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MORFOLOGIA FUNCIONAL DE LA ROSETOFILIA:
¿PLANTAS QUE COSECHAN LA NEBLINA?

T E S I S

QUE PARA OBTENER EL GRADO DE:

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P R E S E N T A :

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Mayahuel, "La que está Rodeada de Manos",
Divinidad mexica del Maguey y la fertilidad exuberante.
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Resumen

Gracias a su morfología infundibuliforme y su epidermis hidrófoba, las rosetófilas de los desiertos norteamericanos son capaces de captar y conducir a sus raíces el agua de la lluvia con una gran eficiencia. En esta tesis se propone que dicha característica les permite también hacer uso del agua procedente de la neblina. De esta hipótesis se desprenden tres predicciones que abordan aspectos de distribución, morfología funcional y tendencias evolutivas. Estas predicciones son:

1. *En las zonas donde la neblina está disponible, deben presentarse grandes abundancias y diversidad de rosetófilas.* Se describió la vegetación en cuatro gradientes altitudinales en diferentes desiertos mexicanos: El Valle de Tehuacán, la Barranca de Metztitlán, el Desierto Queretano y la Península de Baja California. En Tehuacán se midió además la disponibilidad de neblina durante un año. Se encontró que la distribución de las rosetófilas está fuertemente determinada por la altitud. En puntos intermedios del gradiente altitudinal de cada sitio, dichas plantas son particularmente abundantes y diversas, patrón que otros grupos taxonómicos no presentan. En tales altitudes se desarrolla una formación que denominamos matorral rosetófilo de montaña. En Tehuacán, el matorral rosetófilo de montaña se desarrolla en una franja altitudinal donde las nieblas son frecuentes. Estimamos que una roseta que crece en este sitio puede incrementar su provisión de agua en un 10-100% a partir de la niebla. Fuera de esta altitud, la cantidad de neblina es mínima. En Baja California se encontraron dos pisos altitudinales con alta diversidad de plantas en roseta. El estrato inferior coincide con la altitud de las nieblas costeras.

2. *Las plantas que dependen de la neblina deben de presentar características morfológicas que incrementen la captación de dicho recurso.* Por razones físicas, se esperaba que la forma de la hoja tuviese un efecto significativo sobre la intercepción de niebla. Las superficies angostas presentan una menor capa limítrofe, por lo que su eficiencia de intercepción debiera ser mayor. Otras características accesorias incrementarían la cantidad de niebla obtenida, conformando lo que denominamos el "síndrome de hoja angosta". Se construyeron modelos de aluminio de plantas rosetófilas modificando el número y forma (relación longitud/anchura) de las hojas, así como el tamaño de la planta. Éstos modelos se sometieron a niebla artificial y se midió la cantidad de la niebla interceptada. Lo mismo se hizo con siete epífitas del género *Tillandsia* representativas del gradiente de formas del taxón. En las grandes rosetófilas del desierto se aplicó niebla artificial a plantas de los géneros *Agave, Brahea* y *Dasylirion,* y se midió el escurrimiento inducido. Se encontró que la forma y tamaño del modelo de aluminio tiene un efecto importante sobre la cantidad de agua obtenida. A partir de este resultado, y considerando las restricciones evolutivas de las rosetófilas, se puede predecir que la intercepción de neblina sería máxima en plantas con un el síndrome de hoja angosta. Los resultados obtenidos a partir de las *Tillandsia* y las rosetófilas xerófilas concuerdan cercanamente con este patrón.

3. *Las plantas que crecen en sitios áridos con abundante niebla debieran mostrar una tendencia evolutiva hacia el síndrome de hoja angosta.* En 31 especies de rosetófilas de desiertos se midieron once parámetros morfológicos relacionados con el síndrome de

hoja angosta, con los cuales se elaboró un índice de forma. En un extremo del índice se encontraron las plantas que presentan el síndrome. Con base en filogenias publicadas, se propuso un árbol filogenético para las especies estudiadas. Se utilizaron los datos de distribución altitudinal de especies generados en el primer objetivo de la tesis. Con estos datos se aplicó un análisis de comparaciones independientes. Se encontró que en las zonas elevadas, plantas de diferentes orígenes han convergido hacia el síndrome de hoja angosta. La prueba no nos permite discernir entre la evolución hacia el uso de niebla en zonas altas, o la selección de plantas de hojas masivas para almacenar agua en las zonas bajas. Sin embargo, la presión evolutiva para el desarrollo de la suculencia está también presente en las plantas de altura, pues éstas han desarrollado grandes órganos de reserva fuera de las hojas, que así pueden permanecer delgadas.

Los diferentes enfoques de este trabajo nos permiten concluir que la neblina es un factor que ha tenido un fuerte impacto en la evolución de las rosetófilas. Existe una tendencia evolutiva presente en varias familias hacia una forma que optimiza, dentro de las restricciones evolutivas del grupo, la captación de niebla. La distribución de estas plantas está fuertemente ligada a la disponibilidad de dicho recurso, que puede duplicar la cantidad de agua disponible por lluvia. La niebla ha sido un fenómeno ignorado en las zonas áridas fuera de los ambientes costeros, pero que también puede tener un impacto importante en los desiertos del altiplano mexicano.

Abstract

Because of their funnel-like morphology and their hydrophobic epidermis, the rosette plants of the North American drylands are capable of capturing rainwater and conducting it towards their roots with great efficiency. I propose that this morphology allows rosettes to use fog water too. From this hypothesis three predictions can be made in terms of distribution, functional morphology, and evolutionary trends. These predictions are:

1. *In drylands where fog is available, a large abundance and diversity of rosettes is expected.* I described the vegetation in four altitudinal gradients in different Mexican drylands: Tehuacán Valley, Barranca de Metztitlán, Queretaroan desert, and Baja California Peninsula. In Tehuacán fog availability was measured for a year. It was found that the distribution of rosettes depends largely on altitude. At intermediate altitudes in each site, those plants are more abundant and/or diverse, a pattern that is not followed by other taxonomic groups. In those altitudinal belts a formation that I call montane rosette scrub occurs. In Tehuacán, this rosette scrub develops at the altitudes where fogs are frequent. It is estimated that rosettes growing in this area may increase their water uptake in 10 - 100% by using fogs. Outside this altitude the amount of fog is negligible. In Baja California, high-diversity rosette scrubs occurs at two belts. The lower one is found at the zone where coastal fogs usually occur.
2. *The plants that depend on fogs should show morphological traits that increase the capture of that resource.* Based on physical reasons, we expected that narrow leaves should intercept more fog than wide ones, because slender bodies have thinner

boundary layers. This, altogether with other ancillary traits that were expected to increase droplet interception, constitutes what I call the "narrow-leaf syndrome". Aluminum models were built, each showing different number, size and form (length-width ratio) of leaves. The models were exposed to artificial fog, and the amount of intercepted fog was measured. The same protocol was applied to seven species of *Tillandsia* that represented the morphological variability of the genus. Artificial fog was also applied to the large xerophytic rosettes in the genera *Agave, Brahea* and *Dasylirion,* and the resulting stem-flow was measured. It was found that the size and form of the aluminum models affects the quantity of water intercepted. From this result and taking into account the evolutionary constraints in the rosette plants, it can be predicted that the interception is maximum in plants showing the narrow-leaf syndrome. The results from the *Tillandsia* species and the xerophytic rosettes confirm this pattern.

3. *The plants growing in drylands with abundant fog should exhibit an evolutionary trend towards the narrow-leaf syndrome.* In the 31 species of rosette plants found at the four study areas (see first prediction), I measured eleven morphological traits related with the narrow-leaf syndrome. A form index was developed from this data. Plants showing extreme index values exhibited the whole syndrome. Based on previously published data, the phylogeny of the 31 species was reconstructed. By means of the independent contrasts method, we correlated the form index with the altitude at which plants occurred. It was found that at higher altitudes, plants from different families have converged into the narrow leaf syndrome. The test does not tell us if this trend is related with the use of fogs at higher zones, or with the need to store water in the leaves at lower, dryer areas. However, there is also an evolutionary pressure to impound water at higher sites, since montane rosettes are succulents too. In this group, large succulent organs develop outside the leaf, which may then remain slender.

The different approaches used in this research allow us to conclude that fog is a resource that has had a large impact in the evolution of rosettes. There is an evolutionary trend found in different families towards a form that maximizes, within certain evolutionary constraints, the fog interception. The distribution of these plants is closely related to fog, which may even double the amount of water available from rain. Fog has been a phenomenon ignored in non-coastal deserts, but it may also have a significant impact on the Mexican Plateau's drylands.

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PRESENTACIÓN

Nada se parece tanto al caos como una paciente lógica
Rosario Castellanos "Oficio de tinieblas"

Agave silvestre. Mapa de la Sierra Gorda.
Siglo XVI

En las regiones áridas del mundo, por definición, el agua es un recurso escaso. Esta limitación es uno de los factores que más fuertemente restringen el desarrollo de los organismos vivos en los desiertos. Como sucede en otros ambientes estresantes, los moradores de los desiertos presentan una serie de características que les permiten enfrentar las condiciones adversas. Se trata de adaptaciones en cuanto a que les permiten a los seres sobrevivir y reproducirse en su medio ambiente (Lincoln *et al.* 1982). Dichos rasgos se presentan a todos los niveles: fisiológicos, conductuales, anatómicos, morfológicos, reproductivos y de historia de vida. De éstos, el factor morfológico pudiera ser crucial, pues se ha encontrado que la intensidad de la selección natural sobre la morfología se encuentra entre las más altas. Es mucho mayor incluso que aquella que opera sobre características de reconocido impacto sobre la adecuación como los atributos de historia de vida, incluyendo a la reproducción (Kingsolver *et al.* 2001). Esto se refleja en la excepcional variedad arquitectónica que muestran las plantas de las zonas áridas (Cody 1989).

Los desiertos del mundo están habitados por plantas de formas tan extrañas como la gimnosperma africana *Welwitschia*, una especie de tubérculo del cual salen dos larguísimas hojas rastreras de crecimiento indeterminado, los nopales (*Opuntia*) con sus cladodios aplanados creciendo uno sobre el otro, o los *Litops* sudafricanos, que pasan por guijarros mientras no lucen sus flores. Incluso plantas tan cercanamente emparentadas como las del género *Fouquieria* de México adoptan una gran variedad de formas, desde árboles típicos (*F. formosa*) hasta columnas (*F. columnaris*), pasando por arbustos compuestos por ramas monopódicas que salen de una corona común (*F. splendens*). Las cactáceas muestran una variedad semejante, con ejemplares arbóreos, globosos, trepadores, barriliformes, colgantes, columnares y candelabriformes, además de las ya mencionadas opuncioides.

En los desiertos también se observan un número importante de convergencias. Quizá la más célebre es la enorme similitud entre algunas cactáceas americanas y euforbias africanas. Más interesante por la gran cantidad de familias involucradas es la convergencia hacia la forma de roseta con hojas suculentas. En las zonas áridas del mundo podemos encontrar especies de las familias Agavaceae, Aizoaceae, Asphodelaceae, Bromeliaceae, Crassulaceae, Dracenaceae, Doryanthaceae, y Nolinaceae con esta morfología. Hay además otras rosetófilas que muestran suculencia en tallos y raíces, tales como varias compuestas y numerosas monocotiledóneas (Liliaceae, Hyacinthaceae, Amarilidaceae etc.).

Esta excepcional variedad de formas y convergencias en las zonas áridas ha llamado la atención de varios ecólogos, quienes han tratado de explicarla desde el punto de vista de la adaptación. Se ha propuesto que la diversidad arquitectónica es resultado de la adaptación de las plantas a diferentes nichos funcionales a fin de evitar la competencia por los escasos recursos del desierto (Cody 1989). Por otro lado, se ha considerado que la convergencia es resultado de las fuertes presiones del medio ambiente árido, y que diferentes organismos adoptan una estrategia similar para afrontarlas, desarrollándose formas parecidas (Harvey y Pagel 1991, Pagel 1994, Farnsworth y Niklas 1995).

La forma de las rosetófilas

La repetida evolución de la forma rosetófila ha llamado la atención de numerosos investigadores. Quizá el sistema más estudiado sean los páramos (*sensu* Monasterio y Vuilleumier 1986), un tipo de vegetación típico de las montañas tropicales, por arriba del límite de vegetación arbórea. Entre los dominantes fisonómicos de los páramos

encontramos grandes rosetófilas caulescentes, las cuales pertenecen a varias familias en distintos continentes: Araliaceae (Oceanía), Asteraceae (Sudamérica, Norteamérica, Oceanía y África en forma independiente en cada caso), Blechnaceae (Oceanía, Sudamérica), Boraginaceae (Canarias), Brassicaceae, Bromeliaceae (Sudamérica), Campanulaceae (África), Cyatheaceae (Oceanía), Eriocaulaceae (Sudamérica), Gentianaceae (Norteamérica), Papilionaceae y Plantaginaceae (Sudamérica, Smith 1979, Young 1990, Monasterio y Sarmiento 1991, Luteyn 1999). En las investigaciones realizadas en estos ambientes se ha hecho hincapié en el papel de la disposición de las hojas (vivas o muertas) en la termorregulación y en la reducción de la transpiración de las rosetófilas (Smith 1975, 1979, Baruch 1979, Mabberley 1986, Monasterio 1986, Fetene *et al.* 1998). Smith (1979) señaló que, gracias a la disposición de las hojas en las rosetófilas de los páramos, el agua de lluvia sería captada en una superficie grande por las láminas foliares y posteriormente conducida hacia la raíz como sucede en un embudo. Gentry (1982) llegó independientemente a la misma conclusión trabajando con los agaves de los desiertos norteamericanos. En efecto, posteriormente se demostró que las características arquitectónicas de las agaváceas les confieren una enorme eficiencia en lo que se refiere a escurrimiento caulinar. *Agave karwinskii* es capaz de escurrir esencialmente toda el agua de lluvia que recibe aún a precipitaciones muy bajas (Ramírez de Arellano 1996). Esto resultó congruente con la frecuente presencia de neblinas en algunos páramos venezolanos (Smith 1979, Azocar y Monasterio 1980), que pueden fungir como lluvias someras.

El paralelismo entre las rosetófilas de desiertos y páramos ya había sido señalado en lo referente a la termorregulación (Mabberley 1986, Monasterio 1986, Mandujano 2001). Sin embargo, no se le ha prestado atención suficiente al posible papel de la neblina en la evolución de la rosetofilia en ninguno de los dos ambientes. Apenas una mención casual de Smith (1979) hace alusión al fenómeno en el páramo andino. Es en un tercer grupo de rosetófilas donde el uso del agua de niebla ha sido ampliamente documentado: las bromeliáceas epífitas atmosféricas. Es bien conocido desde el siglo antepasado que numerosas *Tillandsia* obtienen agua fundamentalmente a través de sus hojas luego de que la niebla o el rocío la depositan en su superficie (Martin 1994). En el presente trabajo proponemos que a las plantas que adquieren un aporte importante de agua a partir de la niebla se les denomine *nebulófitas* (de *nebula*, nube, en forma análoga a freatófita, que se aplica a las plantas que obtienen agua del manto freático a partir de una larga raíz pivotante, Lincoln *et al.* 1982).

Para poder afirmar que una planta es una nebulófita es preciso demostrar antes que la niebla es un recurso abundante en el ambiente donde crece. El primer artículo, *Rosettophyllous scrubs and fog availability in arid mountains of Mexico*, busca establecer la asociación entre algunas rosetófilas de zonas áridas y la niebla. Para ello se analizó la distribución de las plantas y de la niebla en el valle de Tehuacán-Cuicatlán, Puebla. La distribución de las rosetófilas en otros desiertos mexicanos (en Hidalgo, Querétaro y Baja California Sur) fue analizada en busca de patrones similares al encontrado en Puebla.

Admitir que una planta está presente en los sitios donde hay niebla no es suficiente para afirmar que se trata de una nebulófita. Tampoco se puede generalizar que todas las rosetófilas utilicen el agua de las nieblas. El diente de león (*Taraxacum officinale*) es una rosetófila que crece prácticamente adpresa al suelo, lo que (por razones físicas) le impide el acceso efectivo y directo a las microgotas suspendidas en la atmósfera. No basta la forma de roseta, sino que esta debe presentar una arquitectura específica. Esto es bien sabido por los estudiosos de las bromeliáceas, quienes desde hace más de cien años trazaron una línea

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divisoria en los géneros *Tillandsia* y *Vriesea*, separando a ciertas formas de hojas angostas y lepidotas de otras de hojas anchas y glabras. Al primer grupo se le conoce como bromeliáceas "atmosféricas" debido a que su principal fuente de agua es el agua suspendida en el aire (Mez 1904, Martin 1994).

