^{-2}, and vertical cladodes facing North and South will intercept only 5 mol m^{-2} (Cano-Santana et al. 1992). In the case of *C. columna-trajani*, an approximate conversion of our model's predictions from direct solar radiation into PAR indicates that the plants in the field intercept around 12 mol photons $m^{-2}day^{-1}$. Although this value is well above the compensation level reported for cacti, which is around 3 mol m^{-2} day^{-1}, it is also below the daily PAR level that results in maximum net uptake of CO_2, which is around 30 mol $m^{-2}day^{-1}$ (Nobel, 1988), and it is also well below the maximum measured PAR interception for a plane surface in the region (41 mol m^{-2} day^{-1}).

In this framework, tilting appears to be a morphological adaptation that allows the fine-tuning of a columnar morphology to its thermal and radiation environment. By tilting north-northwestwards with an angle that is greater than the northern declination of the sun during the summer solstice, the plant achieves a series of changes in its radiation-interception pattern. It intercepts less radiation at midday and during the afternoon than a vertical columnar plant during the hotter months of the year (Figs. 4 and 5). This is especially important as it is frequently the case that summer rains may arrive as late as July. The tilted stem intercepts more light than an erect structure during the September equinox, the time of the year when the summer rains have commenced and the soils are moister, and also when the plant shows greatest growth (Fig. 3). By tilting the stem, the non-photosynthetic pseudocephalium can develop without significantly losing PAR interception. In fact, tilting actually improves global PAR interception by about 2%, and it particularly improves PAR interception during favorable seasons and during the most favorable hours of the day. The spiny pseudocephalium, in turn, protects the flowers from potential nectar robbers, and also keeps the night-blooming flowers shaded during the day. Finally, the simulation shows that by shifting the pseudocephalium NNW instead of directly North, the plant increases light interception during the cooler hours of the morning (when the apparent position of the sun is in the East), and decreases interception in the afternoon (when the sun is in the West).

Thus, tilting has a direct bearing on the plant's reproductive system, and ultimately on its fecundity, as a mechanism that allows the protection of the flowers (that bloom in the dry season) from excessive evaporative demand and from potential predators. Additionally, tilting does not hinder PAR interception which is fundamental for successful plant growth. In short, our simulations suggest that tilting may have a positive effect on plant reproduction (an important component of fitness) without compromising plant growth (a second fundamental component of fitness). The obvious cost of tilting in a giant columnar cactus such as our study species is that branching becomes almost impossible without serious risk of stem breakage.

Thus, *C. columna-trajani* faces a trade-off compared with other columnar species in the region, such as *Neobuxbaumia tetetzo*: while tilting may increase its capacity to intercept PAR and at the same time to passively regulate stem temperature, the species cannot benefit from the increased PAR interception and CO_2 uptake (Geller & Nobel 1986, 1987), as well as the increased reproductive potential (Yeaton et al. 1980), that derive from stem branching.

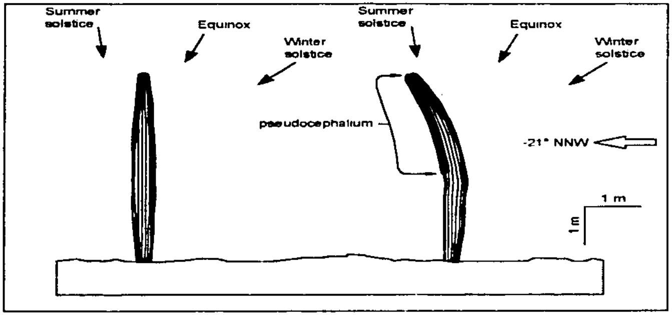

Fig. 5. Angle of incidence of direct solar radiation at midday for an erect unbranched columnar cactus compared with an average *C. columna-trajani*, for the summer and winter solstices, and for the equinox.

This interpretation of the results of our model can be tested with field data on the orientation of the pseudocephalii. In open plain habitats, the azimuth of the pseudocephalium is NNW (angular mean = 339°), but in plants growing on steep slopes, which obstruct part of the incoming radiation, the angular location of the pseudocephalium is shifted towards the slope, i.e. both tilting and the development of the pseudocephalium shift in the direction where the plant receives less direct solar radiation and less PAR.

It is interesting to note that the geographic range of this species is extremely restricted in terms of latitude. *C. columna-trajani* is only found in the Tehuacán Valley between Zapotitlán and Zinacatepec; ranging from 97°13' to 97°30' W, and from 18°18' to 18°21' N (Bravo-Hollis 1978). That is, the species transverses the Tehuacán Valley occupying some 40 km from East to West, but less than 10 km from North to South. The development of a tilting stem may be adaptive in this narrow area, but could be non-adaptive at other latitudes, as the success of the tilting strategy is strongly dependent on the apparent position of the sun during the growing season, and hence on the latitude of the site. The extreme degree of architectural specialization of this species may be at the same time the cause of its local success and also of its geographic rareness.

The northern orientation of the flowers in *C. columna-trajani* and the tilting away from the equator, in contrast with the equatorwards tilting and flower production in other cacti deserve some attention. The difference between our study species and other reported cactus species with stem directionality lies in the fact that *C. columna-trajani* grows in a frost-free intertropical zone, where a vertically-oriented columnar plant receives light on both its southern and northern face at different times of the year (Peters 1993). By tilting slightly to the North, this species intercepts less radiation during the hotter months of the year. Tilting thus allows the passive regulation by the plant of its thermal and radiation environment. Extra-tropical cacti, on the other hand, are often limited both by low temperatures in winter and high temperatures in summer. The apparent position of the sun for these plants is always towards the equinox. Tilting towards the equator may help to regulate radiation interception during the hot summers, while still allowing the interception of significant amounts of radiation during the cold months of the year. The interaction between the yearly radiation pattern, the radiation interception by tilted stems, and the growth season, remains to be studied in more detail for these plants.

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Appendix. Characteristics of the model cactus and their variations, used in this study for estimating the irradiance received by an actual or hypothetical *Cephalocereus columna-trajani* individual with similar characteristics.

Total heights and stem diameters were used for obtaining the overall shape of a cactus by means of the following regression equation:

$$D(H) = [\ 0.03844 + 0.09673\ H/T - 0.1080\ (H/T)^2\ ]\ T \qquad (1)$$

where

$D(H)$ = Stem diameter (cm) at any height (H) of the stem (cm),

T = Total height of an individual (cm).

This equation was obtained by polynomial regression on field data from 10 plants growing in open plain areas ($R^2 = .75$; $F_{2,59} = 86.5$; $P < .00001$).

With the tilting angles measured for the plant segments, a data set was constructed for statistical analyses. As tilting of the upper part of the plant may bend the lower part of the stem in the opposite direction, negative signs were assigned to the angles of sectors that were bent away from the azimuth of the pseudocephalium. The tilting angles for the midpoint of these three categories was fitted to an arbitrary exponential function ($r = .72$ on a semi-log scale; $n = 105$; $p < .05$) which allowed us to interpolate the mean angle of deviation from the basal point for any height of the stem. The function obtained was

$$\beta = [\ 3.8798\ .\ \exp(1.2777\ H)\ ] - 7.0 \qquad (2).$$

Where β is the angle of deviation and H is the height of a standardized plant 6 m high. This function allowed us in turn to model the tilting angle of any specific stem segment.

For a plant with a total height of 600 cm, Equation (1) was used in the computation of diameters at every 50 cm from 0 to 550 m high, and at 595 cm high. With these data, each of the twelve stem stretches was approximated as a truncated pyramid composed by 16 equal trapezoidal sides, or facets. The calculated diameters at each height were ascribed to the maximum width of the bottom and the top of the truncated pyramids. Finally, the plant apex was simulated by a 5-cm-high truncated pyramid with 16 lateral sides and a 8.45-cm-wide flat top. Equation (2) was used to calculate the expected tilting angle of the stem axis for each of the twelve segments. Standard trigonometric equations were used for assigning an azimuth and a vertical angle to each truncated pyramid with respect to the main axis of the stem. Spherical trigonometry was used to calculate the azimuth and the inclination of each facet with respect to the local horizontal coordinates, knowing their azimuth and inclination with respect to the main axis of the stem, and the inclination and azimuth of each stem sector.

Thus, the basic characteristics of the model plant (which are similar to the mean characteristics of actual plants in the field) were the following:

No. of segment	height class (cm)	stem diameter (cm)	tilting angle (°)	number of facets	facet area (cm²)	segment area (cm²)	pseudocephalium	
							number of facets	% covered
1	0-50	23.06	-2.68	16	246.60	3945.60	0	0.00
2	150-100	27.45	-1.71	16	284.94	4559.00	0	0.00
3	100-150	30.94	-0.58	16	314.49	5031.87	0	0.00
4	150-200	33.52	0.74	16	335.28	5364.43	0	0.00
5	200-250	35.21	2.28	16	347.30	5556.84	0	0.00
6	250-300	36.00	4.05	16	350.58	5609.20	0.40	2.48
7	300-350	35.88	6.11	16	345.10	5521.52	0.99	6.22
8	350-400	34.87	8.47	16	330.86	5293.77	1.59	9.96
9	400-450	32.96	11.17	16	307.86	4925.84	2.19	13.71
10	450-500	30.14	14.23	16	276.10	4417.55	2.79	17.45
11	500-550	26.43	17.68	16	235.54	3768.62	3.39	21.19
12	550-595	21.82	21.33	16	170.14	2722.24	3.99	24.93
13	595-600	16.89	21.53	16	16.04	256.64	4.59	28.68
14	(crown)	8.45		1	56.81	56.81	0	0.00

III. REPAIR, GROWTH, AGE AND REPRODUCTION IN THE GIANT COLUMNAR CACTUS *Cephalocereus columna-trajani* (KARWINSKI EX. PFEIFFER) SCHUMANN (CACTACEAE).

Morir...
¿podré resistir tamaño acontecimiento,
o moriré en el momento
en que me tenga que ir
sin pena y sin sentimiento ?
Morir, morir no quisiera...
morir para siempre,
¡no!
Espérate muerte, espera
y déjame que me muera
cuando te lo pida yo.

(Miguel Hernández)

Repair, growth, age and reproduction in the giant columnar cactus *Cephalocereus columna trajani* (Karwinski ex. Pfeiffer) Schumann (Cactaceae)[§].

José Alejandro Zavala-Hurtado and Amaury Díaz-Solís

Departamento de Biología, Universidad Autónoma Metropolitana-Iztapalapa.
Ap. Postal 55-535, México 09340, D.F. México.

Abstract.- Loss of shoot tip because of severe, but non-lethal, injury is a common event in the life-cycle of giant columnar cacti. Repair (reiteration) could adversely affect further growth and reproduction because of a reassignment of resources. We studied a population of *Cephalocereus columna-trajani* in Central Mexico, comparing growth rates, age of first reproduction and number of flowers produced per individual between repaired and undamaged cacti. A fitted generalized linear model, using a binomial error distribution and a logit link function, describes the probability of survivorship after the cactus shoot is broken. According to this model, only individuals exceeding some critical height before damaged are able to survive, and also only reproductive individuals not surpassing an upper threshold height (or age) would survive. We did not find significant differences in flower production between injured and non-injured individuals. The cost of repair would imply a delay of *ca.* 60 years before the damaged cacti could resume reproduction.