¿Son entonces las hojas angostas una adaptación al nebulofitismo?

La demostración de la adaptación a través del estudio de los procesos evolutivos que conducen a esta convergencia se dificulta, pues las rosetófilas de desiertos presentan ciclos de vida muy largos, incluso centenarios. No nos es posible estudiar varias generaciones en busca de cambios genéticos o morfológicos (al menos dentro de los plazos a los que se ha visto restringida la investigación moderna). Como resultado, la adaptación morfológica en las xerófitas se ha abordado desde un punto de vista funcional. Para ello se recurre al concepto de desempeño como "la habilidad de un organismo para ejecutar conductas y labores específicas" (Wainwright 1994). El desempeño constituye el enlace entre forma y función, y nos puede brindar información valiosa desde el punto de vista evolutivo.

El estudio de la adaptación morfológica en un contexto funcional requiere de la comparación de organismos con diferentes atributos morfológicos, los cuales son evaluados en términos de su desempeño. En ocasiones, la variabilidad requerida no se encuentra dentro de los individuos de una especie en forma natural, por lo que algunos estudios la generan manipulando a los organismos, utilizando representantes de diferentes especies o bien mediante modelos matemáticos (Nobel 1988, Ezcurra *et al.* 1991, Harvey y Pagel 1991, Eggleton y Vane-Wright 1994, Zavala-Hurtado *et al.* 1998). Se considera que, en caso de encontrarnos ante una adaptación, la selección natural debe haber moldeado a los organismos de modo que se desempeñen mejor que otras formas posibles. Las morfologías que se comparan dependen en gran medida de la pregunta que se pretende abordar. A menudo se las elige tratando de cubrir en su totalidad cierto morfoespacio, a fin de encontrar diseños óptimos dentro de él (Farnsworth y Niklas 1995). Otras veces la comparación se centra en una apomorfia y el carácter ancestral respectivo (Wenzel y Carpenter 1994).

Existe la propuesta de que las hojas pequeñas, al incrementar la relación superficie - volumen, aumentan la tasa de absorción de agua en líquenes nebulófitos (Larson 1994). Sin embargo, el mismo incremento en superficie se puede lograr con láminas amplias pero de escaso grosor. La escasa amplitud de la hoja no es, entonces, un requisito indispensable para incrementar la tasa de absorción. Algunas bromelias nebulófitas de láminas angostas no sólo no tienen hojas de escaso grosor, sino que éstas son abultadas, e incluso suculentas. Un caso de ello es la atmosférica por excelencia, Su Majestad el Heno (*Tillandsia usneoides*). La tasa de absorción no parece ser el único factor involucrado en la forma de las hojas de las nebulófitas. Más aún, muchas de las rosetófilas de zonas áridas y neblinosas poseen hojas angostas, pero no son capaces, hasta donde sabemos, de absorber cantidades significativas de agua a través de la lámina.

En el segundo capítulo, *The narrow leaf syndrome: A functional and evolutionary approach to the form of fog-harvesting plants*, exploramos el papel funcional de la hoja angosta en la intercepción de la neblina, al margen de su posible papel en la absorción de la misma. El texto tiene dos vertientes fundamentales. En la primera exploramos los aspectos físicos involucrados en la captación de agua de niebla. Para ello utilizamos maquetas de

aluminio a partir de las cuales se desarrolló un modelo matemático. Éste se validó posteriormente utilizando *Tillandsia* de diferentes formas. La segunda parte del artículo es una extensión de los procesos físicos antedichos, aplicándolos a las grandes rosetófilas de los desiertos, y su efecto sobre la distribución de las plantas. Se decidió presentar en forma de un único artículo la información de ambos estudios, puesto que ambos recaban evidencia que apunta hacia la existencia de un "síndrome de hoja angosta" en las rosetas nebulofíticas.

Hasta aquí, el papel adaptativo de la forma de roseta se exploró desde un enfoque funcional a través del desempeño. Para que ello sea completamente válido, deben de verificarse dos supuestos: Que el desempeño esté correlacionado con la adecuación, y que las características morfológicas que están bajo estudio sean heredables. La evidencia en torno a ambas proposiciones parece sólida. En primer término, al medir el desempeño a través de la captación de agua, estamos evaluando uno de los factores que más fuertemente inciden en el ciclo de vida de las plantas en ambientes xéricos tales como son los desiertos o las copas de los árboles (Benzing 1990). Es muy probable entonces que la adecuación se vea afectada por la cantidad de agua disponible. En lo que se refiere a la heredabilidad de la variación, el problema queda salvado al estudiar diferentes especies, pues a esta escala las diferencias morfológicas son innatas y determinadas en forma genética.

El uso de numerosas especies nos invitó a adoptar un enfoque comparativo más allá del estudio del desempeño. En el mismo artículo *The narrow leaf syndrome: A functional and evolutionary approach to the form of fog-harvesting plants* se exploró la posibilidad de que el síndrome de hojas delgadas constituyera una tendencia evolutiva en las nebulófitas de las zonas áridas. El fenómeno ya había sido reportado para las bromeliáceas, donde la forma atmosférica ha evolucionado numerosas veces dentro del género *Tillandsia* (Gilmartin 1989). Hasta cierto punto, la misma tendencia es también observable en las rosetófilas de los páramos. Para evaluar esta posibilidad se aplicó el método de comparaciones independientes (Harvey y Pagel 1991) sobre el conjunto de características arquitectónicas de las rosetófilas de cuatro desiertos mexicanos.

Esta tesis busca establecer, pues, la relación entre un importante grupo de rosetófilas y la neblina. El papel del nebulofitismo en los desiertos mexicanos ha sido generalmente desdeñado por los ecólogos (con la excepción de los desiertos costeros bajacalifornianos), pero que puede ser de gran importancia. La disponibilidad de neblina no sólo influye sobre las nebulófitas, sino sobre comunidades enteras, como lo son las "lomas" del desierto peruano (Rundell *et al.* 1991), y puede ser un factor fundamental para entender mejor esa vegetación que, ante su desconcertante complejidad, se ha clasificado simplemente como "matorral xerófilo".

NOTA: El capítulo 1, "Rosette scrub and fog availability in arid mountains of Mexico" se encuentra actualmente en prensa en la revista *Journal of Vegetation Science*. El texto que aquí se presenta corresponde a la versión que será publicada en la revista, con sólo algunos cambios de formato para facilitar su lectura en esta tesis.

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CAPÍTULO 1.

ROSETTE SCRUB AND FOG AVAILABILITY IN
ARID MOUNTAINS OF MEXICO
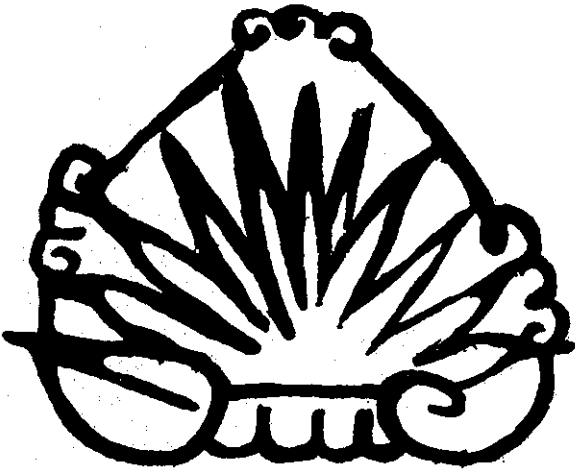
Glifo de Metepec, "En el cerro de los magueyes".
Historia Tolteca- Chichimeca

Rosette Scrub and Fog Availability in Arid Mountains of Mexico

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Abstract: Large succulent-leaf rosettes are characteristic life forms in many deserts. In certain areas they become dominant life forms, forming vegetation types known by their physiognomy as rosette scrub. The large number of rosette species suggests a close relationship between form and environment. Rosettes are excellent harvesters of low-intensity rains and fogs. In this paper we propose that some rosette-dominated formations of the Mexican drylands, the montane rosette scrub, occurs in altitudinal belts around mountains where fog is abundant. We sampled four altitudinal gradients in mountains with different floras, recording the abundance and richness of plants. At one site, the Tehuacán Valley, we also measured for a year the amount of fog along the gradient, below, above, and in the rosette scrub. We found a marked association between the abundance and richness of succulent rosette species and altitude, with maximum values observed on well-defined elevational belts where the montane rosette scrub occurs. Other life forms, such as stem-succulent cacti or woody shrubs, do not show this mid-elevation pattern. The elevational ranges where the montane rosette scrub occurs usually coincide with areas where clouds and fog accumulate. Our micrometeorological measurements indicate that rosette plants growing within a cloud belt can increase their water supply by 10–100% by harvesting fog. Outside these belts, fog harvest is negligible. Desert rosettes constitute one of the most common fog-harvesting growth-forms.

Keywords: Montane rosette scrub, Agavaceae, Nolinaceae, Bromeliaceae, Fog-harvesting, Vegetation.
Nomenclature: Gentry (1982) Agavaceae, Smith & Downs (1974) Bromeliaceae, Roberts (1989) Flora of Baja California.
7853 words

Introduction

The vegetation of the arid and semi-arid lands of Mexico shows a large number of different associations (Rzedowski 1978) that are often found forming a complex spatial mosaic. In a relatively small area, a thorn woodland, a cactus scrub and a chaparral may coexist. Several authors worldwide have studied the factors determining the occurrence of different associations, focusing mainly on elevational gradients (see, for example, Whittaker and Niering 1965, Mooney and Harrison 1972, Arce and Marroquín 1983, Montaña and Valiente-Banuet 1998, Gutiérrez *et al.* 1998). Since the different vegetation units are frequently defined as formations (i.e., communities characterized by the abundance of plants with a distinctive architecture, Walter 1990), close attention has been paid to the morphological changes along environmental gradients (Mooney *et al.* 1974, Box 1981, Rundel and Vankat 1989).

Succulent rosettes are conspicuous life forms among the very diverse spectrum of architectural designs in the arid zones of North America. Plants of different families have converged to that morphology. Among the most widespread genera in North America we find *Agave, Furcraea* and *Yucca* (Agavaceae), *Nolina, Beaucarnea* and *Dasylirion* (Nolinaceae), *Hechtia* (Bromeliaceae), and *Echeveria, Dudleya* and *Graptopetalum* (Crassulaceae). Most of these plants are leaf succulents with massive leaves arranged in rosettes that allow the storage of large quantities of water. These large-leafed, rosette plants are known as megaphytes. It has been proposed that the distinctive traits of megaphytes, such as large leaves and short internodes, are strongly interrelated, so selection upon one of them results on the development of the whole set of characteristics (Begon *et al.* 1987). Therefore, large, succulent leaves are presumably correlated with the rosette habit. Water impoundment is likely the main factor explaining the frequent occurrence of rosettes in drylands.

There are some communities where rosette plants belonging to different families become the dominant species. The vegetation in those areas is known as "rosettophyllous scrub" (Rzedowski 1978).

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To simplify terminology, we shall refer to this formation as "rosette scrub". Since other succulents, such as cacti, are rarely abundant in these formations (see Rzedowski 1978), it seems that water storage is not the only trait that makes plants with rosettes succeed. Succulence may be closely related to rosette growth in drylands, but desert rosettes do not behave merely as succulents; there is something, possibly related to their peculiar architecture, which makes them outperform other water-storing plants in some dry environments.

There is a close relationship between the form of organisms and their environment (Wainwright and Reilly 1994). The morphological convergence of species has been interpreted as evidence of adaptation, and even of optimal design (Harvey and Pagel 1991, Ricklefs and Miles 1994, Farnsworth and Niklas 1995). Thus, a match should be expected between the morphology of desert rosettes and some environmental factors at the areas where the rosette scrub develops, that results in a successful performance of these species. These factors, however, have not been identified and described. The rosette-habit's performance needs to be measured in terms of the environmental characteristics that determine their success in the field.

Some of the most intensively studied rosettes in terms of their form and environment are those of the high altitude "páramo" (*sensu* Monasterio and Vuilleumier 1986), a community occurring on tropical highlands throughout the world, where rosettes may be the most conspicuous species. Like deserts, páramos show a large number of convergent rosette species. Here, the morphology of rosette-plants has been interpreted as a mechanism to avoid sub-freezing temperatures, optimize light interception, and protects and keeps warm the apical meristems (Smith 1974, Monasterio 1986, Mabberley 1986, Monasterio and Sarmiento 1991, Körner 1999). Despite the climatic differences, some of these functions have been attributed to desert rosettes (Woodhouse *et al.* 1980, Gentry 1982, Nobel 1986, Nobel 1988). Both for desert páramos and lowland deserts, it has been proposed that rosettes intercept rainwater and canalize it to the root through stem-flow due to their funnel-like architecture (Smith 1974, Gentry 1982). It has been shown that agaves are most efficient in canalizing rainwater: While most plants need a copious amount of rain in order to get soaked and initiate stem-flow, the waxy epidermis of agaves shows a very high efficiency even for very light (one millimeter) rainfalls (Ramírez de Arellano 1996). This means that agaves are capable of using shallow, low-intensity rains that are not normally accessed by other plants. Therefore, rosette scrub should develop in environments where precipitation occurs in the form of light drizzles. In these conditions, funnel-like architectures could confer plants an adaptive advantage over other morphologies.

We have observed that in certain altitudinal belts on large mountains a rosette scrub develops, which we will name montane rosette scrub (Plate 1). In these areas fogs seem frequent, forming (sometimes very narrow) "cloud belts" around mountains. In some tropical mountains, as many as three of such cloud belts have been reported. They are areas of longest persistence of fogs. It has been recognized that cloud belts may be a factor of great ecological importance in the distribution of certain vegetation types (Van der Hammen and Cleef 1986). Examples of this are the "lomas" formations of the Chilean-Peruvian desert (Rundel *et al.* 1991, Rundel and Dillon 1998, Galán de Mera *et al.* 1998). Many lomas are characterized by the dominance of rosette bromeliads and are highly associated with mountains.

At the altitudes where the cloud belts occur, it is likely that the highly efficient stem-flow of xerophilic rosette plants may be intercepting water from the fogs and drizzles and canalizing it to the roots. Rosette scrub, defined as an area of large density and diversity of rosette species, should develop in these elevational belts. We believe that increased fog availability in the mountain cloud belts is the reason for the widespread occurrence of the montane rosette scrub throughout Mexico.

Since the main idea we are proposing deals with water availability in Mexican drylands, we need to consider the other two main sources of water that a rosette plant may use at a given moment: rain and succulent tissues. These two sources may be of different importance at different altitudes, and their effects may be superimposed to that of fog. To screen between succulence, rain, and fog, the rosette-plant distribution can be compared with those of cacti and shrubs. The Cactaceae have CAM metabolism and are succulents, as many rosettes, but have a different morphology. This means that they should be also adapted to aridity, but should not strongly respond to fog. There is a general trend for aridity to diminish

with altitude as a result both of a reduced temperature and evapotranspiration, and of a higher precipitation (Valiente 1991). Because of the aridity at low altitudes, water-storing plants may be important components of vegetation. Thus, we expect cacti and succulent rosettes to be well represented in the lower parts of the gradients. We will name this increased succulent-plant abundance "aridity effect" (Figure 1).

Figure 1. Hypothetical distribution of three life forms in relation to rainfall and fog. (a) While rainfall is reported to increase linearly with altitude, fog occurs only in narrow fringes, or "cloud belts". (b) Succulent plants are expected to show an "aridity effect", increasing towards the lower, more arid slopes, but rosettes may also benefit from the fog effect. Shrubs would have a distribution similar to that of rain (see text for details)
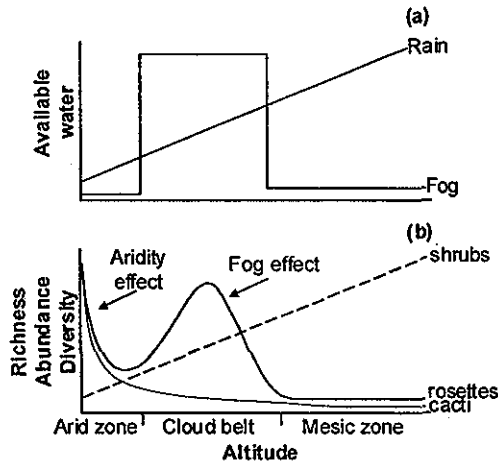
Since most shrubs have no succulent organs where water may be stored, they should not show an aridity effect. They are not as efficient as rosette plants in terms of stem-flow (Ramírez de Arellano 1996), so it is unlikely that they can use fog water as efficiently as rosettes. Shrubs, therefore, basically depend on rain. Several authors have shown a positive correlation between rainfall and diversity (Noy -Meir 1985, Morton and Davidson 1988, MacKay 1991, Tilman and Pacala 1993). Productivity and biomass are laso greater in more humid sites (Polis 1991, Tilman and Pacala 1993). As the precipitation often increases linearly with altitude in some tropical deserts (Valiente 1991, Montaña and Valiente-Banuet 1998), the abundance of woody perennials should follow the same pattern. An altitudinal increase of rosette-plants, resembling the behavior of shrubs, may be the mere result of an enhanced amount of rains. If rosettes use fog water additionally, their distribution should display a peak of abundance and diversity around the cloud belts, as it happens in South American coastal deserts (Rundel and Mahu 1976, Rundel and Dillon 1998). Plants with other morphologies would not follow this pattern (Figure 1).

In this paper we will explore the altitudinal distribution of plants with contrasting morphologies and physiologies to demonstrate that rosettes follow a distinctive distributional pattern that results in the widespread occurrence of the montane rosette scrub. We will also show that this formation develops at definite altitudinal belts where large amounts of fog are available for the use of succulent rosette plants. Finally, we will explore hypothesis on the likelihood of alternative explanations for rosette dominance at certain elevations.

Methods

Study sites

We chose four different arid zones with steep elevational gradients: The Tehuacán Valley, in Puebla, (18°17'N 97°28'W, altitude 1500-2200 m), Barranca de Metztitlán in Hidalgo, (20°34'N 98°42'W, 1400-1900 m) and Sierra de El Doctor, in Querétaro (20°53'N 99°39'W, 1700-2400 m), and Sierra de San Francisco (27°32'N 113°08'W, 400-1500 m) in the central Baja California Peninsula (Figure 2). The Pueblan, Hidalgan and Queretaroan arid zones are small rainshadow deserts in central-southern Mexico, with an extremely high degree of endemism species richness (Bravo-Holis 1978, Sánchez-Mejorada 1978, Zamudio *et al.* 1995, Dávila *et al.* 1993, Reyes 2000). Sierra de San Francisco, in contrast, is an extra-tropical desert, where Pacific coastal fogs constitute an important feature.

Figure 2. Study sites. 1. Sierra de San Francisco, Baja California Sur, 2.Sierra de El Doctor, Querétaro, 3. Barranca de Metztitlán, Hidalgo and 4. Tehuacán Valley, Puebla.
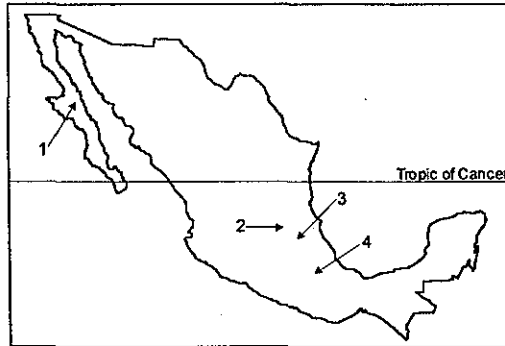
In all cases, mountains with similar geology over their entire elevational gradient were selected. The vegetation is composed of deciduous elements in the lowlands, and perennial ones in the highest portions. At Tehuacán, El Doctor and San Francisco, desert scrub develops in the lower parts of the gradient, whereas at Metztitlán a tropical dry forest occupies the lower ranges. The highest zones were covered by chaparral (San Francisco, Tehuacán and Metztitlán), and pine forest (El Doctor). At all sites but San Francisco, clouds were observed as fog banks both in summer (rainy season) and winter, and often limited to a narrow belt around the mountains. At San Francisco, a layer of thin coastal fogs was observed at an altitude of 400 m, and lasted for all the days we spent working at the site.

Vegetation analysis

The vegetation was sampled every 100 m of altitude through a set of three 50×6 m transects placed randomly. We sampled only in zones with approximately the same slope and aspect when possible, in order to reduce the variation induced by these factors. On each transect, the number of individual rosette plants of each species was recorded. Rosettes were assigned to different individuals if they were separated by more than 0.5 m, and no aboveground connection existed among them. The species and number of individual cacti were also recorded. The abundance of shrubs was measured as percent cover for each species by the line intercept method (Brower *et al.* 1990).

There are two attributes of vegetation that may define montane rosette scrub as a unit: the great number of species and individuals with rosette morphology, and the high abundance of rosette plants compared to other life forms. The measurement of these attributes was achieved by recording the species richness, abundance and diversity (Shannon's Index) of all three life forms, and by calculating two dominance indices. Rosette dominance over cacti and over shrubs were measured, respectively, as the

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number of rosette-plants divided by the total number of succulent plants, or divided by the shrub-cover. To compare between altitudes and life forms we used Generalized Linear Models. Since richness and abundance are count variables, log-linear regressions were fitted. The dominance over cacti, a proportion, was analyzed through logistic regression. Re-scaling was conducted when necessary to correct for overdispersion (Crawley 1993). For Shannon's diversity and dominance over shrubs, both continuous variables, linear regressions were performed. We found no significant deviations from the regression assumptions as evaluated through Lilliefors test (Conover 1980). Species richness, abundance and diversity were tested against altitude as a continuous predictor, and life form as discrete predictor with three levels (rosettes, cacti and shrubs). The dominance indices were regressed only against altitude. Because of aridity- and fog-effects (Figure 1), we expected rosette indices to have two inflections along the gradient. Rosettes should increase towards the arid extreme of the gradient, where succulence provides the adaptive advantage of water storage, and they should also show a peak of abundance in the cloud belts, where rosette morphology allows fog-harvesting. Thus, third degree polynomials and their interactions were fitted as full models. The non-significant terms were then deleted sequentially, and non-significant differences between life forms were removed by collapsing categories (Crawley 1993). Model fitting was conducted using GLIM 4 (Royal Statistical Society 1992), and Lilliefors tests were run on STATISTICA (StatSoft 1993).

Several factors change together with altitude, soil being one of the most relevant among them. Also, elevational position in the geomorphological formations affect biota. The crests, scarps, debris slopes and pediments that characterize the topographic catena of arid elevations have very different inclinations and soil characteristics (FitzPatrick 1980, Small 1984). In order to control the possible effect of edafic and other factors on rosettes, abiotic-environment descriptions were made for each transect. At the middle of every 50 m transect, aspect was recorded with a compass corrected for true north, and slope was measured with a clinometer. A profile of the top 30 cm of soil, where most of the roots of rosettes are found, was made. We recorded the following soil parameters: Acidity (with pH indicator paper), organic matter and carbonate contents (through bubbling intensity of concentrated Hydrogen Peroxide and 0.1N Hydrogen Chloride), dry and wet color (Munsell charts, Soiltest 1975), depth to rock (if shallower than 30 cm), presence of a calcic horizon, percent of leaf-litter cover, and type of A horizon (FitzPatrick 1980). The reactivity of parent material to hydrogen peroxide was also measured as a baseline control for the *organic matter test*.

In order to evaluate the relative importance of the abiotic factors, a multivariate analysis was conducted for the abundance of rosette plants. Since we expected rosette species not to be distributed linearly, but rather unimodally along the elevational gradient, correspondence analysis was chosen (Ter Braak 1995). The degree to which species distribution is determined by abiotic factors was measured through the correlations between environmental variables and the first species axis (inter-set correlations, Ter Braak 1995). Since several coefficients were calculated, the overall probability of committing Type I error increases. This probability was kept below the overall 0.05 value by correcting critical significance level by means of Sidak's transformation (Sokal and Rohlf 1995). The fog hypothesis predicts that altitude should be strongly related to rosette distribution, but that the other variables should not appear as strong predictors at all four sites.

Fog measurements

After describing vegetation at Tehuacán, we made precipitation measurements along the studied gradient. We placed six sets of raingauge/fog-catcher pairs (Nagel 1956) at different altitudes: at 1450 m (microphyllous scrub), 1800 m (montane rosette scrub) and 2050 m (chaparral), with one replicate at each altitude. The raingauge collector was a funnel 10.5 mm in diameter. The fog-collecting instrument was a mesh cylinder 10 cm tall and 8.66 cm in diameter, so its vertical cross-sectional area was equivalent to that of the funnel. The fog-catcher was made of metallic mesh with wires 0.25 mm in diameter, forming a lattice 2.18 mm wide and 1.38 mm high. According to the calculations proposed by Nagel (1956) this fog catcher will intercept 82.5% of the fog particles that reach it, underestimating the amount of fog by 17.5%. To correct for this bias, we multiplied the quantity of collected fog-water by a factor of 1.21 (=1/0.825).

Since fog interception depends on wind speed, which in turn depends on height above ground, fog interception was measured at 0.3, 1 and 2 meters above ground level. The raingauge/fog-catcher pairs where checked monthly during the dry season and fortnightly during the rainy season. Measurements took place between May 1998 and April 1999.

Results

In all, thirty-four rosette species where found. The most important genus was *Agave* with twelve species, followed by *Yucca* with four taxa. This makes the Agavaceae the most diverse and widespread rosette family, with sixteen species (Table 1). Nolinaceae, with seven species in three genera was the second most important family, with Crassulaceae and Bromeliaceae in third place with four species each. Bromeliaceae were of great importance, not so much because of the family's diversity but because of their large abundance in El Doctor, Metztitlán and Tehuacán. These three zones showed a very high species richness, with eleven to fourteen rosette taxa. San Francisco was relatively species poor, with only six taxa. This site was different from the other three, not just in its relative scarcity and low diversity of rosettes, but also, as we shall see, in the overall elevational patterns of rosette distribution. The taxonomic similarity among sites was low except for El Doctor and Metztitlán, with a Sorensen's index of 64.0%. Tehuacán clearly constituted a different floristic unit, resembling El Doctor 14.8% and Metztitlán 8.3%. San Francisco shared no species with the other study sites (Sorensen = 0%, Table 1).

The richness, abundance and diversity of the different life forms changed along elevational gradients. Life forms showed significantly different distributions on every site, with the exception of richness of cacti and rosettes at Metztitlán. Richness did not change with altitude for rosettes in San Francisco and for shrubs in El Doctor, but elsewhere the fitted curves for richness and diversity are very similar. Therefore, only results for diversity are shown.

At El Doctor and Tehuacán, rosette plants behaved as expected, with a well-defined maximum richness, abundance and diversity at intermediate parts of the gradient, 2200 m and 1800 m of altitude respectively (Figures 3.1 and 3.2). Metztitlán only showed this trend for abundance, while richness and diversity did not change with altitude. However, in the intermediate parts of the Metztitlán gradient rosette plants became significantly more rich and diverse than shrubs. At this site, the area where rosettes are more important is at an altitude of 1600 m (Figure 3.3). Only at El Doctor there was a significant aridity effect for rosettes, with increased richness, abundance and diversity in the lower zones of the gradient (Figure 3.1).

At Tehuacán and El Doctor, cacti showed peak diversity and abundance in the lower parts of the mountains. At Metztitlán no significant trend was detected in richness, abundance and diversity of cacti as altitude increased. Shrubs did not show the expected trend to increase diversity and cover with altitude, except at Tehuacán. At El Doctor the trend was found only in terms of diversity. Metztitlán showed a concave curve, due probably to the lack of trees at middle altitudes compared to tropical forests low in the gradient. Dominance indices showed a convex form in all cases except for dominance relative to cacti at Metztitlán, which did not change with altitude. Additionally, in Tehuacán and El Doctor, the dominance of rosettes relative to cacti tended to increase with altitude (Figures 3.1, 3.2 and 3.3).

At San Francisco there was a general trend to reduce richness and abundance of shrubs and cacti at higher altitudes. Rosette plants showed an increased abundance at intermediate altitudes. However, the peaks of diversity, dominance, and abundance of rosettes did not seem to coincide at the same altitudes, as happened elsewhere: Maximum richness and diversity, took place at 400 and 1300 m. The largest abundance occurred at 600 m, and the dominance relative to cacti was greater at 800 m. The dominance over shrubs did not show any significant trend with altitude (Figure 3.4).

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Table 1. Species found in the four study sites and their densities shown as the number of individuals per hectare averaged over the entire elevational range of each site.

Family	Species	El Doctor, Querétaro	Tehuacán, Puebla	Metztitlán, Hidalgo	San Francisco Baja Calif. Sur
Agavaceae	Agave asperrima	176.4			
	Agave cerulata				1037.4
	Agave kerchovei		745.8		
	Agave lechuguilla	366.7		1153.7	
	Agave marmorata		305.5		
	Agave peacockii		1.4		
	Agave potatorum		300.0		
	Agave salmiana	38.9	11.1	22.2	
	Agave striata	211.1		1113.0	
	Agave stricta		26.4		
	Agave xylonacantha	16.7		92.6	
	Agave sp.	6.9			
	Yucca filifera	4.2		16.7	
	Yucca periculosa		68.1		
	Yucca valida				14.8
	Yucca whipplei				9.3
Nolinaceae	Beaucarnea gracilis		12.5		
	Beaucarnea purpusii		4.2		
	Dasylirion acrotriche	52.8	519.4		
	Dasylirion glaucophyllum			285.2	
	Dasylirion longissimum	1.4			
	Nolina palmeri				92.5
	Nolina parviflora	5.6		3.7	
Bromeliaceae	Hechtia argentea	51.4		1450.0	
	Hechtia podantha		627.7		
	Hechtia sp.	166.7			
	Tillandsia albida			577.8	
Arecaceae	Brahea nitida				
	Erythea brandegeei		1.4		6.5
Hyacinthaceae	Hemiphylacus alatostylus	12.5		337.0	
Crassulaceae	Dudleya acuminata				111.9
	Echeverria subsesilis		34.7		
	Echeverria sp1	4.2			
	Echeverria sp2			27.8	

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Figure 3. Richness, diversity, abundance and dominance of three life-forms at four Mexican drylands. (a) Diversity of rosettes (——▲——), shrubs (---□---) and cacti (—O—), (b) Abundance of the three life forms, measured as density for rosettes and cacti, and as cover for shrubs. (c) Dominance indices over shrubs (—◇—) and cacti (---✕---). Error bars correspond to standard errors. The arrow at the bottom shows the altitudinal range at which the montane rosette scrub occurs. Note the significant aridity effect at lower altitudes in Sierra de El Doctor. Two altitudinal belts with significant fog input and high rosette diversity are believed to be present in Sierra de San Francisco, and are indicated by the arrows at the bottom.

3.1 Sierra de El Doctor, Querétaro

3.2 Tehuacán Valley, Puebla

3.3 Barranca de Metztitlán, Hidalgo

3.4 Sierra de San Francisco, Baja California

16
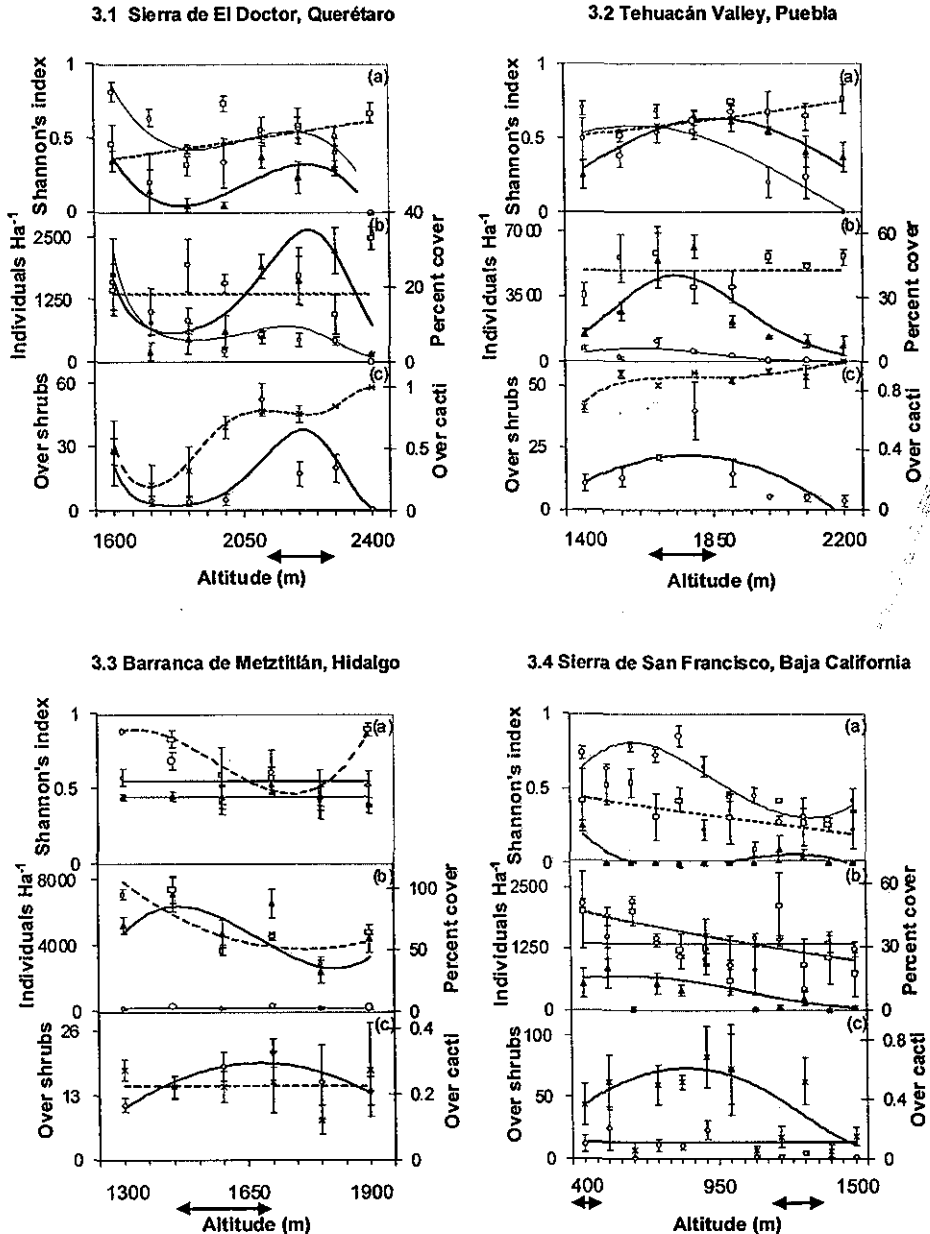
In all sites altitude was the most important variable in determining species distribution, as shown by the high correlation coefficients for this factor (El Doctor: 0.869, Metztitlán: 0.886, Tehuacán: 0.825, San Francisco: 0.825). Most of the other thirteen variables were irrelevant, except for aspect ($r = 0.803$ in El Doctor), slope, and soil color value ($r = 0.811$ and 0.723 respectively, both in Metztitlán). However, not one of these factors was meaningful at more than one site.