Keywords: *Cephalocereus columna-trajani; giant columnar cacti; repair; growth; age; reproduction*

Introduction

It is almost inevitable for organisms to suffer some sort of physical damage during their life span due to their interactions with the environment. In a wide

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[§] **Publicado en:** *Journal of Arid Environments* (1995) **31**:21-31 sense, the role of regeneration, or biological repair, is to maintain the life of the organism and to postpone death due to physical damage. Repair, the power to replace lost or damaged cells, is a fundamental biological process seen in almost all organisms (Elder 1979). Such process is expected to have a cost for organisms in terms of long-term survival and reproduction, but it is also expected to yield a benefit, namely, the immediate survival after damage (Harris 1989).

There is an important link between repair and the life-history of an organism. The main focus of this link is the distribution of resources to different metabolic activities, not only to growth and reproduction but also to restoration. Resource assignment to somatic repair in iteroparous species is of particular interest, as iteroparous life-span may be indefinite. Reproduction occurs various times during maturity and does not coincide with the termination of the individual life cycle, as in semelparous organisms (Kirkwood 1981).

Repair in plants is different from that in animals. Although some repair is analogous to wound healing in animals (e.g. bark formation promoted by an injury), the main response to damage in plants is to replace rather than repair damaged modules. Modules can die as a result of damage, competence or environmental changes, and their death can promote the production of new units (Kirkwood 1981).

In monopodial, orthotrophic plants such as columnar unbranched cacti, damage that destroys the shoot tip eventually promotes reiteration of one or several healthy areoles near the wound. This is the result of the loss of apical dominance, which is enforced by hormone control from the tip (Phillips 1975, Halpering 1978). When the apical meristem dies the lateral meristems resume shoot growth. If there is not an overwhelming dominance of a leading branch, the result is often a branched individual (Sachs 1988).

C. columna-trajani (Karwinski ex Pfeiffer) Schumann, also known as *Cephalocereus hoppenstedtii* (F.A.C. Weber) is a giant unbranched columnar cactus, endemic of the semiarid region of Puebla and Oaxaca in Central Mexico (Bravo Hollis 1978). This spectacular plant, known locally as *cardón*, reaches a height of 10-12 m and characterises the vegetation unit named *cardonal* in the thorn-scrub cactus vegetation of the Valley of Zapotitlán (Zavala-Hurtado 1982). When individuals of this species reach sexual maturity, they produce a hairy structure, or pseudocephalium (*sensu* Gibson and Nobel 1986), which shows a consistent north-western orientation. The pseudocephalium elongates as the cactus blooms each season, leaving behind the scars of past flowers. In the upper part of this structure, areoles produce flowers, often in dense clusters, with a single nightly anthesis (Bravo Hollis 1978; Gibson and Horak 1978). Blooming usually occurs from March to September, although some isolated flowering individuals can be seen throughout the year

It is common to find huge individuals of *Cephalocereus* with an evident transversal cut giving the appearance of the shoot having been broken and rejoined. Actually, the mark indicates the past death of the apical meristem, or the cutting of the upper part of the plant, followed by reiteration of a new leading branch. It is not as common, but not quite rare, to see individuals with several branches emerging from a transversal cut. In this case, the death of the apical meristem and the ensuing loss of apical dominance, activated the growth of more than one lateral areole. The causes of transversal damage are not fully understood, but some hypotheses can be advanced: (i) it could be due to mechanical properties of the column, which would not support the weight of a shoot over a critical height; (ii) a wound caused by different agents (both physical or biological) would lead to the development of an infection softening the tissue and eventually producing the fracture of the shoot; (iii) sometimes peasants, particularly during drought periods when there is not enough pasture for goats, cut the shoot allowing the animals to eat the parenchyma (these cuttings are transversal only in young individuals of less than 2 meters height: in large cacti the procedure is to expose the parenchyma in the base of the plant by cutting-off the areoles and the epidermis); and (iv) any combination of the above.

In this work we try to approach an answer to the general question: What are the costs of repair in terms of survival, growth, and reproduction in the giant columnar cactus *Cephalocereus columna-trajani*? Thus, we aimed (i) to describe a population of *C. columna-trajani* stratified in undamaged individuals and those with reiterations originated from a physical injury, (ii) to estimate the growth rate and age of both groups, (iii) to estimate height or age of the first reproduction in both groups, (iv) to estimate height or age of the plant when damage occurred, and (v) to compare both groups in terms of the number of flowers produced per individual.

Study site

Our study site was at the semiarid valley of Zapotitlán (18° 20' N, 97° 28' W), a local basin in the Pueblan-Oaxacan Region in the Mexican State of Puebla (Vite *et al.* 1992). This a unique region in terms of its biological richness, about 30% of its species are endemic and it is especially rich in columnar cacti (Villaseñor *et al.* 1991).

The climate is dry with summer rains. Annual mean temperature is 18-22°C and precipitation is around 400 mm/yr. The soils are shallow, stony, and halomorphic (Byers 1967). Arid conditions are produced by the rain shadow of the Sierra Madre Oriental. The vegetation has been classified as *matorral xerófilo* (xerophyllous scrub; Rzedowski 1978) or as thorn scrub cactus (Smith 1965), and is a well-preserved sample of this vegetation type, that supposedly covered the region some 10,000 years ago (Smith 1967; Zavala-Hurtado 1982).

Our research was carried out within the vegetation unit named *cardonal* (Zavala-Hurtado 1982). This unit is physiognomically characterised by *Cephalocereus columna-trajani*, a giant unbranched columnar cactus which emerges from a lower stratum of thorny shrubs.

Methods

In a North-facing slope we marked an area of 2,500 m^2 All individuals of *C. columna-trajani* were tagged and located on a chart. Undamaged individuals were differentiated from those showing an evident transversal damage (those that have lost a section of their shoot, including apex) and a reiterated shoot above it. In this paper, these reiterated cacti are referred to, indistinctly, as 'damaged' or 'repaired' individuals. In each undamaged individual we recorded total height and height of the base of the pseudocephalium to the nearest centimetre using a measuring tape attached to a 10 m rod facing the cactus side bearing the pseudocephalium. Shoot diameter was measured to the nearest millimetre using a caliper, always in an east-west direction at 1.5 m in height. Additionally, we counted the number of ribs at the same height. The same measures were recorded for repaired plants above the damage scar. Additionally, in this group we also measured the height of the damage scar, and the diameter and number of ribs below and above the damage line. To estimate apical growth rates, we measured shoot elongation (absolute difference between two consecutive height measurements) every 6 months from November 1989 to November 1991. Finally, we counted flowers produced during blooming periods from March to September of both 1990 and 1991. Flower counts were carried out at dawn during five consecutive days every 2 weeks to estimate number of flowers produced per individual.

Results

Undamaged plants between 50 cm and 1 meter constituted the best represented height class (Fig 1(a)). This large representation of young individuals is typical of a population of sexually-reproducing organisms. Deviations from an expected exponential model were not significant (p>0.2).

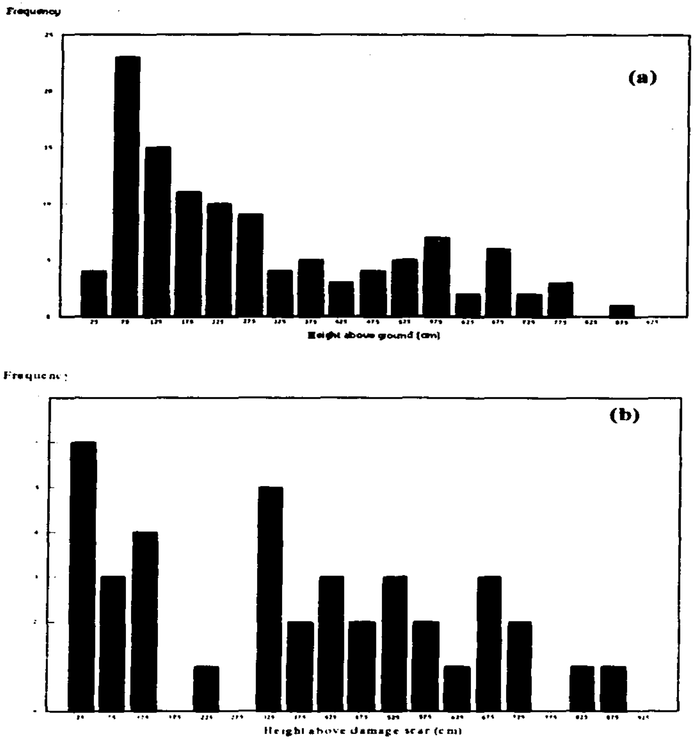

Figure 1. Height distribution of (a) undamaged (n = 114) and (b) damaged (n = 62) individuals in a population of *Cephalocereus columna-trajani*. Height in damaged individuals refers to height of reiterations above the damage scar.

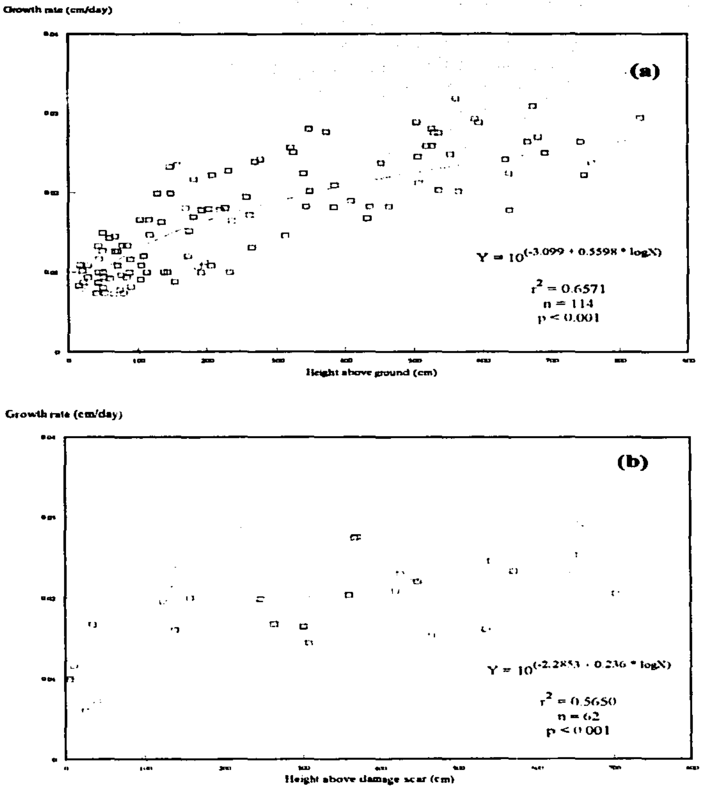

Figure 2. Scatter diagrams and fitted curves of the exponential models relating height and growth rate of (a) undamaged, and (b) damaged individuals in a population of *Cephalocereus columna-trajani*. Height of damaged individuals refers to height of reiterations above the damage scar.