The study period (April 1998 - March 1999) was part of one of the most dramatic El Niño years in Mexico. The rainy season was severely delayed in 1998, and a harsh drought caused several wildfires at the Tehuacán Valley. Even in these dry conditions, an important amount of fog was registered at an altitude of 1800 m, where the montane rosette scrub occurs. The rainy season finally began in July, and for three months more than 100 mm (the average precipitation of the rainiest month) fell fortnightly, overflowing the rain gauges. For this reason, data for July, August and September were lost. From then on, fog kept occurring at the same altitude of 1800 m (Fig. 4). Very little fog occurred at the other altitudes, although it rained about the same quantity everywhere (fig. 5), with an overall mean of 200.9 mm for the study period (excepting July-September, when the gauges overflowed).

As height above ground level of the fog-collector increased, more fog was collected. At an altitude of 1800 m, the fog collected over the whole year was 2.2 mm at 0.3 m above ground level, 74.0 mm at 1 m, and 183.4 mm at two meters. Thus, at the montane rosette scrub, and at two meters above ground, nearly the same quantity of water is available as fog as it is available in the form of rain.

Figure 4. Fog and rain recorded monthly at three altitudes in the Tehuacán Valley. The 1800 m station was located at the montane rosette scrub, while the other stations were above and below that vegetation belt. Fog measurements are shown for two meters above ground.
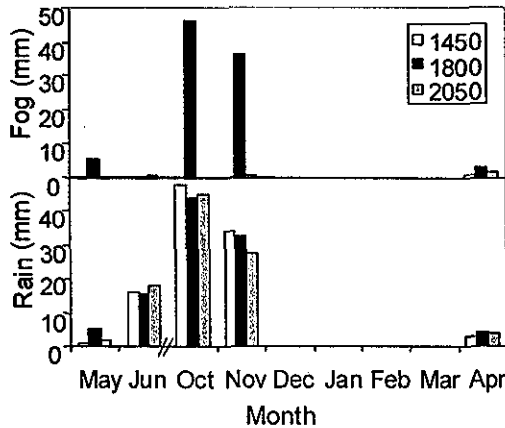
Discussion

The relatively wide range of rosette families (six families in all), as well as the little taxonomic similarity at the species level between most sites, are evidence for the convergence of species from different regional floras into the montane rosette scrub. Therefore, the montane rosette scrub cannot be considered as the result of a few competitively aggressive species incidentally occurring at a given altitude all over Mexico. Different initial conditions —different regional floras, as evidenced by low inter-site similarity— have resulted in the same vegetational life-spectrum patterns. The convergence of different species at different sites suggests that there is a strong environmental factor behind rosette dominance (Harvey and Pagel 1991, Ricklefs and Miles 1994, Farnsworth and Niklas 1995).

Figure 5. Total annual rain and fog at three altitudes and three heights above ground at the Tehuacán Valley. The montane rosette scrub station was located at 1800 m. Rain is the mean from all rain gauges at each altitude.
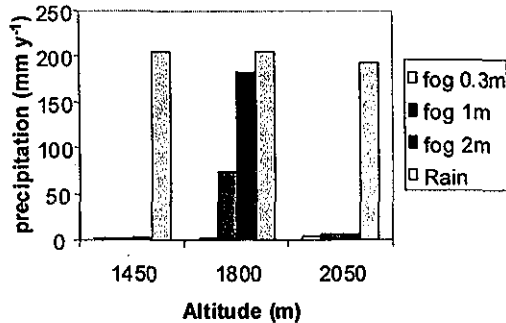
Patterns in the distributions of rosettes and cacti resembling the expected trends shown in Figure 1, were found at the field. At all sites, there was an intermediate altitudinal belt where rosettes were most abundant and dominant (Figure 3). At two of the sites, El Doctor and Tehuacán, rosette diversity and richness followed a similar pattern (Figures 3.1 and 3.2). The data on San Francisco require some comments. In this site, the curves for abundance, diversity and dominance are not easily interpreted. This happens because (unlike intertropical deserts) the maxima for each variable occurred at different altitudes (Figure 3.4). While richness and diversity showed two peaks at 400 and 1300 m, abundance reached a maximum at 600 m and dominance over cacti was greater at 800 m. Our definition of rosette scrub as a formation showing a high diversity and abundance of rosettes, which become the dominant elements of vegetation, cannot be applied to Sierra de San Francisco. Additionally, the abundance (and therefore dominance) curves are not too reliable, since one species alone (*Agave cerulata*) occurs at middle altitudes, from 500 to 1000 m., but it does so in great numbers. This gives this species alone an inordinate influence on the regressions. The convex form of the abundance and dominance curves may be, to a large degree, the result of the bell-shaped distribution that single species show along gradients (Giller 1984). At San Francisco, two zones may be described as relatively rosette-abundant and with higher diversity: the 400 m and 1100-1300 m belts, each with three species. Therefore, we propose that a first montane rosette scrub happens in San Francisco at 400 m, and a second one takes place in higher areas above 1000 m. This seems to have a correspondence with environmental factors, as we will discuss below.

In general terms, our data confirm the existence of the montane rosette scrub as a well defined altitudinal belt around arid mountains, where abundance and diversity of rosette plants are high enough to make them the dominant elements of vegetation. Because of its geographic extent, this is a generalized pattern over the Mexican drylands.

At the Sierra de El Doctor, rosettes showed an increase towards the lowlands (Figure 3.1) similar to the one we expected due to the aridity effect (Figure 1). The fact that the curves calculated for the other sites did not show a minimum between the desert and the montane rosette scrub is not evidence against the aridity effect. Aridity is still likely to be the cause for the overall high abundance of rosettes at the lower extremes of all four elevational gradients. Some very succulent rosette species (e.g. *Agave marmorata*, *Agave xylonacantha*, and *Agave cerulata*) are clearly bound to the more arid lowlands. Cacti, however, were more strongly restricted to the lowlands. At all sites but Metztitlán, the abundance and diversity of the Cactaceae showed a decreasing trend with altitude, displaying maxima close to the lower parts of the gradient. Significant differences between cacti and rosettes along the altitudinal gradients were found in terms of richness, diversity and abundance. The dominance of rosettes over cacti tended to increase with

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altitude. This marks a clear distinction between rosette and non-rosette succulent plants. Both are capable of storing water in drylands, may tolerate about the same harsh drought and high temperature stresses (Nobel 1988), and have been capable of colonizing extremely dry deserts. However, our data show that many rosette species grow also on higher sites, where fog is an important environmental feature.

Shrubs also showed significant differences with rosettes. The abundance of shrubs either remained equal throughout the gradient (El Doctor and Tehuacán), or showed a decreasing trend with altitude (Metztitlán and San Francisco). Only at El Doctor and Tehuacán shrub diversity increased with altitude. It should be noted that shrub diversity did not show any significant convexity at intermediate altitudes.

While the monotonically increasing trend of vegetation cover with rainfall has been reported in several systems, the same is not necessarily valid for diversity. In several studies with plants and animals all over the world it has been found that in low and high productivity environments diversity is poor, but at intermediate conditions large diversities are achieved. The reasons for this pattern remain unclear. Competition, habitat heterogeneity, and predation are among the processes that have been proposed to cause unimodal patterns along productivity gradients (Tilman and Pacala 1993, Rosenzweig and Abramsky 1993). This phenomenon has been found in several drylands, related to altitude and rainfall (Whitaker and Niering 1975, Tilman and Pacala 1993, Rosenzweig and Abramsky 1993 and references therein, Gutiérrez *et al.* 1998). This is of great importance, since we found an area with increased diversity of rosettes at intermediate portions of the altitudinal gradient. However, the lack of significant convexity in the curves for shrubs and cacti renders the usual productivity - diversity patterns an unlikely explanation for the case of rosette species at desert mountains. There is no obvious or *a priori* reason, other than fog, to expect that rosettes should show that peak of diversity on mid-mountain slopes while other life forms would not.

The factor that determines more strongly the distribution of rosette plants is altitude. Its correlation with the species multivariate axis was always higher than 0.82. Other factors were also correlated, but only at one place. Slope was correlated with floristic change at Metztitlán, but not elsewhere. The same happened with aspect at El Doctor. This is important, since certain environmental factors, such as steep slopes or shallow soils usually are present at the intermediate portions of mountains (FitzPatrick 1980, Small 1984), and could account for the occurrence of certain species. If rosette scrub was associated any of such factors, we would have seen a consistent correlation between it and rosette distribution. Thus, we may discard factors associated with topographic catenas as the ones determining the occurrence of the montane rosette scrub at mid elevations.

The floristic importance of altitude supports the idea of cloud belts as a determinant factor. However, in vegetation change this result is not surprising, as altitude is highly correlated with several factors (mainly temperature) which are widely known to have a large effect on plant distribution. At the two sites that are closer, El Doctor and Metztitlán, the rosette scrub occurs at 2200 and 1600 m respectively. The closest weather stations (El Doctor at 1500 m and Metztitlán at 1250 m) show a difference of 4°C in mean temperature, Metztitlán being hotter (García 1987). Thus, it is quite likely that the rosette formations at El Doctor, which occur at a much higher site, are exposed to a far lower temperature. In spite of this, both sites had a high (64%) species similarity. It seems possible that temperature is not the most influential factor determining the distribution of rosette species at different sites.

Our micrometeorological measurements at Tehuacán showed that fog could be a very important resource. As we expected, fog is more available at the 1800 m (the altitude of the rosette belt), and is nearly absent at other zones. This is in complete agreement with the hypothesis that montane rosette scrub develops at mountain cloud-belts. At two meters above ground, fog was nearly as abundant as rain. Even during a harsh drought, there was some fog available and it may even double the water uptake during the occasional winter and early-spring rains. The supplementary humidity provided by fog might alleviate water stress during the driest part of the year. However, there was a clear association between fog and precipitation, as no atmospheric humidity was caught in the gauges without some associated rain.

The differential availability of fog at different heights above ground was also an outstanding pattern. As we expected, greater heights were the best for fog collection. It is noteworthy that at higher

altitudes we found more caulescent rosettes, and their caudices were longer, so the fog-catching leafs are placed higher above the ground, and therefore exposed to more fog. Thus, high-elevations are dominated by caulescent taxa such as Arecaceae, *Nolina, Dasylirion* or *Yucca* rather than *Agave*. At San Francisco the pattern is partially inverted, with *Agave* and the stemless *Yucca whippleii* at intermediate altitudes, and the caulescent *Yucca valida, Erythea brandegeei* and *Nolina beldingi* at the two belts that we have defined as montane rosette scrub.

At San Francisco the distribution of rosette plants seems complex, but so is the altitudinal distribution of humidity. As we have pointed out, the vegetation at two altitudinal belts resemble montane rosette scrub. Both correspond to the observed coastal fog belt at 400 m, and a potential cloud-belt at high altitudes. Although no direct studies on fog formation have been made at the Sierra de San Francisco, the meteorology of coastal fogs has been well studied on Southern California, where clouds form when moist marine air is trapped against the mountains by an atmospheric inversion layer (Bailey 1966). These coastal fogs typically reach around 400 m above sea level, although the altitude of the inversion may fluctuate. In San Francisco, at 400 m a very dense carpet of epiphytes covers almost every shrub (Plate 1), showing intense fog condensation. *Agave cerulata*, being the most succulent rosette species, seems to follow the aridity effect, being more abundant in the lower parts of the gradient.

The South American coastal deserts have also frequent fogs. The Atacama Desert and the Peruvian lomas are two areas with large fog inputs where rosettes are of great importance. In the lower area or "tillandsian lomas", several species of *Tillandsia* are found. Some of them have water-reservoirs that are only functional if there is significant stem flow. In the higher "bromelian lomas", large numbers of *Pitcairnia, Deuterocohnia* and *Puya* occur (Rundel and Mahu 1976, Rundel and Dillon 1998). These are large, rooted leaf-succulents, morphologically similar to those found in Mexican drylands. The latter genus is also common and highly diverse in Andean páramos (Vuilleumier 1986, Luteyn 1999). Some high-altitude areas in the northern Andes are quite arid, but have also frequent fogs. In Venezuela, these "desert páramos" are the areas of highest density of giant rosettes (Monasterio 1980).

So far, there seems to be some correlation between the rosette form and foggy environments in South America. But the pattern is not so straightforward. In the Ecuadorian Andes, giant rosettes are restricted to the most humid páramos (Ramsay and Oxley 1997). The lomas formations of the coast display a high variability in their structure. In some areas there are composed of herbs, while other lomas are characterized by trees (Rundel *et al.* 1991). It has been reported that lomas plants with other morphologies other than rosettes (trees, shrubs and arborescent cacti) are able to condense moisture and to conduct it to the soil in large quantities (Ellenberg 1959). As a result, the fog belt in these fog deserts keeps a large density and diversity of plants of different growth forms (Rundel *et al.* 1991). By looking at our data, it seems that both shrubs and cacti are slightly more abundant and diverse at the montane rosette scrub than would be expected from their respective fitted curves. However, this effect is not significant, and the rosette's response is much stronger, as the dominance indices show.

Rosettes achieve significant amounts of stem flow at shallower rain-events than other morphologies (Ramírez de Arellano 1996). This means that, in environments with massive fog-inputs, such as lomas, plants with different forms may also get soaked and conduct large amounts of water to the soil. Rosettes have an advantage only when water availability is small. By looking at the distribution of rosette formations in Northern Chile and Peru, it becomes obvious that bromelian and tillandsian lomas occur at the margins of the fog belt (Ellenberg 1959, Rundel and Mahu 1976, Rundel *et al.* 1991, Rundel and Dillon 1998). Slight variations in the altitude of the atmospheric inversion layer should result in periods when fog is unavailable near the borders of the fog zone, while in the core of this belt humidity seldom falls below 80% for six months (Rundel *et al.* 1991). Rosettes in the borderline zone may be using eventual or shallow fog events that are inaccessible to plants with other architectures.

The present study shows the widespread existence of the montane rosette scrub at Mexican drylands. As it becomes obvious from the case at San Francisco, the term "montane" makes no reference to high altitude. Rather, it alludes to the topographical relief that plants need to reach the clouds and fogs that otherwise would follow their path without being harvested. Other communities of fog-harvesting rosettes such as the South-American lomas are also known to be associated with topography (Rundel *et al.*

1991, Rundel and Dillon 1998). From our data in the Tehuacán Valley and our direct observations in the Sierra de San Francisco, it is now clear that rosettes develop preferentially at altitudes with large fog inputs, and it is likely that the same phenomenon occurs elsewhere. While succulence might have been an important innovation for the colonization of xeric environments by desert rosettes, the rosette architecture by itself may also alleviate the water shortage by enabling the exploitation of fog, a novel resource in the evolution of these plants.