Damaged individuals did not show any conspicuous pattern of height structure, but peaks at 25 cm, 3.25 m, 5.25 m and 6.75 m could indicate past periods of disturbance (Fig. 1(b)). A log-log regression analysis showed a significant allometric relationship (r^2=0.657, p<0.001) between height and growth rate (Fig.2(a)). It can be seen that the older individuals grow faster than the younger ones, but that growth rate tends to stabilize around an asymptotic value of approx. 0.03 cm/day. The growth rate of reiterations in damaged individuals also showed a significant fit to an allometric model (r^2=0.565, p<0.001; Fig.2(b)).

Additionally, we found a significant allometric relationship between shoot diameter and cactus height (r^2=0.865 p<0.001; Fig.3) similar to the one estimated by Yeaton, Karban and Wagner (1980) for *Carnegiea gigantea* (Engelm) Britton & Rose in Arizona. We used this relationship to estimate cactus height and age when damage was produced.

Figure 4 shows the distribution of estimated heights of cacti at the time the primary shoot was lost. Most of the sampled cacti were damaged when they had attained a height between 2.5 m, and 6 m (x=4.09 m; S.D.=2.00 m). This suggest at least two things: (i) that younger individuals would have low survival probabilities after apical damage, or, alternatively, that younger individuals are less prone to suffer this type of damage; and (ii), as individuals above 7.75 m are poorly represented, there seems to exist a threshold height above which damaged individuals would not survive.

Probability of regeneration after damage depending on cactus height was predicted by generalised linear modelling (GLM), assuming binomial error distribution of the response variable (presence or absence of repaired individuals after a damage at a given height) and using a logit link function (McCullagh & Nelder 1983). The independent variables were height and its quadratic form to allow a non-monotonic response. The fitted model was ($p<0.001$, Fig.4):

$$R = e^{lp} / (1 + e^{lp})$$

where:

$lp = -6.161 + 0.028x - 0.000031x^2$ is a linear predictor,

R = probability of reiterating,

e = 2.7183, the base of natural logarithms,

x = height of cactus

Figure 5 shows the frequency distribution of height (Fig.5(a)) and age (Fig.5(b)) of first reproduction, *i.e.* the height above the damage scar of the base of the pseudocephalium in damaged individuals, and the height above the ground of the base of the pseudocephalium in non-damaged individuals. We did not find significant differences using height of first reproduction, but a significant one does exist considering age of first reproduction (Table 1). Finally, although damaged individuals produced more flowers per individual in the 1990 and 1991 flowering periods, a Kolmogorov-Smirnov test showed that this contrast was not significant (*p*>0.25).

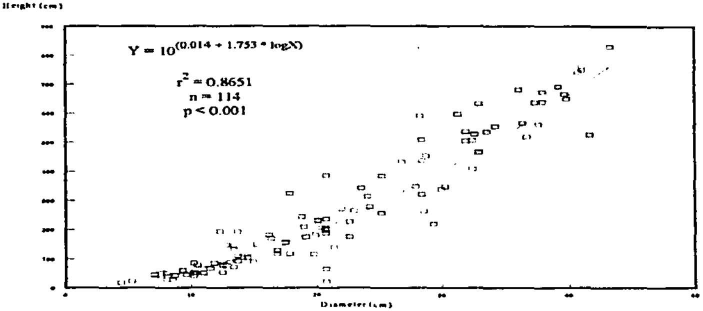

Figure 3. Scatter diagram and fitted curve of the exponential model relating shoot diameter and column height of undamaged individuals of *Cephalocereus columna-trajani.*

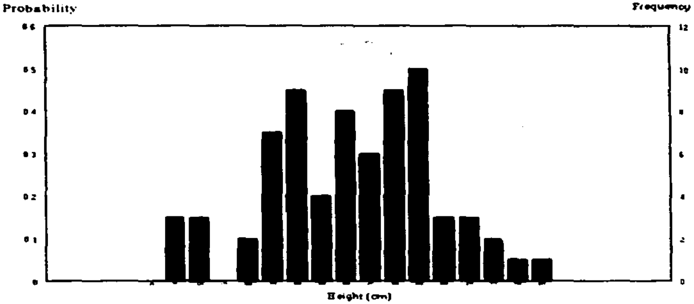

Figure 4. Frequency distribution of estimated height when cacti were damaged, and probability of successful repair according to a fitted generalized linear model (see text for details) in a population of damaged *Cephalocereus columna-trajani.*

Discussion

From the height distribution of undamaged individuals (Fig.1(a)), and according to our age estimation, it could be inferred that some 88-123 years ago, there were high rates of recruitment, perhaps due to relatively benign environmental conditions (Parker 1989). Height structure of reiterations does not show any apparent pattern but peaks could indicate past disturbance events.

The regression model relating growth rate with height of individuals allowed the estimation of cactus ages. Thus, an undamaged individual with a height of 2 cm would be about 1-year-old, whereas a reiteration of the same height would be about 6-months-old, and a 1 m undamaged individual would be almost 23-years-old. These differences are due to a higher growth rate for reiterations below 3 m height. Although non-damaged individuals above this height grow faster than reiterated modules, these would be younger than undamaged cacti for any given height within the sampled range of heights. Following this, a mature individual of 3.30 m would be almost 70-years-old in the case of an undamaged cactus, while a reiteration of 3.30 m would be around 60-years-old, irrespectively of the age of the plant when damaged. A reiteration of 10 m height would be 135-years-old, and an undamaged cactus of the same height would be 145-years-old. According to our estimation, taller (and hence, older) individuals grow faster than younger ones (Fig.2(a)). Opposed to our results, Turner (1990), using a complex exponential model, found younger individuals of the giant columnar cactus *Carnegiea gigantea* growing faster than the older ones. This contrast could, at least partially, be due to different growth habits of both species. Whereas *C. columna-trajani* usually does not branch, expenditure of resources in branching in the older individuals of *Carnegiea gigantea* could lead to a reduction in the overall elongation rate of the leader shoot (E. Ezcurra, pers. comm.).

The exponential regression model that predicts height (and age, by extension; Fig. 3) by the simple measure of shoot diameter allowed us to estimate height (and age) of a given repaired cactus when it was damaged (Fig. 4). Underlying this estimation is the assumption that the observed damage was unique, and that healing and repair did not modify diameter-height allometric relationships.

Under-representation of repaired individuals damaged when they were below 2.75 m (about 61 years) or above 6 m (about 103 years) leads to the hypothesis that these individuals would not survive a damage which breaks their shoot because of a lack of vigour. In young individuals this kind of damages would be caused mainly by predators or diseases. Conversely, rupture of shoot in giant individuals could be caused by severe winds or diseases as well. In small individuals, a relative large damaged surface with respect to the remaining shoot portrays a serious handicap against the feasibility of allocating a huge amount of energy for a successful repair. On the other hand, it is possible that the remaining biomass after damage could become literally embodied in the repaired module, being almost impossible to discriminate between a healthy and a damaged individual. The lack of vigour for repair in older cacti could be related to its previous expenditure in reproduction.

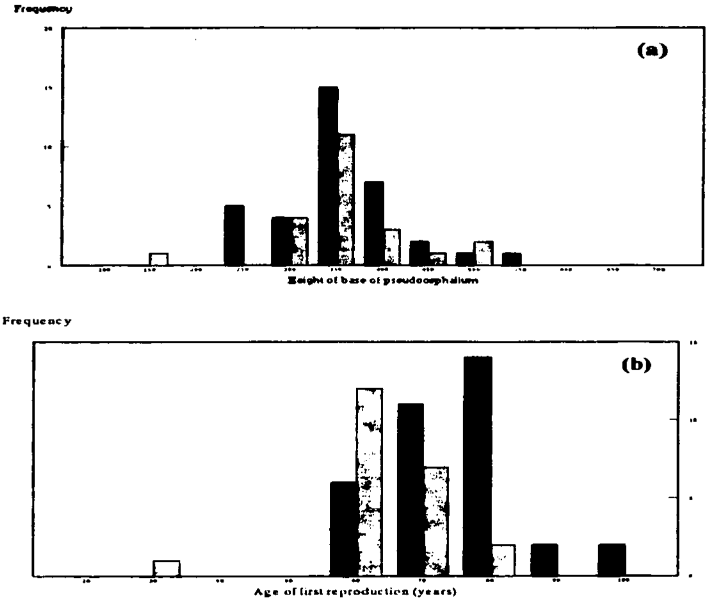

Figure 5. Frequency distribution of (a) height when first reproduction occurred (height of base of pseudocephalium), and (b) age of first reproduction in a population of *Cephalocereus columna-trajani*. Height and age of damaged individuals refers to height and age of reiterations above the damage scar (■ = undamaged ; ☐ = damaged.)

Most repaired individuals were reproductive at the time when they were damaged. Besides, increase in growth rate slows down when reproduction begins at a mean height of 3.33 m (Figs.2(b) and 5(a), and Table 1). There is a significant linear correlation between cactus height (age) and length of the pseudocephalium ($r^2=0.77$, $p<0.001$). The length of the pseudocephalium measures the time span an individual has been reproductive for. This applies because the pseudocephalium is built up by flower scars. So, according to the fitted GLM, there is a maximum probability of repair (0.57) when damaged individuals are around 4.30 m height (83-years-old); that is, they have been reproductive for about 13 ± 1.5 years. Individuals beginning or about to begin they reproductive life increase their probability of surviving after the loss of their shoot tip. Above this height, there is an inverse correlation between height and probability of successful repair, presumably due to a lack of resources for the replacement of the shoot leader.

Table 1. Height and age of first reproduction (height of base of pseudocephalium) and average number of flowers produced per individual in each of the two flowering periods considered for both damaged and undamaged individuals. Height of damaged individuals refers to height of reiterations above damage scar.

	Damaged	Undamaged	*p*
Mean height of first reproduction	329.95 ± 14.47 cm	333 4 ± 10.90 cm	NS
Mean age of first reproduction	59.35 ± 2.003 year	69.91 ± 1.52 year	<0.001
Average number of flowers per individual:			
1990 (135 days)	15.14 ± 2.57	13.06 ± 3.56	NS
1991 (126 days)	18.68 ± 4.58	16.24 ± 3.53	NS

A damaged reproductive cactus would have some possibility of resuming growth at an initial higher rate than non-damaged *C. columna-trajani* individuals, and eventually blooms again. Nevertheless, the type of damage discussed here would delay reproduction for a period of about 60 years (Fig.5(b), and Table 1). This could represent important ecological implications with consequences both at the individual and population levels.

A somewhat surprising result was that for the two studied years there were no significant differences in flower yields between both groups (Table 1). According to assumptions of life history theory there should be trade-offs between resources allocated to growth (repair) and reproduction (Waller 1988; Stearns 1992). Accordingly, a lower reproductive output in damaged individuals was expected.

On the other hand, pruning to promote flowering in cultivated plants is a common practice among horticulturists. Paige and Whitham (1987) found an overcompensation response on clipped plants of the herb *Ipomoeopsis aggregata* (Pursh) V. Grant which produced twice the number of flowers than control individuals. Yeaton, Karban and Wagner (1980) proposed branching in *Carnegiea gigantea* as an adaptation to increased reproductive potential. The mechanisms that promote overcompensation following damage and repair probably include complex and correlated physiological responses (Paige & Whitham 1981). The unveiling of these responses is outside the scope of this paper.

Conclusions

Injuries causing loss of the shoot tip in *Cephalocereus columna-trajani* promote reiteration, usually with a single shoot taking over apical dominance, although in some cases several branches succeed.

Reiterations of a given age after damage, grow faster than undamaged individuals of the same age after establishment during the first 3 m of height (about 54 and 65 years for damaged and undamaged individuals, respectively). After that, growth rate of severed cacti is lower than growth rate of undamaged ones.

A fitted GLM predicts that only individuals exceeding some critical height before damaged, are able to survive. The model also predicts that cacti over an upper threshold height will not survive as well. No significant differences in flower production were found between damaged and non-damaged individuals.

A reliable measure of damage effects could be the elapsed time before a damaged individual resumes reproductive activity after its fracture. Although we did not find differences in number of flowers produced between damaged and undamaged plants, there could be a potential decline in the quality of pollen, fruits and seeds produced by repaired individuals because of insufficient maternal resources (Paige & Whitham 1987, Schoen & Dubuc 1990). These aspects were not analysed in this study.

The possibility also remains that, given the decades elapsed between damage and reproduction in successfully repaired individuals, they could have compensated the diversion of resources to repair.

Finally, there is a call for an experimental approach to answer questions related to the ecological and evolutionary meaning of repair.

We especially thank E. Ezcurra for his continuous academic support. We also thank C. Montaña, J. Meave and F. Vite for ideas, comments and suggestions, and P. Valverde for his assistance in the field. This work was supported by CONACYT (P220CCOR892149) and SEP-DGICSA (91-01-775) grants.

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IV. VEGETATION-ENVIRONMENT RELATIONSHIPS BASED ON A LIFE-FORMS CLASSIFICATION IN A SEMIARID REGION OF TROPICAL MEXICO.

Los árboles todos están tan disformes de los nuestros
como el día de la noche, y así las frutas, y así las yerbas
y las piedras y todas las cosas.

(Cristóbal Colón)

Vegetation-environment relationships based on a life-forms classification in a semiarid land in Tropical Mexico[§].

Zavala-Hurtado, J.A*, P.L. Valverde*, A. Díaz-Solís+, F. Vite* and E. Portilla*.

* *Departamento de Biología, Universidad Autónoma Metropolitana-Iztapalapa. Ap. Postal 55-525, México 09340, D.F. México.*

\+ *Jardín Botánico y Vivero de Cactaceas "Dra. Helia Bravo-Hollis", Zapotitlán, Puebla, México.*

Abstract.-Taking the view that morphological characteristics represent behavioural strategies of plants to cope with environmental pressures, we defined 18 life-forms, using multivariate classification techniques in a tropical semiarid ecosystem in Central Mexico. A multiple discriminant analysis confirmed the existence of these groups. A null model of random membership of species to life-forms was significantly different from our classification. Vegetation-environment relationships were examined with Detrended Canonical Correspondence Analysis (DCCA). Ordination axes were interpreted mainly by altitude and soil moisture. Response curves of life-forms along these gradients were explored fitting generalised linear models (GLIM's). We believe that the life-forms approach for the study of vegetation-environment relationships is a valid alternative to the traditional species approach usually used in phytosociological research because: i) life-forms number showed to be an excellent species diversity predictor, ii) this approach enables considerable reduction in the bulk of data without losing ecological information, and iii) life-forms represent ecological strategies per se and they constitute an index of the number of different ways the desert's resources are utilised.

Keywords: Morphological attributes; morphological strategies; ordination; multiple discriminant analysis; response curves; xerophyllous scrub; desert plants

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Introduction

The occurrence of structural similarities among desert plants, independently of their phylogenetic relationships and geographical distribution, is well known . There is a preponderance of certain growth forms in desert floras that are rare or restricted in other types of ecosystems. Nevertheless, the causes of these presumed convergences are not quite well understood (Solbrig *et al.* 1977; Bowers & Lowe 1986; Cody 1989). A fundamental problem is to understand how the environment acts as a selection pressure on shape and function of plants. How do desert plants coexist interacting with each other and with the physical environment?

There have been several attempts to define morphological strategies of desert plants to face environmental pressures (Shreve 1942; Cody 1989; Leishman and Westoby 1992). These attempts vary widely in the number and nature of the morphological traits used and in the number of life-form groups produced.

In this paper we describe a multivariate classification of 107 perennial plant species based on morphological characteristics in a semiarid region of tropical Mexico. The basic assumption is that plant species would be naturally clumped in a few morphological categories each of which represents a convergence of strategies to cope with the desert environment. Our purpose was to describe vegetation-environment relationships based on these life-form categories.

Vegetation-environment relationships are usually studied along gradients. The concept of environmental gradients has been a cornerstone in the development of ecological theory (Okland 1992). Austin *et al.* (1984) recognise three basic environmental gradients types: (i) indirect gradients, those which have not a direct influence on plant growth (*e.g.* altitude); (ii) direct gradients, those which have direct influence on plant growth but are not resources potentially subject to competition (*e.g.* pH); and (iii) resource gradients, those environmental variables which are direct resources influencing plant growth (*e.g.* soil nutrients). Using certain assumptions, direct environmental gradients can be regarded as dimensions of the Hutchinsonian niche concept. Following this, species response curves along direct gradients would represent their realized niches in one dimension (Austin *et al.* 1990) and, hence, would be subject of measurements of niche amplitude and overlap.

Taxonomical nomenclature in this paper follows Davila *et al.* (1993).

Material and Methods

Our study site was located in the semiarid valley of Zapotitlán (18° 20' N, 97° 28' W), a local basin in the Pueblan-Oaxacan Region in the Mexican State of Puebla (Vite *et al.*, 1992). This is a unique region because of its biological richness. About 30% of its species are endemic and it is especially rich in columnar cacti (Villaseñor *et al.*, 1991).

The climate is dry with summer rains. Annual mean temperature is 18-22°C and precipitation is around 400 mm/yr. The soils are shallow, stony, and halomorphic (Byers 1967). Arid conditions are produced by the rain shadow of the Sierra Madre Oriental. The vegetation has been classified as xerophyllous scrub (Rzedowski 1978) or as thorn scrub cactus (Smith 1965), and is a well-preserved sample of this vegetation type, that supposedly covered the region some 10,000 years ago (Smith 1967; Zavala-Hurtado 1982). Zavala-Hurtado (1982) describes four vegetation units in the Zapotitlán Valley: thorn scrub (dominated by thorny shrubs and trees, mainly legumes, Agavaceae and low cacti), cardonal (thorn scrub with the columnar cactus *Cephalocereus columna-trajani*), izotal (thorn scrub with *Yucca periculosa* or *Beaucarnea gracilis*, and tetechera (thorn scrub with the columnar cactus *Neobuxbaumia* spp). There are permanent sites for research on vegetation dynamics in the tetechera, izotal and cardonal units.

The site for the study of the vegetation-environment relationships is a protected area adjacent to the 'Helia Bravo Hollis' Botanic Garden, located in the middle of the Zapotitlán Valley, 28.5 Km far from Tehuacan city. This area occupies an extension of 1 Km^2 and is occupied with the tetechera vegetation unit.

Five 10 x 10 m permanent plots have been established at each site where vegetation dynamics studies are carried out. In these 15 plots we recorded 107 perennial plants. In every 10 x 10 m plot we selected 10 individuals of each species that was present, and recorded the presence or absence of 30 morphological attributes (Table 1). These attributes have clear adaptive significance in terms of photosynthesis optimisation (presence of leaves, photosynthetic stems, etc.), and thermic regulation (morphology of stems, hairy leaves, etc.).

Table 1. Morphological attributes used for classification and multiple discriminant analysis

1 Spines present
2 Succulent stem
3 Exfoliant cortex
4 Perennial stem
5 Spiny stem (*)
6 Photosynthetic stem
7 Waxy stem
8 Woody stem
9 Erect stem
10 Flattened stem
11 Solitary stem
12 Globose stem
13 Candelabrous shape (*)
14 Ribs present
15 Tubercles present
16 Branched
17 Extensive branching
18 Plagiotrophic branching
19 Wide base
20 Leaves present (*)
21 Rosetophyllous leaves (*)
22 Simple leaves
23 Microphyllous leaves
24 Hairy leaves
25 Succulent leaves
26 Glabrous leaves
27 Waxy leaves
28 Perennial leaves
29 Caudex present
30 Epiphytic habit

(*) attributes not entered by multiple discriminant analysis

On the species-attributes matrix (107 x 30) we carried out an agglomerative cluster analysis using Ward's method (1963) with SPSS+Pc package (Norusis 1988). The number of groups in the species classification was chosen subjectively, based on a visual inspection of the dendrogram obtained (Fig. 1). Each of these groups was regarded as a life-form (LF).

Results of the classification were evaluated by a stepwise multiple discriminant analysis from SPSS+PC. This method was also applied to a null model of random assignment of species to the same number of groups detected with the cluster analysis. The objective of this comparison was to test the null hypothesis of random membership to life-forms.

The null model was constructed permuting at random the life-form constituency of each species (maintaining its own morphological attributes).

Analysis of vegetation-environment relationships was carried out in the protected area of the 'Helia Bravo Hollis' Botanic Garden where we set-out a grid of 100 x 100 m squares in an area of 1 km^2. In the Southeast corner of each of the 100 resulting squares we located a 5 x 5 m plot. As 22 edge sites were occupied by cultivars, we were left with 78 5 x 5 m plots. Within each plot we recorded presence/absence data for perennial plants, considering their life-forms membership according to the classification analysis. Also, we recorded 11 continuous and 12 categorical environmental variables for each plot (Table 2).

Incident radiation was estimated using the unpublished computer package INSOL (Sánchez-Colón 1987 unpubl.) considering geoposition of the plots and topographical interference.

Soil moisture was estimated as a percentage of the soil dry weight (Avery and Bascomb 1974). pH was measured in a water-saturation percentage preparation' (Jackson 1958) using a pH-meter Chandos type M43.

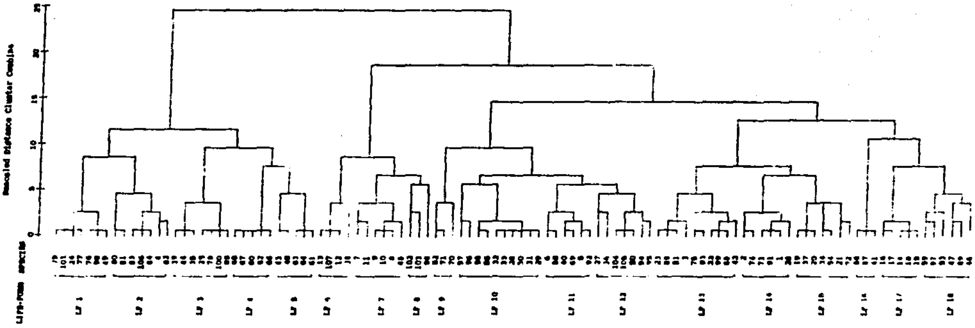

Fig. 1. Dendrogram showing agglomerative schedule of the classification of 107 species from the semiarid valley of Zapotitlán, Mexico into 18 life-forms (indicated by LF#) using Ward's method. See App. 1 for species names.