Conclusions

1. In mountainous slopes in Mexican deserts there is a marked association between the abundance and richness of succulent rosette species and altitude, with maximum values observed on well-delimited elevational belts. These formations are defined as montane rosette scrub.
2. Other life forms, such as stem-succulent cacti or woody shrubs, do not show this mid-elevation pattern of increased richness and abundance. Cacti tend to increase towards the lower, more arid altitudinal end of the gradient, while shrubs do not show a predictable trend in abundance or species richness.
3. In different sites, the montane rosette scrub is composed of different species, frequently of widely different taxonomic origins, a fact that suggests that the succulent rosette morphology is indeed an adaptive response to environmental conditions prevailing in the mid-slopes.
4. The elevational ranges where the montane rosette scrub occurs usually coincide with areas where clouds and fog accumulate. Because some rosettes have been reported as excellent harvesters of low-intensity rains and —probably— of fogs, it seems very likely that the succulent rosette morphologies are associated with cloud belts because of their high capacity to harvest fog.
5. Our micrometeorological measurements indicate that fog harvesters growing within a cloud belt can increase their water supply by 10–100%. Outside these belts, the increase is negligible.
6. Fog-harvesting plants are common in coastal deserts such as Baja California, Atacama and the Peruvian coastline, and also in the mid-ranges of many dry tropical mountains, where clouds tend to concentrate. Desert rosettes constitute one of the most common fog-harvesting growth-forms.

Acknowledgments

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Plate 1. Views of the four study sites (a) Tehuacán Valley, Puebla, (b) Sierra de El Doctor, Querétaro, (c) Barranca de Metztitlán, Hidalgo, and (d) Sierra de San Francisco, Baja California Sur at an altitude of 400 m. Note the fog in Tehuacán and El Doctor, and the high abundance of epiphytes in San Francisco.

a)   Tehuacán Valley

b) Sierra de
El Doctor

Plate 1 (Continued)

c) Barranca de Metztitlán

d) Sierra de San Francisco

CAPÍTULO 2.

THE NARROW LEAF SYNDROME:
A FUNCTIONAL AND EVOLUTIONARY APPROACH
TO THE FORM OF FOG-HARVESTING PLANTS.
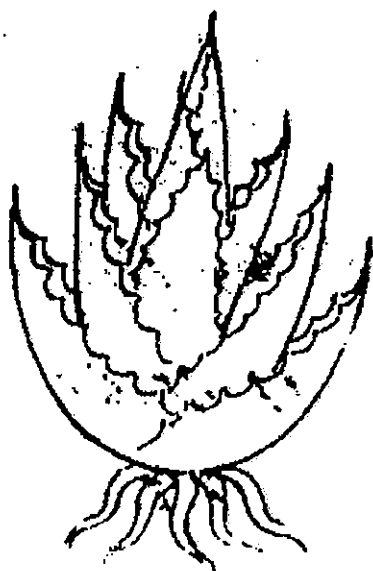
"Maguey o *Metl*"
Códice Florentino

Running head: The narrow leaf syndrome

TITLE: THE NARROW-LEAF SYNDROME: A FUNCTIONAL AND EVOLUTIONARY APPROACH TO THE FORM OF FOG-HARVESTING PLANTS

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ABSTRACT

1. Several plants that use fogs as important water-sources have a rosette growth habit. The performance of this morphology in relation to fog interception has not been studied. Some first-principles from physics predict that narrow leaves, together with other ancillary traits (large number and high flexibility of leaves, caudices, and/or epiphytism) which constitute the "narrow-leaf syndrome," should increase fog-interception efficiency. This was tested using aluminum models of rosettes that differed in leaf length, width and number and were exposed to artificial fog. The model was validated using seven species of *Tillandsia* and five species of xerophytic rosettes.

2. The total amount of fog intercepted in rosette plants increases with total leaf area while narrow leaves maximize interception efficiency (measured as interception per unit area). The range of forms is constrained because wide-leafed rosettes can only have a few blades. Within this physical constraint, both net fog interception and interception efficiency are maximized by a large number of narrow leaves.

3. Atmospheric *Tillandsia* species show the narrow-leaf syndrome. Their fog interception efficiencies were close to the ones predicted by our model. In the larger xerophytic rosette species, the efficiency was greatest in plants showing the narrow leaf syndrome.

4. The adaptation to fog-harvesting in several narrow-leaved rosettes seems to be phylogenetically convergent. We tested convergence using comparative methods in 31 xerophytic rosette species, and we examined the ecological distribution of these plants in relation to fog availability in the environment.

5. There was a significant evolutionary tendency towards the development of the narrow-leaf syndrome in xerophytic rosettes that grow at higher altitudes where fog is frequently available. Xerophytic rosette plants with narrow leaf morphologies are major vegetation components of cloud belts in arid mountains, where large amounts of fog are available.

Keywords: fog, rosette, xerophyte, functional morphology, comparative method, phylogeny, montane rosette scrub, nebulophyte.

INTRODUCTION

While in most plants the main source of water is rain, several species have resorted to the utilization of fog. Most of them live on environments where rainwater is unavailable, either because rain is scarce, or because soils are unable to retain it. We suggest the term *nebulophytes* for species where fog is an important water source. Such is the long-known case of several epiphytic bromeliads (Mez 1904, Smith and Downs 1974, Martin 1994), but nebulophytes may also be large ground-living plants. For instance, several trees, shrubs, and columnar cacti are nebulophytes from the Atacama and Peruvian Deserts, hyperarid areas where fogs are frequent (Rundel and Mahu 1976, Halit 1984, Rundel *et al.* 1991). We have shown that large rosette xerophytes from North-American deserts, such as some Agavaceae and Nolinaceae, occur in large numbers in arid mountains where fog is a very important source of water. It is likely that those plants are nebulophytes too (Martorell and Ezcurra in press).

Many nebulophytes, both epiphytes and xerophytes, show the same rosette habit. The reason for this may be that rosettes resemble funnels that conduct water to the plant's roots. The stem flow of some Agavaceae is highly efficient, even at very shallow (1 mm) rain events (Gentry 1982, Ramírez de Arellano 1996). The flow of water towards the base of the plant may also be crucial for those bromeliads that store water in a central tank (pitcher plants). Since fog may be conceived as a light rain, rosettophyllism can be viewed as a trait that allows the utilization of fog, which is inaccessible to other plants. The fact that fog can cause significant stem flow in rosettes can be ascertained from the large amounts of liquid found in the tanks of some Peruvian-desert bromeliads (Rundel and Dillon 1998). However, several epiphytic Bromeliaceae absorb humidity directly at the leaf surface, and their roots serve merely as holdfasts (Smith and Downs 1974, Martin 1994). Thus, they constitute a group of rosettes where stem flow may not contribute to water capture.

The role of the form of rosette plants on fog-water interception, rather than on its subsequent conduction to certain parts of the plant, has not been studied. Since rosette morphology itself is related to stem flow, other morphological traits must be taken into account when assessing fog-interception efficiency, such as leaf size or the presence of caudices. In this sense, a clear pattern arises: It has been noted that the nebulophytic Bromeliaceae have very narrow leaves (Benzing 1990). Plants with this attribute are known as "atmospheric" bromeliads, and have evolved several times, at least within the genus *Tillandsia* (Gilmartin 1983). Nebulophytic lichens and mosses also have thin thalli, a trait that Larson (1981) has shown to increase water uptake rates at the plant's surface. Our field observations suggest that nebulophytic Agavaceae and Nolinaceae also have narrow leaves. The reiterated convergence of narrow leaves or thalli suggests that it might be an adaptive trait perhaps related to fog utilization. However, it is unlikely that Agavaceae or Nolinaceae may have a rapid, if any, water uptake at the leaf surface. Larson's (1981) explanation can be discarded for these plants, and an alternative hypothesis is needed. In this paper we suggest that the narrow-leaf syndrome (in addition to enlarging water-absorption rates in some plants, as it happens in lichens and mosses) is an adaptation that increases the fog interception of nebulophytes.

As a result, there must be some association between plants showing the narrow-leaf syndrome and fogs in natural conditions. We have demonstrated the existence of "montane rosette scrub" characterized by a high density and diversity of rosettes in arid

zones with large fog inputs (Martorell and Ezcurra in press). So far, we have not studied the factors that determine the membership of different rosette species to that formation. In this paper we explore the prediction that rosette plants showing the narrow-leaf syndrome should be more frequent in the montane rosette scrub.

To tackle questions dealing with adaptation, two methods may be followed: The homology and the convergence approaches (Harvey and Pagel 1991, Coddington 1994, Pagel 1994, Wenzel and Carpenter 1994). The supporters of each mode have frequently claimed that theirs is the only valid method for demonstrating adaptation, but we believe both approaches are complementary, and assess the same problem from the two viewpoints. According to the homology approach, a trait can be proved to be adaptive if it increases the performance of the organisms that show that trait. To test this hypothesis, meticulously detailed studies on the evolution of the trait are often needed. This results in a lack of generality, because the evolution of a trait on any species is a "historical unique" (Coddington 1994). On the other hand, the convergence-method supporters hold that adaptation can be shown through the repeated evolution of the same trait in different taxa as a result of the same evolutionary pressures. Because of its nature, the convergence approach has the advantage of generality. However, as a correlative study, convergence cannot establish a clear causal relation between the traits and the hypothetical pressures that shaped them, but it does provide strong evidence to discard alternative explanatory factors that are not correlated with the hypothesized ones (Coddington 1994, Wenzel and Carpenter 1994). A highly widespread convergence rules out exaptation as highly unlikely, and therefore evinces adaptation rather than mere adaptive value (Harvey and Pagel 1991, Pagel 1994).

In the present study we need both methods. The convergence approach alone cannot tell between Larson's hypothesis (high rate of water uptake) and ours (high fog interception efficiency). We need the type of detailed information on performance that is required by the homology approach. However, this method is unable to embrace and analyze the widespread convergence that we observe. Convergence allows us to establish the narrow-leaf syndrome as a general phenomenon, and generality is needed to understand phenomena at the community level, such as rosette scrubs.

The homology approach requires a measure of performance. It can be defined, in terms of fog interception, as the net amount of water gained per unit time. This is of course of great importance for nebulophytes since they often live in arid environments. However, while a few milliliters of water may be enough for a small plant to live, very large plants may find this quantity to be scarce. Thus, we define a second measure of performance, efficiency, as the amount of water gained per unit of time in relation to total leaf area. The use of leaf area is both an estimator of plant size and of the amount of resources (plant surface) invested in fog-catchment.

If the narrow-leaf syndrome is related to fog use, it should render better efficiency. As we shall see, physical laws predict that narrow surfaces should catch more fog-droplets than broad ones, and therefore be more efficient.

The physics of fog interception

The air moves the humidity that constitutes fog, so some aerodynamics is needed in order to understand its usage by plants. Air moves at a lower speed as it gets closer to surfaces, forming an envelope of nearly-still air around objects, known as the boundary layer. The thickness of the boundary layer depends both on the wind speed

and on the size of the object. For a flat surface, such as a leaf, the following relationship holds:

$$\delta^{bl} = 4\sqrt{\frac{l}{v}} \qquad (1)$$

where δ^{bl} is the thickness of the boundary layer in millimeters, l is the size of the surface in the downwind direction in meters, and v is the wind speed in m s^{-1}. This means that large leafs have thicker boundary layers (Nobel 1991).

Fog is composed of water droplets that must cross the boundary layer before they make contact with the plant's surface. These droplets have an average size of 20 µm, so they have a large surface/volume ratio (Jones 1992). When small particles cross the still-air boundary layer, their large surfaces are subject to strong friction forces, while their reduced mass keeps little kinetic energy of its own. As a result, the fog droplets are easily arrested by the boundary layer before they impact the plant surface. Only a small fraction of the water-drops, known as impaction efficiency, finally collides with the plant. Impaction efficiency is inversely proportional to the thickness of the boundary layer (Jones 1992).

Turbulence has an important effect on impaction efficiency. In laminar air-flow, movement is mostly parallel to the leaf surface, while in turbulent eddies the motion occurs in all directions. A water droplet has little chance of impacting a surface if it moves parallel or oblique to it, since it must move a larger distance through the boundary layer. If movement is perpendicular to the surface, as in certain areas of eddies, the droplet crosses the still-air layer following the shortest possible trajectory. That is why aerodynamically rough bodies, which induce turbulence, have large impaction efficiencies (Jones 1992). The movement of the leaves in the wind also increases turbulence.

So, three factors may facilitate fog-water transfer to plants: First, having small or narrow leafs results in thin boundary layers. As we have pointed out, many epiphytes that are known to use fog have this kind of leafs, the same as some xerophyte rosettes such as *Dasylirion* spp. or *Agave striata*. Second, fast winds, which reduce boundary layers and provide sufficient kinetic energy to droplets. Since wind-speed increases with distance from the ground, rosettes should be placed away from the soil level. This may be achieved either by having a stem or caudex, as in some *Yucca* and *Nolina,* or by growing on branches of other plants, that is, as in epiphytes. Third, turbulence induction by means of complex, aerodynamically-rough surfaces, such as many-leafed rosettes. Flexible leaves that whisk in the wind also promote turbulence.

We have used thin leaves as the main characteristic to describe the morphology of certain plants. From physics we may predict that three other characters (distance from the ground, flexibility of the leaves, and a large number of them) constitute ancillary traits that should occur together in efficient nebulophytes. These four attributes constitute what we have named the narrow-leaf syndrome.

For this study we measured the fog-interception efficiency of rosettes with different morphologies. We were especially interested in the effects of three attributes, number, length and width of leafs, because of their expected effect on boundary layer thickness and on turbulence. The classical homology approach demands sister taxa, with and without the traits that are thought to be adaptive, to be compared. However,

several other traits change from species to species, and they may have an effect on fog-capture. To solve this problem, we used aluminum models exposed to artificial fog to evaluate the effect of length, width and number of leaves. To validate our results, they were compared to data obtained from living plants of the genus *Tillandsia* (Bromeliaceae), to which the same method was applied. The taxa were selected for their wide differences in the same three attributes. This genus is an interesting system to address this question, since it shows a large variation on water usage and morphology: For some species stem flow is very important, as for the pitcher plants already discussed. Other taxa take in water at the leaves (the so-called atmospheric *Tillandsia*), and yet other species have abandoned the ancestral rosette habit.

Once the adaptive value of the narrow-leaf syndrome is established, its generality is to be established by means of the convergence approach. This method requires the comparison of attributes between species by statistical procedures. Since species are not independent data, we need to include phylogenetic information into the analysis. A set of appropriate comparative methods is available for that purpose (Harvey and Pagel 1991). For this part of our study we used xerophytic rosettes, because they come from a larger set of families than the epiphytes, allowing us to achieve a greater level of generality. Finally, we tested the hypothesis that narrow-leafed rosettes should occur mainly at the areas where fog is available, that is, at the montane rosette scrub.

METHODS

Fog-interception modeling

Aluminum models

To test the hypothesis that rosettes with many thin leafs are the best fog interceptors, we used artificial models. Using models overcomes the difficulty of finding different plant species that differ in the characteristics we are interested in, without showing simultaneous changes in other morphological variables. We chose aluminum for building the rosette models because it is a light material that allowed the precise measurement of water interception.

Because of the non-linear effect that size was expected to have on water interception (see eq. 1), it was important to use models of at least three different sizes. Leaves were triangular, with lengths of twelve, eighteen and twenty-four cm. For each size, three leaf-form variants were constructed. Leaf form was defined as the ratio of length to width. Models with larger form indices had more leafs, so the overall area was the same for all models of the same size. This was achieved by means of form indices of 2.67, 4 and 8 (Table 1). Finally, for each combination of leaf length and form, two variants were assembled, one with twice as many leafs as the other.

Fog was simulated by means of a "Hurricane" 2790 fogger (Curtis DynaFog ltd., Westfield, IN. USA). The device was placed inside a wind tunnel, in order to have a uniform wind stream carrying the water droplets against the models. However, the wind flow produced by the fogger inside the tunnel induced a very turbulent fog stream. The flux produced by the device alone was more uniform, so simulations were carried without a tunnel in a closed, windless environment. The distance between the fogger and the models was 3 m, where the size of the fog droplets was 5-50 µm. To obtain a

measure of weight change immediately after the application of the experimental fog, the models were mounted on top of a weighing scale. To avoid the boundary layer of the ground and the interference of the weighing scale, each model was placed 25 cm above the balance, attached to a cubic, thin-wire structure that induced minimal perturbations on the fog stream. The aluminum rosettes were exposed to the fog for one minute (about 310 ml of water droplets), and the change in its weight, due to intercepted water, was then measured. The amount of water intercepted by the wire structure alone was subtracted from the whole data set. No dripping from the model was observed.