Table 2. Environmental variables used for ordination by DCCA

Continuous	Categorical
1 Altitude (m.a.s.l.)	1 North-eastern aspect
2 Winter incident radiation (MJ/m^2)	2 South-eastern aspect
3 Spring incident radiation (MJ/m^2)	3 South-western aspect
4 Summer incident radiation (MJ/m^2)	4 North-western aspect
5 Fall incident radiation (MJ/m^2)	5 Indeterminate aspect
6 Yearly incident radiation (MJ/m^2)	6 Concave topography
7 Soil moisture at 10 cm depth (%)	7 Plain topography
8 Soil moisture at 20 cm depth (%)	8 Convex topography
9 Soil pH at 10 cm depth	9 Stoniness (0-25%)
10 Soil pH at 20 cm depth	10 Stoniness (25-50%)
11 Slope (°)	11 Stoniness (50-75%)
	12 Stoniness (75-100%)

Altitude, aspect and slope were measured using conventional methods. Topography (concave, plain and convex) and stoniness were estimated visually

With these data , we built-up two matrices: life-forms x samples and environmental variables x samples. Both matrices were analysed simultaneously with a Detrended Canonical Correspondence Analysis (DCCA) using the CANOCO package (ter Braak 1987).

To explore the relationship between the defined life-forms and the environmental variables considered, we made a biplot of the life-forms ordination on the sample space. The vectors show direction and relative importance of the environmental variables significantly correlated to the sample ordination axes

Response of different life-forms to environmental gradients was estimated fitting Generalized Linear Models (GLIMs, Baker & Nelder 1978) to the defined life-forms. Independent variables (gradients) considered were the environmental variables that explained significantly the sample ordination axes. This approach is useful to predict the probability of a life-form being present (in a quadrat of 5 x 5 in this case) at a given point along the gradient. We assumed a binomial distribution for presence/absence data and used a logit transformation to link this distribution with the linear predictor (Austin *et al* 1984)

Results

Cluster analysis grouped the 107 species in 18 life-forms (Fig. 1). All morphological attributes listed in Table 1 were used for the definition of life-forms. The dendrogram in Fig. 1 shows the agglomeration schedule. Two large groups are evident: species without (life-forms 1 to 5) and with leaves (life-forms 6 to 18). All the former life-forms have succulent stems.

The first group of life-forms is constituted entirely by members of the Cactaceae family (31 species). LF1 (seven species) includes columnar (solitary stem) and branched (candelabrous shape) species ; LF2 includes seven species with branched flattened stems. Columnar non-branched cacti are clumped in LF3 (seven species), whereas five species of solitary globose cacti (tubercles present) belong to LF4, and LF5 is formed by gregarious globose plants (tubercles present). A single case of misclassification was found in this group: *Coryphanta palida* Brit. & Rose, a solitary globose cactus was located in LF3 bearing more morphological affinity with members of LF4.

The second outstanding group (leaves present), with 77 species, is subdivided in two further groups: species with succulent leaves (LF's 6 to 8) and with non-succulent leaves (LF's 9 to 18). Within the life-forms with succulent leaves LF6 (four species) is formed by arboreal rosette-like plants, LF7 (six species) with acaulescent rosette-like species, and LF8 (three species) with small rosette-like plants (some of them epiphytes). The group with non-succulent leaves is composed of a variety of trees and shrubs with and without spines. Life form 9 (three species) is built up of climbing species, LF10 (ten species) of short shrubs with unarmed simple leaves, LF11 (six species) of medium-sized shrubs with microphyllous leaves. LF12 (seven species) includes short shrubs with hairy leaves. Unarmed trees and shrubs, mainly with composed leaves were grouped in LF13 (ten species), whereas LF14 (seven species) includes thorny trees and shrubs. Medium sized unarmed shrubs with simple leaves are in LF15. Species with ephemeral leaves, succulent photosynthetic and unarmed stem were grouped in LF16 (three species). LF17 (five species) includes trees and shrubs with exfoliant cortex, and LF18 (six species) is made up of shrubs with simple waxy leaves.

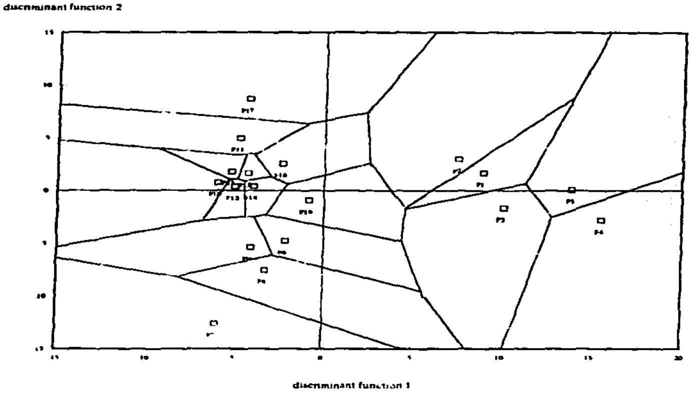

Fig. 2. Centroids and polygonal territories of 18 life-forms in discriminant space given by the first and second functions of multiple discriminant analysis.

Multiple Discriminant Analysis validated the 18 group classification (Fig. 2), with 99.07% of the species being correctly classified. The first two discriminant functions accounted for 55.25% of variance (39.99% and 15.26% for discriminant function 1 and discriminant function 2, respectively; $p < 0.001$). The structuring of groups shown in the dendrogram of Fig. 1 is clearly depicted in the discriminant space of Fig. 2, although according to the multiple discriminant analysis, segregation between the two main groups is not given by the presence or absence of leaves. The first discriminant function separates these two groups by the presence or absence of succulent stems, spines, ribs and tubercles.

The Multiple Discriminant Analysis of the null classification revealed that only 15.89% of the species were classified correctly. The life-forms classification differs significantly from this random assignation (Chi square = 1414.26; $p < 0.001$).

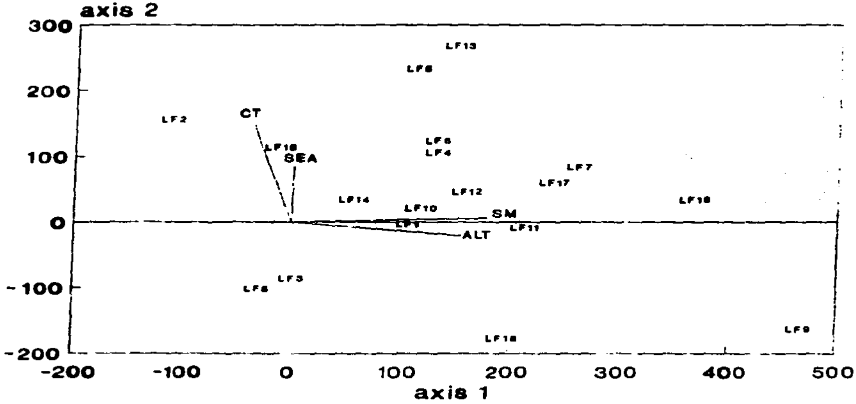

Fig. 3. Biplot of life-forms ordination in the sample space with respect to four environmental variables (lines). CT= concave topography; ALT= altitude; SEA= South-eastern aspect; SM= soil moisture at 20 cm depth.

Fig. 3 shows ordination of life-forms on axes 1 and 2 of DCCA. These axes accounted for 60.54% of variance (37.77 and 22.99%, respectively). The same Figure shows the biplot of life-forms ordination on the sample space and the direction and relative importance of the most influential environmental variates. Axis 1 was significantly explained by altitude ($r^2 = 0.55$; $p < 0.001$) and soil moisture at 20 cm depth ($r^2 = 0.44$; $p < 0.001$). Axis 2 was explained by concave topography ($r^2 = 0.80$; $p < 0.001$) and south-eastern aspect ($r^2 = 0.19$; $p < 0.001$). On the other hand, axis 1 showed a significant relationship with number of life-forms ($r^2 = 0.48$; $p < 0.001$). So, this axis conforms a life-forms diversity gradient (Fig. 4).

It can be seen that climbing deciduous plants (LF 9), unarmed shrubs with succulent stems and ephemeral leaves (LF 16), trees and shrubs with simple leafs and waxy stems (LF 18), acaulescent rosette-like succulents (LF 7) and trees with microphyllous leaves and exfoliant stems (LF 17) would be restricted to relatively high altitude and/or relatively high water soil content. On the other hand, unarmed trees with composite leaves (LF 13) and small globose gregarious spiny succulents (LF 5) would be found in lower and less humid sites. Succulents with spiny flattened photosynthetic stems (LF 2), unbranched columnar cacti (LF 3) and small rosette-like epiphytes (LF 8) occupy moderately xeric sites. The other eight life-forms are expected to be found in intermediate conditions or to have a wider range of tolerance.

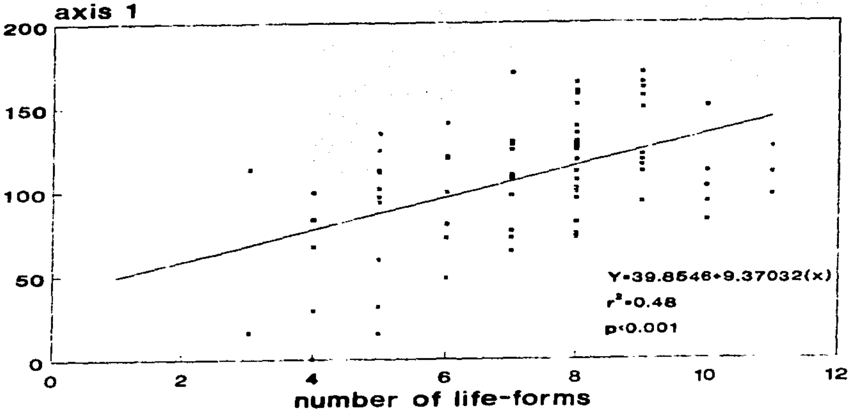

Fig. 4. Relationship between ordination axis 1 (exp. Var= 37.77%) and life-forms diversity.