Table 1: Number of leaves in the eighteen aluminum models used in fog simulations

Leaf density	Leaf length	Leaf form index[1]			Total area
		2.67	4	8	
Low	12 cm	12	18	36	648 cm^2
	18 cm	12	18	36	1458 cm^2
	24 cm	12	18	36	2592 cm^2
High	12 cm	24	36	72	1296 cm^2
	18 cm	24	36	72	2916 cm^2
	24 cm	24	36	72	5184 cm^2

[1]Leaf form index is the ratio of leaf length to width

During the transport of particles from the fogger to the models, evaporation can potentially change the size of the water droplets. The amount of evaporation should change with relative humidity, which, in turn, depends both on air temperature and the amount of water in the atmosphere. These variables were expected to change with time, so the models were sequentially exposed to fog in blocks, allowing us to remove the effect of the changing relative humidity. All the levels of each morphological factor were randomized and were represented the same number of times in each block, to form a quasi-Latin square design (Cochran and Cox 1957). The plan was replicated four times.

As a measure of the aluminum model's performance we used the total amount of water captured. The relationship between size and boundary layer thickness follows a power function (eq. 1), so the data on morphology (leaf width, length and number) and water interception were both log transformed. The results were subjected to an ANOVA. We used GLIM 4.0 (Royal Statistical Society 1992) to perform model simplification following the procedure recommended by Crawley (1993), and we tested the ANOVA's assumptions using STATISTICA (StatSoft 1993). The resulting equation was used as a mathematical model for net interception, and was divided by total leaf area to produce a model for interception efficiency.

Experiments with live bromeliads

Seven species of *Tillandsia* were selected from the Sierra Mazateca and the Mixteca Alta Mountains in Oaxaca, southern Mexico. The chosen plants ranged from *Tillandsia imperialis*, a tank bromeliad with very broad leafs (leaf form index = 2.8) to the "atmospheric" *T. chaetophylla*, which displays a few thread-like leafs (Leaf form index = 400). The other species selected were *T. plumosa, T. concolor, T. butzii, T. recurvata,* and *T. usneoides.* The last two species do not show the typical rosette morphology of

the genus, showing instead long internodes (Table 2). Nomenclature follows Smith and Downs (1974).

Table 2: Morphological traits of the seven species of *Tillandsia* used in the study.

Species	Leaf form index[1,2]	Number of leaves[1]	Other traits
T. butzii	79.0	8.3	Bulbous sheaths.
T. concolor	12.3	33.3	Succulent blades
T. chaetophylla	378.8	37.5	Succulent sheaths.
T. imperialis	3.7	19.0	Central tank; glabrescent blades.
T. plumosa	44.9	148.0	Long hair-like trichomes; succulent sheaths
T. recurvata	47.3	12.0	Non rosette; densely pubescent.
T. usneoides	68.7	24.5	Non rosette; densely pubescent.

[1]Values are means for the three plants employed.
[2]The leaf form index is the ratio of leaf length to width.

The plants were exposed to fog in the same way as the aluminum models. The order of exposure was selected randomly. Three replicates were conducted using different individuals from each species. Because some of these species are clonal, only one ramet per clone was used. After the experiment concluded, the length and width of three fully-developed leafs of each ramet were measured, and the total leaf area was measured using a ΔT area meter (delta-T devices, Cambridge, UK). In some species the leaf had a wide sheath. In such cases (*T. plumosa*, *T. butzii* and *T. chaetophylla*), sheaths form a tight bundle similar to the tank of other *Tillandsia* or to the heavy stem of xerophytic rosettes, so only the exposed leaf blade was measured.

Model validation

The mathematical model was validated by comparing the predicted and observed interception efficiencies of the species of *Tillandsia*. The mathematical model's predicted efficiencies were calculated using the observed length, width and number of leaves in each plant. We expected to find a high correlation between predictions and observations if our model was realistic. As a measure of accuracy we used the percentage explained by the model of the variation in *Tillandsia* interception efficiency:

$$R^2 = 1 - \frac{\sum(O_i - E_i)^2}{\sum(O_i - \overline{O})^2}$$

where R^2 is the proportion of variance explained, O_i is the ith observation, E_i the corresponding expected datum calculated from the model, and $\overline{O}$ the mean of all observed values.

The predicted data accounted only for the effects of leaf size, form and number, because they are based upon aluminum models that only differ in those attributes. The observed data reflected those same effects plus the effects of other traits, which can be assessed by means of the differences between predicted and observed data. We used the *Tillandsia* species to test the role of the rosette morphology *per se* on fog interception. We applied a Mann-Whitney test over the differences between observed and expected efficiencies, comparing *T. usneoides* and *T. recurvata*, which are not rosettes, against the rest of the species.

Experiments with xerophytic rosettes

The results obtained from the aluminum models are only valid within the subset of the morphological space explored. Extrapolations to xerophytic rosettes are possibly inaccurate because their real morphologies may be quite removed from the ranges of the models: leaves of two meters compared to 24 cm, or several hundreds of leaves compared to 72. Besides, unlike *Tillandsia*, xerophytes cannot take water through the leaves, so the efficiency needs to be measured in terms of the amount of water that flows from the plant into the soil.

We selected five species with contrasting morphologies: *Agave kerchovei, Agave salmiana, Agave stricta, Brahea nitida* and *Dasylirion acrotriche.* Five plants from each species were selected at random from an area near the city of Tehuacán in Central Mexico. In each individual, dead leaves were removed from the base of the plant. A fabric sheet was placed over the soil beneath the plants. A layer of liquid impermeable sealant was applied to the cloth, pasting it to the base of the plants. Thus, all of the stem flow was collected in the waterproof basal cover. We simulated fog with a backpack sprayer. The flux of the sprayer was not uniform; it tended to form a cone with more droplets on the sides. After some experiments, we determined that a continuous circular movement damped a flat area uniformly. Fog was simulated for fifteen seconds at a distance of two meters from the plant, moving the nozzle as described. The water on the plants was left to flow for one minute. After that, water was gathered from the waterproof collector with previously weighed paper sheets, which were weighed again after collection. The difference in weights was transformed into water volume.

As was the case with aluminum models, we were interested in measuring efficiencies relative to leaf areas. However, the total leaf area of the selected plants could not be accurately estimated because of the large number of leaves and the difficulty in tearing them apart. Thus, efficiency was standardized by the area exposed to the fog, estimated as the product of the height and width of the whole plant. In a uniform horizontal fog flux, this efficiency will estimate the amount of fog intercepted and conducted to the soil, out of a given and constant amount of fog available in the atmosphere. The observed efficiencies were compared to the expected ones in the same way as was done with the *Tillandsia* species. Efficiency was also compared with a plant form index derived from a PCA (see below). This was done in order to evaluate if a multivariate index of "form", as measured by PCA, was also related to fog interception and stem flow.

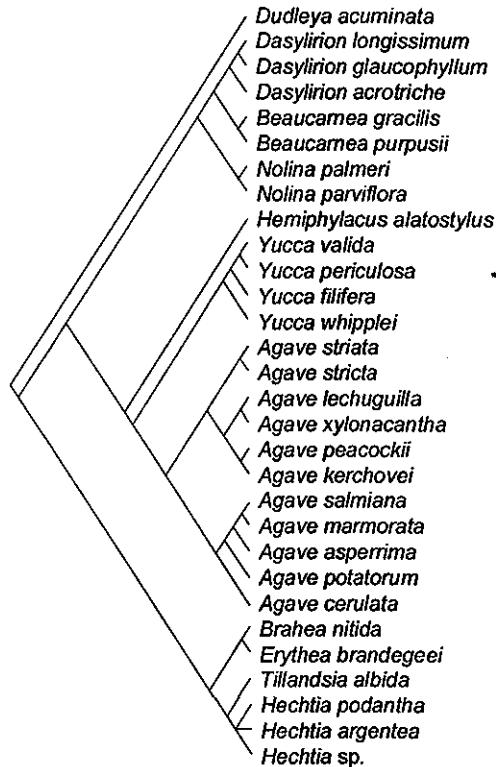**Comparative analysis of rosette morphologies**

Phylogenetic relationships

To test how widespread the convergence of rosette species towards the narrow-leaf syndrome is, we used data from four localities in Mexican arid zones. In each zone one mountain was sampled along its whole altitudinal gradient, recording the density and species of all the rosette plants found in three replicate transects placed at 100 m altitude intervals (see Martorell and Ezcurra in press for details). In total, rosette plants from six families were found. The most important ones were Agavaceae and Nolinaceae, but also Bromeliaceae, Crassulaceae, Arecaceae and Hyacinthaceae were present.

The study of adaptation based on a convergence approach requires a set of independent data, which is usually produced taking into account the phylogeny of the studied species. No single study has undertaken with the required detail the phylogenetic relationships within and among the six families we found. To build a cladogram useful for our purposes, we used taxonomy as well as phylogenetic data from several sources. The taxonomic information for the genus *Agave* down to series was based on Gentry (1982). The same author points out that in the series *Marginatae, Agave xylonacantha* and *A. lechuguilla* are close relatives, so we placed them in the same clade, while *A. peacockii* was derived from *A. kerchovei* thus forming a second clade. Within the subgenus *Agave,* species from several series were found. The relationships between them are based on the work of M. Tambutti on floral and vegetative traits (pers. comm.). Several authors agree that the series *Striatae* is basal to the genus (Gentry 1982, Eguiarte 1995). For the genus *Yucca* we used the work of Clary and Simpson (1995). Bogler (1995) has studied relationships within the Nolinaceae. Finally, the relative position of families in the cladogram was taken from Eguiarte (1995), except for the Hyacinthaceae (*Hemiphylacus*), which was considered as a sister taxa of the Agavaceae based on genetic and serologic information (Hernández 1995, Eguiarte pers. comm). The resulting cladogram was fairly well resolved, showing only one polytomy at *Hechtia* (Figure 1).

Morphometric analysis

We were interested in evaluating the four ancillary traits related to the narrow-leaf syndrome. The first, leaf form, comprised measurements of leaf length, width and thickness. The second, distance from soil, was evaluated by the presence or absence of a well-developed caudex, a trait frequently related to the presence of a marcescent collar (*sensu* Mabberley 1986). A complex and/or compact spatial arrangement of leaves was taken as a measure of the third trait: aerodynamic roughness. Thus, the following estimators were also included: number of leaves, packing of leaves measured as the number of Fibonacci series (parastichies), and the mean and variance of the angles of the leaves. We also recorded the presence of ornamentations such as grooves or striations, which increase boundary layer thickness. The curvature of leaves, related to stem flow, was also evaluated.

Figure 1. Phylogenetic relationships among 32 species of xerophytic rosette species (see text for details).

Dudleya acuminata
Dasylirion longissimum
Dasylirion glaucophyllum
Dasylirion acrotriche
Beaucarnea gracilis
Beaucarnea purpusii
Nolina palmeri
Nolina parviflora
Hemiphylacus alatostylus
Yucca valida
Yucca periculosa
Yucca filifera
Yucca whipplei
Agave striata
Agave stricta
Agave lechuguilla
Agave xylonacantha
Agave peacockii
Agave kerchovei
Agave salmiana
Agave marmorata
Agave asperrima
Agave potatorum
Agave cerulata
Brahea nitida
Erythea brandegeei
Tillandsia albida
Hechtia podantha
Hechtia argentea
Hechtia sp.

In fifteen individuals of each species, the eleven traits were recorded. The curvature, angle and number of leaves were measured on photos using IMAGETOOL 2.00 (Wilcox *et al.* 1995). For the Arecaceae, curvature and angle were measured at the petiole (which largely determines the position of the leaflets), but length, width, thickness and number were measured using the leaflets, because they are the main fog-catching areas.

In order to have a unique measurement of the form of the plants, the eleven traits were standardized (substracting the trait's mean and dividing the result by the trait's standard deviation) and then summarized by means of principal components analysis (PCA). We evaluated the significance of the axes by comparing the percentage variance explained by each axis against the predicted values of the broken-stick distribution (Jackson 1993). The significant axes were interpreted as form indices. As a measure of the degree of non-independence of indices due to phylogeny, the amount of variation accounted for by the different taxonomical levels was estimated by means of a nested analysis of variance (Harvey and Pagel 1991).

Comparative Analysis

The phylogenetic model and the form indices were used in a comparative analysis. The hypothesis to be tested was that rosette plants showing the narrow-leaf syndrome occur preferentially in areas with high fog availability.

In a previous work we reported the presence, at mid altitudes in four Mexican arid zones studied, of an area of large abundance and diversity of rosettes, which we have called the montane Rosette Scrub following Rzedowski's (1978) nomenclature for desert scrubland. This formation occurs in certain altitudinal belts on mountains where clouds are frequent. For each of the 32 succulent rosette species found in our study, the elevational centroid of its distribution was calculated as the weighted mean of the altitudes at which it was recorded, using abundances as weights. The altitudinal ranges were very different at each site, and the montane Rosette Scrub occurred at different elevations, invalidating direct comparisons between sites. To make data comparable, we used the differences between the centroids of the altitudinal distribution of each species and the median altitude where the montane Rosette Scrub occurred.

A relationship between the form index and the relative position of the elevational centroids was then sought. To do so, we used the method of independent comparisons. This method is appropriate for continuous variables, and makes use of all the information in the data set (Harvey and Pagel 1991). The significance of the association was assessed by means of a sign test (Grafen 1989).

Distribution of nebulophytic rosettes in drylands

For this last analysis we used only data from the Tehuacán Valley, because for this site we have the best data for fog distribution. There is a clear condensation belt at 1800-1900 m (Martorell and Ezcurra in press). Here we tested the prediction that plants showing the narrow-leaf syndrome should be relatively more abundant near areas with more fog. This was assessed by means of regression of the average of the mean form composition (mean form index of all the plants found at each transect) against altitude along the transect as independent variable. A quadratic term was tested in the regression analysis because a non-linear trend, with a maximum at 1800 m, was expected.

RESULTS

Fog-interception modeling

Aluminum models

Length, width and number of leaves had a significant effect on the amount of fog interception. No interactions were found to be significant (Table 3). The equation that best described the relationship between form and fog interception was:

$$i = 0.0026 l^{1.48} w^{0.502} n^{0.604} \qquad \text{(eq. 2)}$$

where l is leaf length in cm, w leaf width in cm, and n number of leaves. The resulting value of interception (i) is expressed in ml.

Table 3: Analysis of variance of the total amount of fog intercepted regressed on morphological traits (R^2=92.64).

Source	Sum of squares	Degrees of freedom	F	P
Leaf length	6.146	1	165.5	<0.0001
Leaf width	1.378	1	37.1	<0.0001
Leaf number	3.152	1	84.9	<0.0001
Blocks	0.531	11		
Error	2.117	57		

The efficiency is defined as the ratio of the total amount of water to the total leaf area. Because the aluminum leaves were triangular, efficiency (e) expressed in $\mu l/cm^2$ equals:

$$e = \frac{i}{A} = \frac{2i}{lnw} = 5.24 l^{0.477} w^{-0.498} n^{-0.396} \quad \text{(eq 3)}$$

We expected efficiency to be related to square-root functions (powers of 0.5) of the size of the leaves, because it depends on their boundary-layer thickness (eq 1). From eq. 3 this seems to be confirmed for both size parameters, leaf length and width. The regression was then repeated setting the power of length to 1.5 and of width to 0.5. This resulted in a minimum increase of deviance that was not significant (F=0.07, p=0.93), meaning that the simplification of the equations was compelling (Crawley 1993). The relationships of form to fog-interception and efficiency were:

$$i = .00266 \, n^{0.602} \, l\sqrt{lw} \qquad (4)$$

$$e = 5.33 n^{-0.398} \sqrt{\frac{l}{w}} \qquad (5)$$

Both equations predict that, to maximize the interception efficiency, leaves should be few and narrow, while the opposite is needed to optimize net interception (Figures 2 and 3). However, optimality in net interception seems unreachable, since there are no plants in nature that have many broad leaves; there is obviously no physical space to accommodate hundreds of leaves with large basal areas on the reduced stems of rosettes. Evolution should therefore maximize interception within the limits imposed by this constraint.