Fig. 5 shows significant ($p< 0.05$) response curves of eight representative life-forms to (a) altitude and (b) soil moisture at 20 cm depth, the most important environmental variables in the determination of samples ordination. Climbing deciduous plants (LF 9) show low probabilities of occurrence along both gradients and are restricted to moderately high soil moisture contents and relatively high altitudes. Unarmed shrubs with succulent stems and ephemeral leaves (LF 16) are restricted to high altitudes. Rosette-like acaulescent succulents (LF 7), unarmed trees with composite leaves (LF 13) and small rosette-like plant (some of them epiphytes, LF 8) raise their probability of occurrence as both altitude and soil moisture increase, but

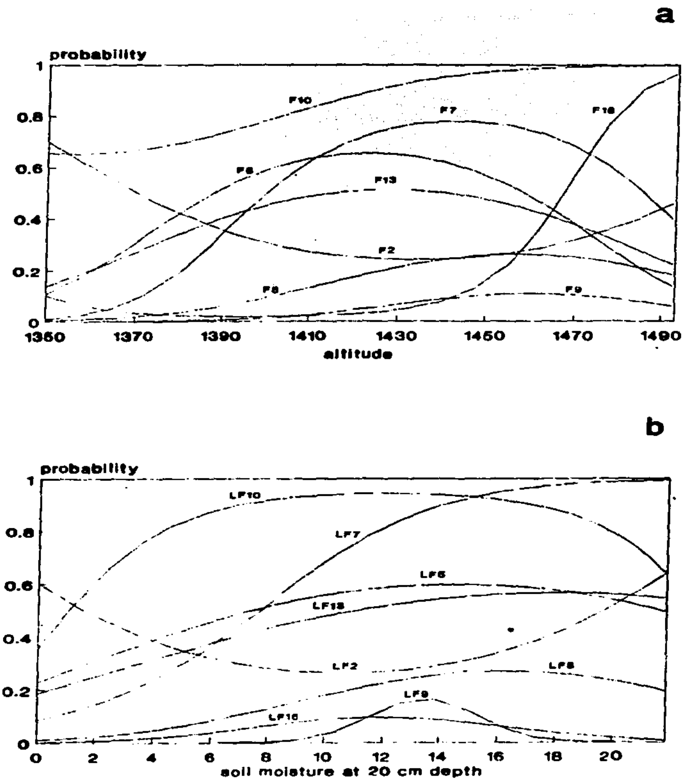

Fig. 5. Significant ($p<0.05$) response curves of eight representative life-forms to (a) altitude and (b) soil moisture at 20 cm depth. Response curves were fitted to GLIM's assuming a binomial distribution.

become rarer in the upper part of the altitude gradient. Succulents with spiny flat photosynthetic stems (LF 2) show bimodal response curves for both gradients with relatively high probabilities of occurrence at both ends of the soil moisture gradient and at low altitudes. Finally, short deciduous unarmed shrubs (LF 10) and small globose gregarious spiny succulents (LF 5) show wide bell-shaped response curves with highest probabilities of occurrence in the middle of both gradients.

Discussion

The 18 defined life-forms represent different strategies to cope with environmental pressures characteristics of this arid region in central Mexico Although the considered attributes represent only structural traits, they characterise the plant's function (Bowers & Lowe 1986). Grouping of cacti in life forms 1 to 5, on the basis of morphological attributes (succulent stem, absence of leaves and presence of spines) has important functional implications on water storage and photosynthetic pathway. For the rest of life forms (LF6-18), attributes as succulent, rosette-like, microphyllous, waxy and deciduous leaves have influence in both sun light interception and storage and use of water (Fitter & Hay 1983). Cody (1989), reviewing several authors, mentions ecological implications on light interception of stem geometry in cacti, and leaf shape in shrubs.

Our classification of 18 life-forms using multivariate techniques resembles, in some way, Shreve's (1942) life-forms described for the Sonoran Desert. In that study life-forms were classified subjectively using morphological and phenological characteristics, although the categories used were not completely equivalent with those in the present study. On the other hand, Leishman and Westoby (1992), using multivariate techniques, classified 300 semiarid Australian species in only five functional life-forms. Such differences may be in part due to the fact of the absence of succulents and rosette-like forms in the region in which they worked. Other life-forms systems (*e.g.*, Raunkier 1934) are not adequate to express adaptations to environmental conditions of arid ecosystems (Montaña 1990).

Life-forms territories determined on discriminant space (Fig. 2) allow the classification, on their proper life-form, of species of the Zapotitlán region not considered in this study. This could be achieved with the simple substitution of their attribute values (1/0) on discriminant functions 1 and 2. Then, the scores of the species for these two functions could be plotted on the territories map and the assignation would be complete. The first two discriminant axes explain 55.25% of inter-group variability. Although this figure is low for practical purposes, would raise to 69.30%, if the third discriminant function is considered as well. Also, it is expected that the inclusion of a greater number of species, and the use of dynamic traits (*e.g.*, phenology) would improve the classification.

Comparison of our life-forms classification with the random grouping (null model), supports the evidence that the former exhibits a non-random pattern. It is proposed that such a pattern reflects similarities and differences on morphological, and hence ecological, attributes of species with each other.

One major drawback of direct gradient analysis is the subjectivity involved in defining important environmental gradients. An indirect approach to the ordination of community data is likely to overcome this problem, because the extracted gradients are defined by the vegetation itself and are expected to reflect the effect of important environmental factors acting on the vegetation (Gauch 1982). A successful environmental interpretation of the major axes of vegetational variation could provide a bridge to return to the direct gradient analysis approach but with less subjective defined gradients. Canonical Correlation Analysis produced an interpretable ordination of the community data in environmental terms.

Although altitude is not a resource or direct gradient (*sensu* Austin 1980), it is associated with the water regime of a site (Ezcurra *et al.* 1987). The positive significant correlation between altitude and the first ordination axis, and between the later and life-forms diversity could be explained by an increment in the complexity of habitat structure (Noy-Meir 1985). So, higher altitudes would be associated with topographic heterogeneity (land forms) and microtopography (soil texture, rockiness, etc.). On the other hand, soil moisture is a direct gradient that represents available water for plants. So, it seems that differences in available soil moisture would be the main cause of life-forms distribution in our study site. This agrees with the widespread idea of water as the main controlling factor in arid ecosystems (Noy-Meir 1973).

Nevertheless, the environmental interpretation of the derived axes cannot be a completely satisfactory one because of intrinsic limitations of environmental ordinations caused by the open ended nature of environmental data (Greig-Smith 1983). Although CANOCO is a very popular and reliable method, it assumes Gaussian response curves (ter Braak 1985, 1986; ter Braak and Looman 1986; Austin *et al.* 1994) and its robustness to violations to this assumption remains to be proved (Minchin 1987; Austin *et al.* 1994).

The present study has no intention of contributing to the debate about shape of response curves (Gauch and Whittaker 1972; Austin 1985, 1987; Austin *et al.* 1984; Austin *et al.* 1994), the interpretation of the ordination axes did allow us to get an insight into the performance of life-forms along explicit environmental gradients under a direct gradient analysis approach.

The simple quadratic models used revealed significant bell-shaped (mainly platykurtic, and bimodal in some cases) responses of life-forms to the environmental variates examined. Most of life-forms response curves were wide, perhaps because they encompass realised niches of their constituent species. In this sense, life-form response curves would be a guild level analogous to the qualitative environmental realised niche (QERN) of species (Austin *et al.* 1994; Austin *et al.* 1990). Nevertheless, life-forms response curves should not be regarded simply as cumulative species response curves because these categories may behave in a quite different way to the same environmental gradient (Okland 1992).

The life-forms approach for the study of vegetation-environment relationships is considered a valid alternative to the traditional species approach usually used in phytosociological research: firstly because, life-forms number showed to be an excellent predictor of species' richness ($r^2 = 0.65$; $p < 0.001$). Secondly, the life-forms approach implies a considerable reduction in the bulk of data (18 LF << 107 spp) without losing ecological information. Thirdly, life-forms represent ecological strategies *per se* and, as Cody (1989) states, they constitute an index of the number of different ways that the desert's resources are utilized.

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Appendix 1. Plant species used for the definition of life-forms in the semiarid valley of Zapotitlán, Mexico.

	Species	LF		Species	LF
79	Neobuxbaumia tetetzo (Web. ex K. Sch.) Backeb	1	6	Aeschinomene compacta Rose	11
101	Stenocereus stellatus (Pffei.) Riccob.	1	58	Lippia graveolens Kunth	11
24	Cephalocereus chrisacanthus (Weber) Britt & Rose	1	40	Echinopterix eglandulosa Small.	11
77	Neobuxbaumia macrocephala (Weber) Dawson	1	69	Mascagnia seleriana Loes.	11
76	Myrtillocactus geometrizans (C. Martius) Console	1	5	Actinocheita filicina (Sesse &Moc.) Barkley	11
90	Polaskia chichipe (Gosselin) Backeb.	1	92	Asteraceae 7	11
49	Polaskia chende (Gosselin) Gibson & Horak	1	27	Cnidoscolus tehuacanensis Breckon	12
80	Opuntia decumbens Salm-Dyk	2	36	Croton ciliato-glandulosus Ortega	12
81	Opuntia depressa Rose	2	104	Turnera difussa Willd ex Schult	12
83	Opuntia pumila Rose	2	105	Viguiera sp.	12
106	Peniocereus viperina (Weber) Buxb.	2	50	Hibiscus sp	12
84	Opuntia rosea De Candolle	2	94	Ruellia sp.	12
4	Acantothamnus aphyllus (Schl.) Stanley	2	95	Salvia sp.	12
82	Opuntia pilifera Weber	2	23	Celtus pallida Torr.	13
39	Echinocactus platyacanthus Link & Otto	3	88	Phitecellobium acatlense Benth.	13
44	Ferocactus recurvus (Miller) Lindsay	3	51	Ipomoea arborescens Sweet	13
35	Corypantha palida Britt & Rose	3	3	Acacia subangulata Rose	13
25	Cephalocereus columna-trajani (K. ex Pfeiff) Schumann	3	75	Morkillia mexicana Rose & Painter	13
78	Neobuxbaumia mezcalaensis (Bravo) Backeb.	3	93	Pseudosmodingium multifolium Rose	13
100	Pachycereus marginatus (DC.) Britt. & Rose	3	22	Ceiba parvifolia Rose	13
85	Pachycereus hollianus (Weber) Buxb	3	99	Senna pringlei Rose	13
65	Mammillaria compressa De Candolle	4	68	Manihot sp	13
67	Mammullaria pectinifera (Ruempler) Weber	4	42	Eysendhardtia polystachia Sarg.	14
60	Mammillaria carnea Zucc. ex Pfeiffer	4	2	Acacia sp.	14
62	Mammillaria mystax martius	4	74	Mimosa luisana Brandg	14
66	Mammullaria elegans DC.	4	73	Mimosa lacerata Rose	14
43	Ferocactus flavovirens (Scheidw.) Britt & Rose	5	91	Prosopis laevigata (Humb & Bonpl. ex Willd.) Johns	14
45	Ferocactus robustus (Pfeiffer) Britt. & Rose	5	1	Acacia constricta Bendth.	14
63	Mammilaria sphacelata Martius	5	26	Cercidium praecox Harms	14
64	Mammilaria viperina Purpus	5	19	Caesalpinia melanadenia Standl.	15
61	Mammilaria haageana Pfeiffer	5	37	Dalea sp	15
13	Brahea dulcis Cooper	6	20	Calliandropsis sp	15
107	Yucca periculosa Baker	6	34	Cordia cylindrostachya Roem. & Schult	15
12	Beucarnea gracilis Lemm	6	54	Karwinskia humboldtiana Zucc.	15
38	Echeveria sp	6	21	Castela tortuosa Liebm	15
7	Agave karwinskii Zucc	7	72	Megastigma galeottii Baill	15
11	Agave potatorum Zucc	7	86	Pedilanthus aphyllus Boiss	16
9	Agave macroacantha Zucc	7	87	Pedilanthus sp.	16
10	Agave marmorata Roezl	7	41	Euphorbia antisiphyllitica Zucc.	16
8	Agave kerchovei Lemm	7	16	Bursera fagaroides Engl	17
48	Hechtia podantha Mez	7	17	Bursera hindsiana Engl	17
102	Tillandsia pueblensis Laman Smith	8	14	Bursera sp	17
103	Tillandsia recurvata L.	8	18	Bursera sp	17
98	Selaginella sp	8	15	Bursera arida Standl	17
52	Ipomoea conzatii Greenman	9	59	Lycium sp.	18
71	Metastelma sp.	9	97	Schaefferia stenophylla Standl	18
70	Maximowitzia sp	9	53	Jatropha spathulata Muell. Arg.	18
57	Lappia gratissima (Gill.) Troncoso	10	47	Gymnosperma glutinosa Spreng.	18
96	Sanvitalia fruticosa Hems.	10	89	Plumeria rubra L	18
55	Lantana camara L.	10	46	Fouquieria formosa Kunt	18
56	Lantana sp	10			
32	Asteraceae 1	10			
33	Asteraceae 2	10			
28	Asteraceae 3	10			
30	Asteraceae 4	10			
31	Asteraceae 5	10			
29	Asteraceae 6	10			

V. DISCUSION.

Discusión

Es ya un lugar común en la literatura biológica el decir que las variaciones fenotípicas entre los organismos se reflejan en diferencias en su desempeño ecológico (Wainwright 1994). Así, las relaciones de una planta con, digamos, raíces profundas y hojas pequeñas con su medio ambiente van a ser muy diferentes de las de una planta con raíces someras y carente de hojas. Sin embargo, la elucidación de las relaciones forma-función no siempre es directa y ha generado el desarrollo de una disciplina especializada: la ecomorfología o morfología funcional.

En *Cephalocereus columna-trajani* encontramos una clara relación entre su morfología y su eficiencia en la captación de radiación solar directa que, a su vez, está íntimamente relacionada con la regulación de su régimen térmico, así como con su tasa de crecimiento y producción de flores.

El trabajo presentado en el Capítulo II aborda directamente la relación forma-función analizando la respuesta ecológica de *Cephalocereus columna-trajani* a la radiación solar, un gradiente directo de recurso (*sensu* Austin *et al.* 1984) En este trabajo se resaltan las ventajas funcionales de la morfología dominante en poblaciones de esta especie sobre las variantes estudiadas, inclusive sobre una forma erecta sin pseudocefalio.

Con respecto a la inclinación del tallo observada en este cactus, es relevante mencionar que se trata de un suceso, si bien observado desde hace mucho tiempo (Greenwood 1964), poco probable de acuerdo a expectativas sobre restricciones mecánicas en el sostén del tallo en cactus columnares gigantes (Geller & Nobel 1987, Nobel 1988). En relación a esto, es probable que la altura alcanzada por individuos de esta especie (raramente más de 10 m) sea un conflicto entre una inclinación del tallo con claros beneficios funcionales y un maximización del crecimiento en altura que también tendría importantes ventajas adaptativas (King 1990). Una evidencia circunstancial de esto es la presencia en el valle de Zapotitlán de *Neobuxbaumia mezcalaensis*, cactácea columnar gigante no ramificada que no presenta pseudocefalio ni inclinación del tallo y alcanza alturas incluso mayores a 15 m (observación personal). De hecho, sería muy interesante analizar los patrones de intercepción de radiación solar por individuos de esta especie comparándolos con los de *C. columna-trajani*.

Con respecto a este punto, cabe mencionar que es muy probable que la ventaja funcional que confiere la inclinación del tallo sea una consecuencia secundaria de la ubicación del pseudocefalio que conduce a un crecimiento diferencial que es mayor en el lado (SSE) contrario al que posee la superficie no fotosintética del pseudocefalio ocasionando la inclinación de la columna.

La inclinación del tallo, además de las ventajas mencionadas, puede traer como consecuencia una relativamente alta vulnerabilidad de los individuos ante disturbios como fuertes vientos o tormentas (o incluso el simple crecimiento más allá de lo permitido por restricciones mecánicas de la misma) que pueden ocasionar la fractura de la columna. Esta fractura involucra la pérdida del meristemo apical y, eventualmente, un proceso de reparación que puede modificar las características morfo-funcionales descritas anteriormente, dependiendo si se regenera un solo tallo o varios como ocurre frecuentemente (observación personal). Así, individuos reparados que no producen ramificaciones presentan una morfología similar (en cuanto a la inclinación del tallo y la ubicación del pseudocefalio) a la de cactus no dañados, mientras que en aquellos que generan varias ramas se modifica el régimen de radiación debido al efecto de sombreado que se produce entre las ramas de un individuo.

En el trabajo presentado en el Capítulo III (Zavala-Hurtado & Díaz-Solís 1995) se muestra que existen diferencias significativas en la tasa de crecimiento y la edad de la primera reproducción entre individuos no dañados e individuos reparados después de sufrir un daño severo que involucró la pérdida del meristemo apical. Sin embargo, no se observaron diferencias en cuanto al número de flores producidas por individuo entre las dos categorías mencionadas. Como se menciona en el artículo, este punto requiere de un análisis más profundo pues podrían existir diferencias en el número de frutos y semillas producidos así como en la calidad de estas últimas y de las plántulas que eventualmente pudieran generar.

Un resultado relevante es que, en promedio, un individuo de *Cephalocereus columna-trajani* que sufra el tipo de daño aquí descrito deberá esperar cerca de 60 años antes de continuar con su vida reproductiva. En ese tiempo el escenario medioambiental puede llegar a ser muy diferente (ya sea en su beneficio o perjuicio) al que enfrentaba el organismo antes de sufrir el daño.

Aunque en este trabajo no se profundiza en el análisis de las ventajas y desventajas de la reparación (de lo cual, por cierto, se sabe muy poco). El modelo que describe la probabilidad de una reparación exitosa después de un daño, nos permite hacer algunas inferencias al respecto. Para esto, debemos tomar en cuenta que un daño siempre es perjudicial para el organismo y que la reparación necesariamente implica un costo. Entonces una pregunta relevante es ¿cuándo vale la pena gastar en un proceso de reparación?

Kirkwood (1981) de manera general, argumenta que si **D** es el decremento promedio en la adecuación relativa resultante de un tipo particular de daño no reparado y **R** denota al costo de repararlo, medido en términos del decremento en la adecuación que resulta de canalizar recursos al proceso de reparación, éste nunca debe ocurrir a menos que **D** > **R**. Así, en el caso de C. *columna-trajani*, para un individuo joven de unos 3.30 m (más o menos 70 años de edad) que está por comenzar o que recién ha comenzado a reproducirse, **D** sería relativamente alta pues la no reparación del daño implicaría no reproducirse y **R** sería relativamente baja suponiendo un mayor vigor en individuos jóvenes que en los de mucho mayor edad. Por su parte, para un individuo de 8 m de altura que comenzó su reproducción hace más de 50 años, **D** sería relativamente baja y **R** alta considerando una disminución en el vigor relacionada con la edad. Bajo estas circunstancias, el proceso de reparación se favorecería en individuos jóvenes que inician o están por iniciar su vida reproductiva y sería menos importante en individuos de más de 120 años (cerca de 7.5 m de altura). Además, la inclinación del tallo (ver Capítulo II) y el muy somero sistema radical de los individuos de esta especie pueden hacer que los individuos muy altos se caigan completamente debido a vientos y lluvias fuertes, con lo que no habría posibilidad de reparación.

La ausencia de individuos pequeños reparados exitosamente es menos clara y se puede deber a que el tallo original se vea literalmente embebido en la masa de la reiteración.

El entorno comunitario de Cephalocereus columna-trajani visto en términos de la morfología funcional.

El estudio de estrategias morfológicas a nivel comunitario es abordado en el Capítulo IV (Zavala-Hurtado *et al.* 1996) mediante la clasificación de 107 especies de plantas en 18 grupos definidos por características morfológicas, i.e. formas de vida, gremios o tipos funcionales de plantas. La suposición fundamental es que existiría un número limitado (menor al número de especies presentes) de estrategias morfológicas (funcionales) para enfrentar las presiones selectivas del medio ambiente árido (Cody 1989).

La clasificación obtenida, si bien es limitada pues no considera, entre otras cosas, aspectos metabólicos y solo parcialmente características fenológicas de las especies analizadas, describe tipos morfológicos con una clara implicación funcional. Así, por ejemplo, *Cephalocereus columna-trajani* se diferencia claramente en términos de patrones de captación de luz, crecimiento y reproducción del resto de las formas de vida incluyendo a otras cactáceas columnares que fueron clasificadas en grupos diferentes dentro del cúmulo que aglomeró a las cactáceas.

Por otra parte, la clasificación obtenida resultó significativamente diferente de la obtenida mediante un modelo nulo de asignación aleatoria lo que apoya la idea de convergencias de tipos morfológicos en la zona estudiada aunque la validez funcional de estos tipos esté por probarse. Además, se mostró que la reducción de la dimensionalidad del problema (18<<107) no conlleva una pérdida significativa de información sobre la diversidad de especies.

Finalmente, los intentos de definir tipos funcionales de plantas (fundamentalmente con una base morfológica) si bien tienen una larga historia en la ecología de comunidades, actualmente se consideran de fundamental importancia (aparte de su relevancia intrínseca en los estudios de comunidades) para la modelización de las respuestas de la vegetación a nivel global ante los relativamente acelerados cambios climáticos que se esperan en las próximas décadas (proyecto sobre Cambio Global y Ecosistemas Terrestres del Programa Internacional de la Geosfera y la Biosfera; Woodward y Cramer 1996; Box 1996). Se pretende desarrollar un modelo dinámico global de vegetación (DGVM, por sus siglas en inglés) basado en tipos funcionales de plantas que son especies o grupos de especies con respuestas similares a un conjunto de condiciones medioambientales y en base a cuyas características se pueda interpretar y predecir la conducta del ecosistema (Shao, Shugart y Hayden 1996). Así, un planteamiento morfométrico como el aquí presentado (complementado con otras características de historia de vida) puede contribuir al desarrollo de un modelo como el que se pretende.

Conclusiones

1. *Cephalocereus columna-trajani* presenta características morfológicas peculiares de las que se puede inferir una clara relación con su desempeño ecológico y por tanto es un sujeto idóneo para abordar estudios de diferentes aspectos de morfología funcional, tanto a nivel de individuos, poblaciones y de las comunidades en que habita.