We then asked the question of how many leaves could be placed on the compact stem of rosettes given a leaf form. We assessed this problem graphically, using data for 36 species of xerophytic and epiphytic rosette plants. Arecaceae were not included, because leaflets are not directly inserted to the stem and, therefore, they may not show the same patterns as other rosettes. It is quite clear that several broad-leaved rosettes have few leaves, and that no one was found to contravene this pattern (Figure 4). This confirms that broad-leaved rosettes are restricted in their leaf number. A line passing through the origin (because of the tight cluster of points that is found near it) was drawn separating the areas with and without points in the graph. Only 5% of the species (Agave potatorum and Yucca filifera) lie above this line. This borderline was considered as predicting, for most plants, the maximum number of leaves that a species with a given leaf-form can have: If a rosette is to maximize its net interception, it should have

the largest possible number, or the broadest possible leaves within the constraints imposed by leaf width.

Figure 2: Net interception of fog in aluminum models with (a) 12 cm leaf length, and (b) 24 cm leaf length.
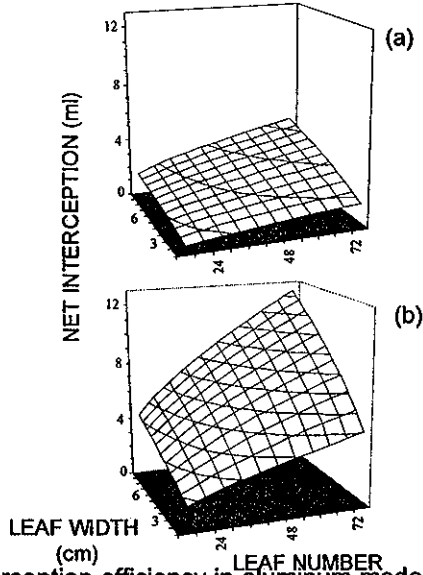

Figure 3. Interception efficiency in aluminum models with (a) 12 cm leaf length, and (b) 24 cm leaf length. Note that the origin in this figure is behind the projected surface.
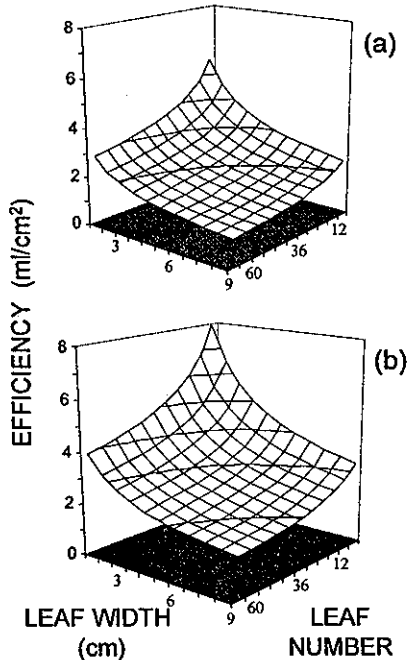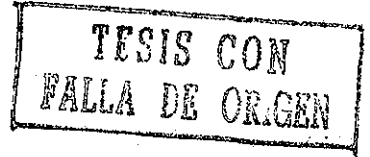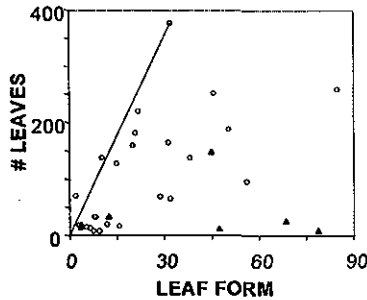

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Figure 4. Number of leaves in plants with different leaf forms: Form was defined as the ratio between length and width of the leaf. open circles represent xerophytic rosettes, black triangles represent *Tillandsia* spp. The line shows the approximate maximum number of broad leaves that can be accommodated around a compact stem.

Using eqs (4) and (5), we calculated the net interception and efficiency for borderline rosettes (i.e. plants having the maximum possible number of leaves). We found that, within the limits set by this physical constraint, having several narrow leaves maximizes plant performance compared to plants with few broad leaves (Figures 5 and 6). Because leaf number is limited by leaf width, plants with narrow leaves can accommodate more leafs and intercept more water. For this reason, and because of the effect of narrow leaves on boundary layer thickness, interception efficiency increases dramatically as width diminishes.

Figure 5. Highest net fog interception by plants modeled within the limits imposed by morphological constraints. The solid line corresponds to a leaf length of 24 cm, the dashed line to 18 cm and the dotted line to 12 cm. The numbers next to each curve represent the number of leaves that maximize interception for leaf widths of 1.5 cm (narrow leaves) and 9 cm (broad leaves).
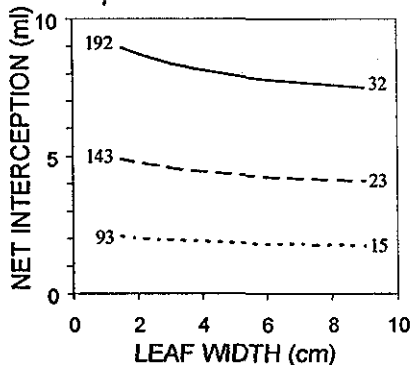
Model validation

The efficiency of bromeliads as predicted by equation 5 is highly correlated with observed values (r=0.82, p=0.0001, figure 7). However, the percentage of the bromeliads variance in efficiency explained by the model is quite low (20.0%). This may

be due largely to the inclusion of two non-rosette species. The Mann-Whitney test performed on the differences between predicted and observed data showed that non-rosettes were more efficient than rosettes ($U = 9$, $p = 0.020$), and, therefore, equation 5 would not be appropriate to predict their efficiencies. After removing *T. usneoides* and *T. recurvata* from the analyses, both the correlation ($r=0.91$) and the fraction of explained variance (64.5%) increased substantially. Notwithstanding this, the observed efficiencies of rosette bromeliads alone were still larger than the values predicted by our model ($t=3.21$, p=0.003).

Figure 6. Fog interception efficiency of plants modeled within the limits imposed by morphological constraints. The solid line corresponds to a leaf length of 24 cm, the dashed line to 18 cm and the dotted line to 12 cm. The numbers next to curves are the number of leaves that maximize interception for leaf widths of 1.5 cm (narrow leaves) and 9 cm (broad leaves).

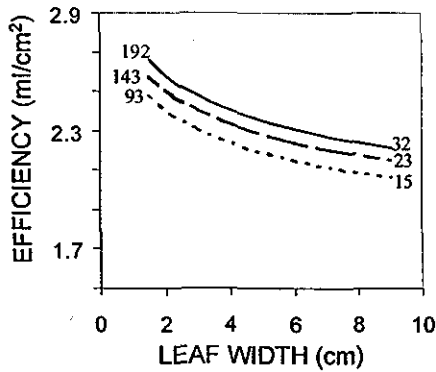Figure 7. Comparison between the observed efficiencies of seven species of *Tillandsia* and the efficiencies expected for aluminum models with the same form. The identity line shows the expected relationship if observed and expected efficiencies were equal. The species depicted are:◆ *T. butzii*, ● *T. chaetophylla*, ▲ *T. concolor*, ■ *T. imperialis*, ▼ *T. plumosa*, ◇ *T. recurvata* and □ *T. usneoides*.
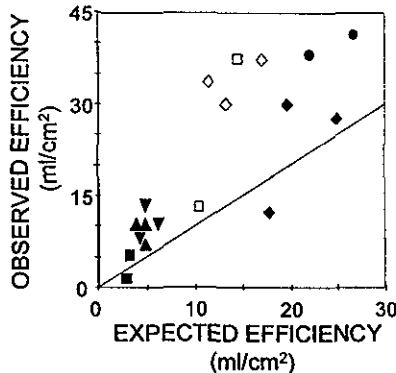
Experiments with xerophytic rosettes

The efficiency of large xerophytic rosettes showed large variation between species. The leaves of *Dasylirion acrotriche* intercepted large amounts of water, but moisture was sequestered at the marcescent collar, and therefore could not be quantified. For that reason this species was excluded from statistical analyses. Our mathematical model (eq. 5) showed a small, non-significant correlation (r=0.28 F=1.54, p=0.23) with the observed fog interception of xerophytes. However, efficiency was highly correlated with plant form measured with a multivariate index (see below).

Comparative analysis of rosette morphologies

Morphometric analysis

The first form index extracted by the PCA on the species × morphological traits matrix explained 35.7% of the total variation. All other axes were non-significant. The axis corresponds largely to the narrow-leaf syndrome. By looking at the signs of the loadings (Table 4), it becomes apparent that high positive values in the index correspond to plants with long, narrow leaves, while low values of the index correspond to plants with wide, thick, fleshy leaves. The ancillary traits are also present in plants that score high in this index: longer caudices, many leaves, no ornaments, and complex (aerodynamically rough) leaf distributions as measured by the Fibonacci number.

Table 4. Principal Component Loadings of the eleven morphological attributes of xerophytic rosettes used to calculate the multivariate form index.

Trait	Loading
Caudex	**0.85**
Collar	**0.74**
Leaf curvature	**-0.42**
Leaf number	**0.55**
Leaf density[1]	**0.57**
Leaf length	0.25
Leaf width	**-0.59**
Leaf thickness	**-0.75**
Mean leaf angle	0.12
Leaf angle variance	0.36
Leaf ornamentation	-0.33

[1]estimated by the number of contact parastichies (or Fibonacci number).

The numbers in bold indicate the traits that are more associated to the narrow leaf syndrome. The sign indicates if the character is positively or negatively associated to the syndrome

The species are not independent points. The nested ANOVA shows that two species in the same genus have very similar form index (80.2%, table 5). The PCA reflects this taxonomic bias by clearly separating the species belonging to different taxa down to the subgenus or series level (figure 8).

Table 5. Nested analysis of variance of the form index by taxonomical level.

	%	Cumulative %
Class	0.54	0.5%
Order (Class)	20.99	21.5%
Family (Order)	39.17	60.7%
Genus (Family)	19.53	80.2%
Subgenus (Genus)	9.55	89.8%
Species (Subgenus)	10.22	100.0%

Parentheses denote the taxon each group is nested in. The cumulative percent of variance explained can be interpreted as the degree of similarity between two randomly chosen species in that taxon

Figure 8. Ordination of 32 species of xerophytic rosettes on a Principal Components Axis (mutivariate form index). Species (i.e., multivariate data points) were grouped according to taxonomy. Species that have the narrow-leaf syndrome (large caudices and collars, high number of narrow, thin leaves arranged in dense whorls) dominate towards the right-hand side of the axis. Broad-leafed plants dominate towards the left-hand side. See Table 4 for details.
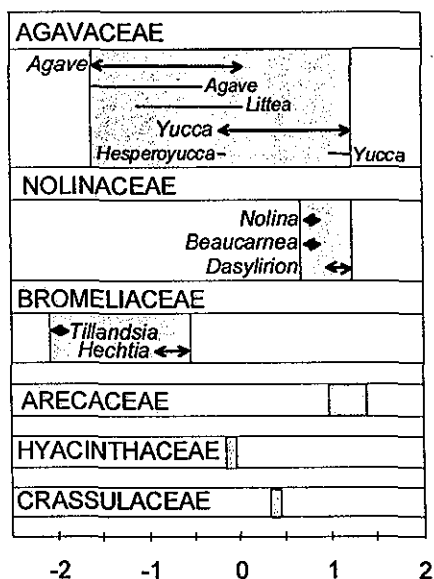
While equation 5 was unable to predict the observed efficiencies of large rosettes, the form index accurately did so ($r=0.76$). It was found that rosettes showing the narrow-leaf syndrome —i.e. with high form index scores— intercepted and conducted larger amounts of fog towards their bases ($F=23.25$, $p=0.0002$. Figure 9).

Figure 9. Relationship between the multivariate form index of four xerophytic rosettes and the amount of fog they intercept and conduct to the soil.
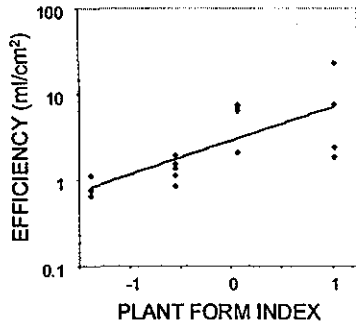
Comparative analysis

The method of independent contrasts revealed a significant relationship between form and altitude (sign test $n=24$, $p=0.049$). The sign-test comparison between the altitudinal range of the species and their multivariate form-index showed that rosettes with narrow leaves and their ancillary traits have evolved at higher altitudes.

Distribution of nebulophytic rosettes in drylands

The mean form composition of the rosette community increased with altitude, indicating that slender-leafed rosettes are dominant in higher elevations ($F=16.9$, $p=0.0005$). A significant non-linear term was found ($F=11.94$, $p=0.0024$), but the curve did not peak at 1800 m, the altitude with the largest fog input. Instead, the form composition seemed to level-off above 1800 m into narrow-leafed morphologies. That is, plants showing the narrow-leaf syndrome were distributed preferentially at higher altitudes. The rate of change in morphological dominance was larger at lower altitudes and tended to stabilize at higher altitudes (Figure 10).

DISCUSSION

Fog-interception modeling

In general terms, the hypothesis that the narrow-leaf syndrome is an efficient morphology for fog interception was largely confirmed. It was found that both aluminum models and *Tillandsia* species with large leaf-form indices had the best performances. However, a comparison of our predictions with the actual results is pertinent.

Aluminum models

As it was expected, efficiency is inversely related to the square root of the leaf width. This is clearly the result of the relationship between fog interception and the

thickness of the boundary layer. As predicted by equation (1), narrower leaves will have shorter surface lengths in the downwind direction, and will thus show thinner boundary layers. Leaf length, in contrast, had an opposite effect. The largest leaves showed a better performance. The reason for this behavior may become clear by noting that, during the fog simulations, it was observed that fog was intercepted mainly at the tips of the leeward leaves. It seems that, as the wind flow reaches the plants, the windward leaves both deplete its fog-contents and slow down its speed. The leaves that the wind reaches subsequently should have lower impaction efficiencies, as only the tips of these leaves project beyond the fog-shadow of the windward leaves.

Figure 10. Mean form composition of communities along an elevational gradient in the Tehuacán Valley, Mexico. The mean form composition was calculated as the average of the multivariate form indices for all the species found at a site, weighed by their abundance.
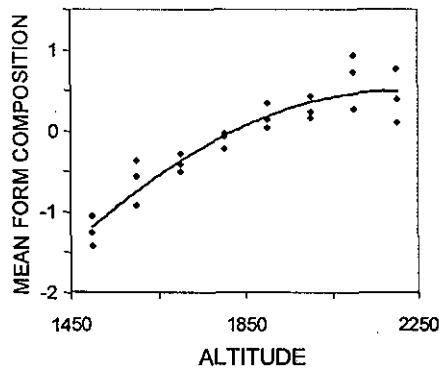
Everything else being equal, longer leaves will be more separated at their apices. Because most of the fog collection occurs at the tips of the leaves, it follows that longer leaves interfere less with each other, as there is more space between one tip and the next one for wind to recover its speed and for turbulent flow to mix the fog particles and recover the moisture that was extracted by the first leaf apex. The idea that longer leaves will receive higher wind speeds at their tips is supported by the fact that in our model (eq. 5) we found a direct relationship between interception efficiency and the square root of leaf length, while the boundary layer model (eq. 1) predicts that efficiencies (an inverse function of the layers thickness) are directly related to the square root of wind speed.

Equations 4 and 5 show an inverse relationship between net interception and efficiency; maximizing net interception reduces efficiency and vice versa (Figures 2 and 3). As we have already discussed, a large size increases both interception and efficiency, but having a few, slender leaves maximizes efficiency while broad, numerous leaves are best to enlarge net interception because it results in a large total surface. There is an obvious trade-off between having a large area and keeping a few narrow leaves. The only way to solve the problem is by having long leaves. Nebulophytes that achieve large areas by means of several leaves should also be under high pressure to

compensate fog-shading. Again, the solution is long leaves that reach out for unshaded, fog-rich air streams.

Model validation

Both our models and our field measurements show that *Tillandsia* with the narrow-leaf syndrome have much larger efficiencies, a result entirely attributable to their leaf form and number. This does not contradict Larson's (1981) hypothesis of fast absorption. In reality, both fog interception and absorption may be two factors that acted synergistically in the evolution on bromeliads, leading to the appearance of atmospheric *Tillandsia* and *Vriesea*. The same can be concluded for lichens and mosses with narrow thalli, and for the thin, velamentous roots that some Orchidaceae project into the atmosphere (Benzing 1990).

While the narrow-leaf syndrome is largely responsible for the high efficiency of atmospheric epiphytes, all the epiphytic species we studied showed larger interception than the aluminum model predicted. Trichomes may be largely involved in the process because they protrude beyond the leaf boundary layer, and increase the interception area. By means of a Mann-Whitney test we found that the glabrescent *T. imperialis* and *T. butzii* efficiencies where much closer to the model's predicted values than the rest of the species (U=9, p=0.019). In effect, no significant difference was found between observed and expected values in glabrescent plants (t=0.59, n.s.). This suggests that pubescence is the main cause for the difference observed between *Tillandsia* species and the aluminum models.