2. La morfología funcional pretende integrar características morfológicas de los organismos con su desempeño en un contexto ecológico. Sin embargo, estamos muy lejos de poder caracterizar el ajuste entre la morfología y la ecología y tampoco sabemos cómo determinar la bondad de ajuste (Ricklefs y Miles 1994).

3. En años recientes, los estudios sobre morfología funcional de plantas han proliferado en la literatura científica. Es promisorio que estos estudios ayuden a resolver problemas biológicos fundamentales mediante el análisis de la conducta de las plantas y sus consecuencias ecológicas y evolutivas.

Sin embargo, todavía es necesaria una revisión integradora sobre este apasionante campo de la ecología.

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Zavala-Hurtado, J.A.; P.L. Valverde; A. Díaz-Solís; F. Vite & E. Portilla. 1996. Vegetation-environment relationships based on a life-forms classification in a semiarid region of Tropical Mexico. *Revista de Biología Tropical* 44:561-570.g

APENDICE.

(Documentos probatorios del estatus de los artículos presentados)

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Publications Office

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Ithaca, NY 14850-5616
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4 October 1996

Dr. José Alejandro Zavala-Hurtado
Departamento de Biología
Universidad Autónoma
Mdtropolitana-Iztapalapa
Ap. Postal 55-535
México 09340 D.F.
MEXICO

Dear Dr. Zavala-Hurtado:

I am pleased to acknowledge receipt of your manuscript entitled: "Stem tiling and pseudocephalium orientation in Cephalocereus columna-trajani (cactaceae): a functional..."

The manuscript was received on 12 September 1996, and was assigned the following number: 96-0636. It has been forwarded to a member of the Board of Editors. If the topic and treatment seem appropriate for the journal, your manuscript will be sent out for peer review by others with expertise in the subject. After the reviewers' evaluations are received, you will be notified of the Editor's decision. This decision is usually reached in less than four months, but delays in obtaining reviews may prolong that period.

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Sincerely,

J. David Baldwin
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University of Colorado at Boulder

Environmental, Population, and Organismic Biology

N122 Ramaley
Campus Box 334
Boulder, Colorado 80309-0334
(303) 492-8981
FAX: (303) 492-8699

Professor Russell K. Monson
(303) 492-6319
monsonr@colorado.edu

November 26, 1996

Dr. J.A. Zavala-Hurtado
Departamento de Biologia
Universidad Autonoma Metropolitana-Iztapalapa
Ap. Postal 55-535
Mexico 09340, D.F.
Mexico

Dear Dr. Zavala-Hurtado,

I have now received two reviews of your ms. "Stem tilting and pseudocephalium orientation in *Cephalocereus columna-trajani* (Cactaceae): A functional interpretation", #96-636. which was recently submitted to *Ecology*. Both reviewers provided positive reviews, though it is apparent that some revision is necessary. Please revise the ms. and send it back to me within four weeks of receiving this letter. Most of the requested revisions deal with the manner in which data is presented or interpreted. Please pay careful attention to address each item covered in the reviews. Please include a cover letter with your revision that explains exactly how you have dealt with each of the items listed by the reviewers. I will then make a decision as to whether the ms. has been successfully revised. Thank you for sending such nice work to *Ecology*.

Sincerely yours,

Russell K. Monson
Professor

Journal of Arid Environments (1995) 31: 21–31

Repair, growth, age and reproduction in the giant columnar cactus *Cephalocereus columna-trajani* (Karwinski ex. Pfeiffer) Schumann (Cactaceae)

José Alejandro Zavala-Hurtado & Amaury Díaz-Solís

Departamento de Biología, Universidad Autónoma
Metropolitana-Iztapalapa, Ap. Postal 55-525, México 09340, D.F.
México

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Loss of shoot-tip because of severe, but non-lethal, injury is a common event in the life-cycle of giant columnar cacti. Repair (reiteration) could adversely affect further growth and reproduction because of a reassignment of resources. We studied a population of *Cephalocereus columna-trajani* in Central Mexico, comparing growth rates, age of first reproduction and number of flowers produced per individual in repaired and undamaged cacti. A fitted, generalized linear model, using a binomial error distribution and a logit link function, described the probability of survivorship after the cactus shoot is broken. According to this model, only individuals exceeding a certain critical height before damaged are able to survive, and also only reproductive individuals not surpassing an upper threshold height (or age) would survive. We did not find significant differences in flower production between injured and non-injured individuals. The cost of repair would imply a delay of *ca.* 60 years before the damaged cacti could resume reproduction.

Keywords: *Cephalocereus columna-trajani*; giant columnar cacti; repair; growth; age; reproduction

Introduction

It is almost inevitable for organisms to suffer some sort of physical damage during their life-span due to their interactions with the environment. In a wide sense, the role of regeneration, or biological repair, is to maintain the life of the organism and to postpone death due to physical damage. Repair, the power to replace lost or damaged cells, is a fundamental biological process seen in almost all organisms (Elder, 1979). Such process is expected to have a cost for the organisms in terms of long-term survival and reproduction, but it is also expected to yield a benefit, namely, the immediate survival after damage (Harris, 1989).

There is an important link between repair and the life-history of an organism. The main focus of this link is the distribution of resources to different metabolic activities, not only to growth and reproduction but also to restoration. Resource assignment to somatic repair in iteroparous species is of particular interest, as iteroparous life-span

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A QUIEN INTERESE

El manuscrito Vegetation-environment relationships based on a life-forms classification in a semiarid region of tropical Mexico" por J.A. Zavala, P.L. Valverde, A. Díaz, F. Vite & E. Portilla ha sido aceptado para publicación en la Revista de Biología Tropical. Probablemente será posible incluirlo en el volumen 43*. Si quedan detalles pendientes antes de poder enviarlo a la imprenta, se le informará pronto al autor principal. De otra manera, nuestra próxima comunicación corresponderá a las pruebas de imprenta, junto con las cuales se enviará un formulario por si son necesarias separatas adicionales.

Muy atentamente,

Julián Monge-Nájera
Editor
Revista de Biología Tropical

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Telefax: (506) 207 5550 **E-mail: julianm@cariari.ucr.ac.cr**

Dear authors

Because of reasons beyond our control, several papers scheduled for volume 43 will be included in vol. 44-2 (1996). We regret any inconveniences that this might cause

The Editor

Estimados autores

Rev. Biol. Trop., 44(2): 561-570, 1996

Vegetation-environment relationships based on a life-forms classification in a semiarid region of Tropical Mexico

Zavala-Hurtado, J.A.[1], P.L. Valverde[1], A. Díaz-Solís[2], F. Vite[1] and E. Portilla[1].

[1] Departamento de Biología, Universidad Autónoma Metropolitana- Iztapalapa. Ap. Postal 55-525, México 09340, D.F. México, e-mail jazh@xanum.uam.mx

[2] Jardín Botánico y Vivero de Cactaceas "Dra. Helia Bravo-Hollis", Zapotitlán, Puebla, México.

(Rec. 15-V-1995. Rev. 23-VI-1995. Acep. 28-VI-1995)

Abstract: Taking the view that morphological characteristics represent behavioral strategies of plants to cope with environmental pressures, we defined 18 life-forms, using multivariate classification techniques in a tropical semiarid ecosystem in Central Mexico. A multiple discriminant analysis confirmed the existence of these groups. A null model of random membership of species to life-forms was significantly different from our classification. Vegetation-environment relationships were examined with Detrended Canonical Correspondence Analysis (DCCA). Ordination axes were interpreted mainly by altitude and soil moisture. Response curves of life-forms along these gradients were explored fitting generalized linear models (GLIM's). We believe that the life-forms approach for the study of vegetation-environment relationships is a valid alternative to the traditional species approach usually used in phytosociological research because: i) life-forms number was found to be an excellent species diversity predictor, ii) this approach enables considerable reduction in the bulk of data without losing ecological information, and iii) life-forms represent ecological strategies per se and, they constitute an index of the number of different ways the desert's resources are utilized.

Key words: Morphological attributes; morphological strategies; ordination; multiple discriminant analysis; response curves; xerophyllous scrub; desert plants.

The occurrence of structural similarities among desert plants, independent of their phylogenetic relationships and geographical distribution, is well known . There is a preponderance of certain growth forms in desert floras that are rare or restricted in other types of ecosystems. Nevertheless, the causes of these presumed convergences are not well understood (Solbrig *et al.* 1977, Bowers and Lowe 1986, Cody 1989). A fundamental problem is to understand how the environment acts as a selection pressure on the shape and function of plants. How do desert plants coexist interacting with each other and with the physical environment?

There have been several attempts to define morphological strategies of desert plants in relation to environmental pressures (Shreve 1942, Cody 1989, Leishman and Westoby 1992). These attempts vary widely in the number and nature of the morphological traits used and in the number of life-form groups produced.

In this paper we describe a multivariate classification of 107 perennial plant species based on morphological characteristics in a semiarid region of tropical Mexico. The basic assumption is that plant species would be naturally clumped in a few morphological categories each of which represents a convergence of strategies to cope with the desert environment. Our aim was to describe vegetation-environment relationships based on these life-form categories.

Vegetation-environment relationships are usually studied along gradients. The concept of environmental gradients has been a cornerstone in the development of ecological theory (Okland 1992). Austin *et al.* (1984) recognize three basic environmental gradients types: (i)

Del interior del cielo vienen
las bellas flores, los bellos cantos.
Los afea nuestro anhelo,
nuestra inventiva los echa a perder,
a no ser los del principe chichimeca Tecayehuatzin.

La amistad es lluvia de flores preciosas.
Blancas vedijas de plumas de garza,
se entrelazan con preciosas flores rojas.
En las ramas de los árboles,
bajo ellas andan y liban
los señores y los nobles.

Vuestro hermoso canto :
un dorado pájaro cascabel,
lo eleváis muy hermoso.
Estáis en un cercado de flores.
Sobre las ramas floridas cantáis.
¿Eres tú acaso, un ave preciosa del Dador de la vida ?
¿Acaso tú al dios has hablado ?
Tan pronto como visteis la aurora,
os habéis puesto a cantar.

Esfuércese, quiera mi corazón,
las flores del escudo,
las flores del Dador de la vida.
¿Qué podrá hacer mi corazón ?
En vano hemos llegado,
hemos brotado en la tierra.
¿Sólo asi he de irme
como las flores que perecieron ?
¿Nada quedará de mi nombre ?
¿Nada de mi fama aqui en la tierra ?
¡Al menos flores, al menos cantos !
¿Qué podrá hacer mi corazón ?
En vano hemos llegado,
hemos brotado en la tierra.

Gocemos, oh amigos,
haya abrazos aqui.
Ahora andamos sobre la tierra florida.
Nadie hará terminar aqui
las flores y los cantos,
ellos perduran en la casa del Dador de la vida

Aqui en la tierra es la región del momento fugaz.
¿También es asi en el lugar
donde de algún modo se vive ?
¿Allá se alegra uno ?
¿Hay allá amistad ?
¿O sólo aqui en la tierra
hemos venido a conocer nuestros rostros ?

(Ayocuan Cuetzpaltzin)

luego vemos eso...

(Enrique Portilla)