Non rosettes (*T. usneoides* and *T. recurvata*) had significantly higher efficiencies than rosettes, as shown by the Mann-Whitney test. This may be the result of a diminished fog-shadow effect, because the leaves, being apart from each other by means of long internodes, interfere less between them. Taking this into account, the rosette habit can be considered an ancestral, rather than adaptive, trait in atmospheric *Tillandsia*. It has been considered that a rosulate shoot was required for the evolutionary transference of absorptive role from root to foliage (Benzing 1990), but it may have become more of a burden for the most derived nebulophytes, which have therefore tended to form long internodes. The same is observed in lichens and mosses, where pendant forms with long internodes are better adapted for fog interception than non-pendant forms with short internodes (Kürschner and Parolly 1998, Kürschner and Frey 1999).

Experiments with xerophytic rosettes

The way different plants cope with the trade-off between leaf size and leaf number may be closely related to the way they use water. Net interception is of obvious importance for all plants. However, in atmospheric bromeliads, where water uptake takes place at the leaf, efficiency is a more appropriate measure of performance, since it is a function of leaf area. For xerophytic rosettes the process is quite different. A minimum amount of water per unit area is needed to achieve saturation and start stem flow into the soil. The total quantity of water driven to the soil will be directly related to net interception. Thus xerophytic rosettes living in foggy areas face both the need for high efficiency, as more efficient leaves will attain saturation earlier, and high net interception, as this will create a significant stem flow. The constraint on plant morphology (figure 4), and its consequences on efficiency and net interception (Figures

5 and 6), means that slender leaves are the best possible solution to the problem. Since several of these plants have very long leaves (nearly two meters in some Nolinaceae), they are able to increase their total surface —and therefore their net interception— by having several leaves, without excessive reduction in efficiency due to fog-shading. The maximization of efficiency in atmospheric *Tillandsia* and net interception in xerophytic rosettes is reflected in Figure 4, where it becomes clear that, for any given leaf-form, epiphytes will have fewer leaves than xerophytes.

A trait frequently found in *Tillandsia* and in xerophytes is leaf succulence. The plants that we studied grow in arid environments, with unpredictable pulses of rain, and water storage seems of great importance. The broadening of leaves to impound water should have a negative effect on interception efficiency, so the blades remain narrow with only the sheaths (*Tillandsia butzii, T. chaetophylla,* and *Dasylirion* spp.), or the stem (*Agave striata, Beaucarnea, Nolina,* and *Yucca*) widened for water storage.

Although more research that incorporates these subtleties is needed, several traits that we have discussed for epiphytes are also found in xerophytes. In the Nolinaceae leaves frequently have a tuft of fibers at their apex, and large filaments are found in the margins of the leaves of some Agavaceae and Arecaceae. These may function as the trichomes of bromeliads to increase fog interception. In several *Yucca* (*Y. filifera, Y. valida*) the internodes are relatively long, as it happens in *T. usneoides.*

The equations derived from the aluminum models were no significantly correlated to the efficiencies of xerophytic rosettes. This can be the result of the differences in the way of measuring both area and efficiency in the models and in the plants. It may also be an outcome of an invalid extrapolation of a mathematical model to much larger and leafier plants. However, if the prediction is numerically incorrect, it is qualitatively right. The plants with narrower leaves (*Agave stricta, Brahea nitida*) have much larger efficiencies than broad-leafed rosettes. This trend became obvious when we applied the multivariate form index (PCA).

Comparative analysis of morphologies

Phylogenetic relationships and morphometric analysis

The evolutionary processes have produced a wide range of forms in the xerophytic rosettes. As a result, there is a clear differentiation among taxa (figure 8), with a large morphologic similarity within taxa (table 5). The Agavaceae is the family that shows the largest morphological variation, with the genus *Agave* and *Yucca* clearly separated. Other families exploit smaller fractions of the morphospace. At least three families, Nolinaceae, Arecaceae, and a part of the Agavaceae (*Yucca,* subgenus *Yucca*), form a compact group at the extreme left of figure 8. We believe this constitutes evidence for a widespread convergence into a narrow range of morphologies. Atmospheric bromeliads (not included in this analysis) would be found morphologically close to this group. Several of the attributes of this polyphyletic set are the ones that we expected for nebulophytes: Narrow, long leaves in large numbers, with caudices and no leaf ornamentation. Leaves are curved towards the apex, so the water intercepted at the tips does not leak outwards (Table 4). Flexible leaves, another trait that is believed to optimize fog interception, were also found in Nolinaceae and Arecaceae. The co-occurrence of several traits in these groups confirms our idea that nebulophytic morphology fulfills the definition of a syndrome.

Comparative analysis

The independent-contrasts method reveals an evolutionary association between high altitudes and the narrow-leaf syndrome. This is in accordance with our hypothesis, for it means that the most efficient forms occur in areas where fog is most likely to be found. Some exceptions to the rule were found, such as some plants in the subgenus *Agave* (*A. salmiana* or *A. potatorum*) that have broad, succulent leafs and are found frequently in the montane Rosette Scrub.

By itself, the analysis does not elucidate the direction in which natural selection has acted. At the base of the mountains, increased temperature and, sometimes, reduced rains, are an important pressure for succulence. During the course of their evolutionary history, narrow-leaved ancestors could have evolved into large, broad-leafed succulents. In that case, the interception of fogs would not be an important evolutionary factor. This could have happened several times. The opposite, however, might also be true. We believe that evolution may have acted in both directions. For example, in the Agavaceae, the series *Striatae* of the genus *Agave* is morphologically very close to the subgenus *Hesperoyucca* of the genus *Yucca*. Both taxa are basal to their respective genera (Gentry 1982, Clary and Simpson 1995, Eguiarte 1995), and are at the center of our ordination diagram (Figure 8). It seems that *Agave* evolved into massive leaf succulents, invading the deserts, while *Yucca* developed the narrow-leaf syndrome moving towards higher altitudes.

We need, then, to clarify whether fog utilization is responsible for the selection of narrow leaves, or if it is the result of environments where the storage of water in large quantities is not necessary. We believe the former is correct because narrow-leaf rosettes have also evolved succulence, but not into massive leaf blades. The caudex stores large quantities of water in *Yucca* and in the Nolinaceae, remarkably so in the giant-stemmed genus *Beaucarnea*. *Dasylirion* stores water both in the stem and in greatly enlarged leaf sheaths. Agaves in the series *Striatae* are leaf succulents growing in the montane Rosette Scrub, but still have several, very narrow leaves. All these rosettes have confronted the problem of water impoundment without loosing the narrow-leaf syndrome. They did not become massive leaf succulents because, as nebulophytes, they evolved under the selective pressure for long, slender leaves.

Distribution of nebulophytic rosettes in drylands

The distribution of plants with different form indices over the elevational gradient in the Tehuacán Valley showed that the broad-leaved rosettes occur at lower altitudes. The plants that are better fog-interceptors increase rapidly up to 1900 m, where their relative abundance tends to level-off (Fig. 10). Although the fog is most abundant in a belt around 1700-1900 m, plants with the narrow-leaf syndrome are also abundant above the cloud belt.

CONCLUSIONS

1. The net interception of fog in rosette plants increases with leaf area. Thus, larger plants with several wide, long leaves intercept more fog. Fog interception efficiency, in contrast, is closely related to the thickness of the boundary layer on the leaf.

Because narrower leaves have thin boundary layers, the most efficient fog harvesting rosettes should have narrow and long leaves in small numbers.

2. There is a physical constraint in the number of leaves a plant may have. Wide-leaved rosettes can only have a few blades, while individuals with many leaves are only found among species with thin ones. Within the limits set by this constraint, both net fog interception and interception efficiency are maximized by having several narrow leaves. This attribute usually occurs in nature simultaneously with other ancillary traits (caudices, epiphytism, and/or flexible leaves) constituting a syndrome that characterizes some fog-harvesting species.

3. Atmospheric *Tillandsia* species show the narrow-leaf syndrome. Their fog interception efficiencies are close to the ones predicted by aluminum-rosette model on the basis of size, form and number of their leaves. Their efficiencies are enhanced by means of trichomes and long internodes. In the large xerophytic rosette species, the most efficient plants in terms of fog interception are also those with narrow leaves and their ancillary traits.

4. There is a significant evolutionary trend towards the narrow-leaf syndrome in xerophytic rosettes that grow in high altitudes where fog occurs frequently. These plants have developed succulence in several organs apart from the leaves, which allows the storage of water while keeping slender blades that are suitable for fog-harvesting.

5. The xerophytic rosette plants with narrow leaf morphologies (i.e., nebulophytes) are major vegetation components of the cloud belts in arid mountains. Fog-harvesting rosettes also occur at higher altitudes, but their abundances are lower.

AKNOWLEDGEMENTS

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DISCUSIÓN GENERAL

Cada juicio es un balanceo al borde del error —explicó
Leto—. Exigir el conocimiento absoluto es monstruoso.
El conocimiento es una aventura sin fin en los confines
de la incertidumbre.

Frank Herbert "Children of Dune"

¿Se trata de una versión poco informada de un maguey en
floración o de una hierba descomunal?
Relación de Tuzantla

En los capítulos anteriores se aborda, a fin de cuentas, la pregunta fundamental de la ecología según la definición clásica de Andrewartha (1961): ¿Cómo se distribuyen las rosetófilas en las montañas mexicanas? ¿Qué determina la abundancia y membresía de diferentes especies en las comunidades montañesas? La evidencia reunida apunta hacia la neblina como un factor de gran importancia, no sólo en los aspectos ecológicos mencionados, sino también en la dimensión evolutiva.

Se encontró una estrecha relación entre la presencia de cinturones de condensación o de nieblas costeras y la distribución de rosetófilas. En tales sitios se puede desarrollar una vegetación (o formación) caracterizada por la dominancia de plantas con forma de roseta. Denominamos a dicha comunidad "matorral rosetófilo montano". El término montano hace referencia la presencia de montañas necesarias para interceptar las nubes y neblinas, lo cual no ocurre necesariamente a grandes altitudes.

Las rosuladas que dominan el matorral rosetófilo montano presentan un conjunto de características morfológicas al cual hemos denominado síndrome de hoja angosta. Se encontró que éste constituye una tendencia evolutiva en las rosetas xerófilas, y que las plantas que lo presentan son mejores captadoras de neblina. Se trata de un proceso de optimización en el morfoespacio de las rosetófilas, dentro de los límites marcados por las restricciones evolutivas que dicha forma de crecimiento conlleva. Otras rosetas nebulófitas, como las bromeliáceas, presentan el mismo síndrome de hoja angosta. Es muy probable que también constituya una tendencia evolutiva en el grupo, como lo sugiere su repetida evolución en los géneros *Tillandsia* y *Vriesea* (Gilmartin 1989).

Al proponer que algunas de las grandes rosetófilas de las zonas áridas son nebulófitas, surge la inquietud de cuantificar la cantidad de agua de neblina que estas plantas pueden cosechar. Por razones técnicas, la medición directa del líquido resultó imposible. La solución fue la cuantificación indirecta a través de neblinómetros. Esto reveló que el recurso está disponible en grandes cantidades. Sin embargo, la cantidad de niebla interceptada depende fuertemente de la arquitectura del colector (Nagel 1956). Es obvio que un cilindro de malla de mosquitero es considerablemente distinto de un maguey. Esta diferencia resulta crítica dentro de nuestro discurso sobre el nebulofitismo. Por ello, se sometió a uno de nuestros colectores de niebla al mismo rocío empleado en los experimentos de campo descritos en el segundo capítulo (ver *methods: experiments with xerophytic rosettes*, p 15). El resultado es que la cantidad de agua colectada por la malla fue inapreciable, mientras que todas las rosetófilas mostraron un escurrimiento sustancial (figura 9). Esto significa que 1. Las rosetófilas pueden producir flujo caulinar aún con nieblas someras, y 2. Que las nieblas observadas en el campo debieron sobrepasar con mucho el umbral necesario para que se produzca el escurrimiento en las plantas. La evidencia con que contamos apunta a que las rosetófilas son extraordinarios escurridores de agua, tal como encontró Ramírez de Arellano (1996).

Por supuesto, todo lo anterior es válido para rosetas de talla considerable o caulescentes. Cerca del suelo, el aporte de neblina es reducido. Ello plantea el problema de la obtención de agua en plántulas, las cuales constituyen a menudo el estadio más susceptible del ciclo de vida de las suculentas. Por el contrario, una vez que una planta alcanza cierta talla, la probabilidad de que muera es muy reducida (Valiente- Banuet y Ezcurra 1991, Esparza 1998, López 1999, Quijas 1999, Contreras 2000). Curiosamente, estos mismos rasgos de la historia de vida pueden ser los responsables de que la forma de los individuos adultos se desempeñe mejor. En términos demográficos, se ha encontrado

que en las plantas xerófitas de larga vida la mayor elasticidad se concentra en la estasis de las etapas reproductivas (Esparza 1998, López 1999, Quijas 1999, Contreras 2000), lo que a su vez puede implicar mayores presiones de selección sobre los adultos (Van Tienderen 2000). De tal modo, si la forma de roseta es eficiente en los adultos, ésta sería seleccionada aún cuando no presente ningún valor en individuos infantiles.

Hay, sin embargo, dos fenómenos que pueden apuntar hacia un desarrollo muy temprano del nebulofitismo. El primero es observable en las nolináceas, las cuales desde muy jóvenes producen hojas largas y erectas, que pueden proyectarse más allá de la capa limítrofe del suelo y captar niebla. El segundo se registra en muchas de las agaváceas, bromeliáceas, crasuláceas y arecáceas estudiadas. Éstas se reproducen vegetativamente, situando a sus vástagos en la base de la planta madre, donde se colecta el flujo caulinar de la roseta plenamente desarrollada. Esta misma estrategia también se presenta en numerosas *Tillandsia*.

En esta tesis proponemos que, para alcanzar mayores estaturas y acceder a más neblina, las rosetófilas han desarrollado el hábito caulescente. Esto genera el problema del transporte del agua desde la base de la roseta hasta el suelo. En el caso de *Dasylirion acrotriche* mencionado en el capítulo dos, no se registró que el agua captada de la niebla llegara al suelo, aunque se le observó escurriendo por la hojas. El líquido seguramente quedó capturado en el collar de hojas marcescentes que rodea al tallo. En algunas plantas (*Cyathea*) se ha reportado que el agua secuestrada por el collar puede ser empleada *in situ* por la planta a través de raíces adventicias (Smith 1979). No tenemos evidencia de que esto ocurra en *D. acrotriche* debido a que es virtualmente imposible separar las hojas del tallo. Por otro lado, en un estudio realizado paralelamente con *Yucca periculosa* en el Valle de Tehuacán, encontramos que el collar marcescente es un excelente conductor del agua colectada por la roseta hacia el suelo. Además, la presencia del collar puede incrementar hasta cinco veces la captación y escurrimiento de neblina (Mandujano 2001). Es probable que, al menos en el caso de *Y. periculosa*, la retención de las hojas secas sea una característica adaptativa al nebulofitismo. Es interesante señalar que las rosetófilas de los páramos de altura presentan esta misma característica (Smith 1979, Monasterio 1986, Mabberley 1986), aunque su función no ha sido interpretada en relación a la cosecha de neblina.

Nuestros resultados señalan que la neblina puede ser un recurso de gran importancia en los desiertos altiplánicos. Fuera de los desiertos costeros, tales como el Atacama en Chile (Evans y Ehleringer 1994), el Negev en medio oriente (Kidron 1999), y el desierto californiano (Bailey 1966), la niebla ha sido francamente ignorada por los ecólogos de zonas áridas. Es innegable que el agua juega un papel fundamental en las zonas secas del globo, por lo que contemplar el aporte de la niebla puede ser clave. Por ejemplo, en todas las zonas estudiadas, el matorral rosetófilo montano se presenta en zonas de arbustos perennifolios o sub-perennifolios. Esto sugiere que la niebla puede determinar en cierta medida la distribución del chaparral en México. Numerosos estudios sobre la flora de la Baja y la Alta California han encontrado cierta relación entre la niebla y los matorrales costeros perennifolios (Shreve 1936, Mooney y Harrison 1975, Parsons y Moldenke 1975).

La morfología funcional nos ha llevado de la fisiología de las bromeliáceas a las comunidadess xerófilas, de la meteorología a las tendencias evolutivas. No cabe duda de que, como señalaban Ricklefs y Miles (1994), el fenotipo contiene gran cantidad de información sobre la ecología de los organismos.

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