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Rosette scrub occurrence and fog availability
in arid mountains of Mexico

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Abstract. Large succulent leaf rosettes are a characteristic life form in many deserts. In certain areas they become the dominant life form, creating a vegetation type indicated 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. We propose that some rosette-dominated formations of the Mexican mountains, namely the montane rosette scrub, occur in altitudinal belts around mountains where fog is abundant. We sampled four altitudinal gradients in mountains with different flora recording the abundance and richness of plants. At one site, the Tehuacán Valley, we also measured the quantity of fog along the gradient, below, above and in the rosette scrub for one year. We found that the abundance and richness of succulent rosette species are strongly associated with altitude, showing maximum values in the 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 altitudinal ranges where the montane rosette scrub occurs usually coincide with areas where clouds and fog form. 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: Agavaceae; Altitudinal gradient; Bromeliaceae; Cloud belt; Fog harvesting; Montane rosette scrub; Nolinaceae.

Nomenclature: Gentry (1982) for Agavaceae, Smith & Downs (1974) and Roberts (1989) for Bromeliaceae.

Introduction

The vegetation of the arid and semi-arid lands of Mexico has a large number of different associations (Rzedowski 1978) that form a complex spatial mosaic. In a relatively small area, a thorn woodland, a cactus scrub and a chaparral may co-exist. Several authors have studied the factors determining the occurrence of different associations, focusing mainly on elevational gradients (see, e.g. Whittaker & Niering 1965; Mooney & Harrison 1972; Arce & Marroquín 1983; Montaña & 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 & Vankat 1989).

Succulent rosettes are a conspicuous life form among the very diverse spectrum of architectural designs in the arid zones of North America. Plants of different families have converged on this morphology. Among the most widespread genera in North America are *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-leaved, 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 in 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). 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 enables plants with rosettes to 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 & Reilly 1994). The morphological convergence of species has been interpreted as evidence of adaptation, and even of optimal design (Harvey & Pagel 1991; Ricklefs & Miles 1994; Farnsworth & Niklas 1995). Thus, a match should be expected between the morphology of desert rosettes and some environmental factors in the areas where the rosette scrub develops which results in the successful performance of these species. These factors however, have not been identified and described. The performance of the rosette habit needs to be measured in terms of the environmental characteristics that determine the 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 & Vuilleumier 1986), a community occurring in tropical highlands throughout the world where rosettes may be the most conspicuous species. In common with deserts, páramos have a large number of adaptationally convergent rosette species. Here, the morphology of rosette plants has been interpreted as a mechanism to avoid subfreezing temperatures, optimize light interception and protect and warm the apical meristems (Smith 1974; Monasterio 1986; Mabberley 1986; Monasterio & Sarmiento 1991; Körner 1999). Despite the climatic differences, some of these functions have also been attributed to desert rosettes (Woodhouse et al. 1980; Gentry 1982; Nobel 1986, 1988). Both for desert páramos and lowland deserts, it has been proposed that rosettes intercept rainwater and canalize it to the roots 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 require copious quantities of rain soak and initiate stem flow, the waxy epidermis of agaves shows a very high efficiency, even for very light (1 mm) 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 high mountains a rosette scrub develops, which we will term montane rosette scrub (Plate 1). In these areas fogs are frequent, forming (sometimes very narrow) 'cloud belts' around mountains. On some tropical mountains, as many as three such cloud belts have been reported. They are the areas of the 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 & Cleef 1986). An example of this are the 'lomas' formations of the Chilean-Peruvian desert (Rundel et al. 1991; Rundel & 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 our main hypothesis deals with water availability in Mexican drylands, we need to consider the other two main sources of water available to rosette plants: rain and succulent tissues. These two sources may differ in 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 succulent, as are many rosettes but these have a different morphology. This means that cacti should also be adapted to aridity, but should not strongly respond to fog. There is a general trend for aridity to diminish with altitude as a result of both reduced temperature and evapotranspiration and of increased precipitation (Valiente 1991). Due to aridity at low altitudes, water storing plants may be important components of the 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' (Fig. 1).

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, are basically dependent on rain. Several authors have shown a positive correlation between rainfall and diversity (Noy-Meir 1985; Morton & Davidson 1988; MacKay 1991; Tilman & Pacala 1993). Productivity and biomass are also greater in more humid sites (Polis 1991; Tilman & Pacala 1993). As the precipitation increases linearly with altitude in some tropical deserts (Valiente 1991; Montaña & Valiente-Banuet 1998) the abundance of woody perennials should follow the same pattern. An altitudinal increase of rosette plants, resembling the behaviour of

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.

shrubs, may be the mere result of an enhanced quantity of rain. However, if rosettes use additional fog water their distribution should display a peak of abundance and diversity around the cloud belts, as happens in South American coastal deserts (Rundel & Mahu 1976; Rundel & Dillon 1998). Plants with other morphologies would not follow this pattern (Fig. 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 in well defined altitudinal belts where large amounts of fog are available for the use of succulent rosette plants. Finally, we will explore the likelihood of alternative explanations for rosette dominance at certain elevations.
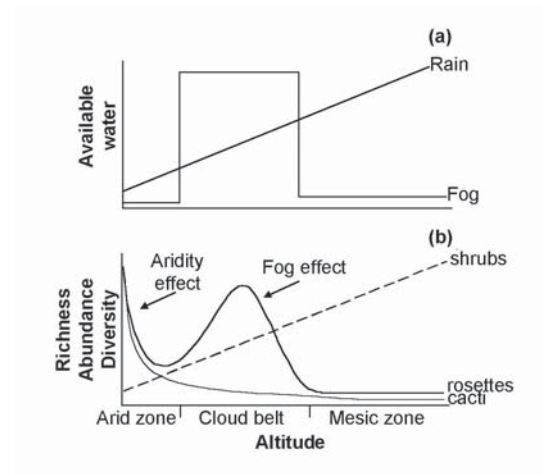

Fig. 1. Hypothetical distribution of three life forms in relation to rainfall and fog. **a**. While rainfall is reported to increase linearly with altitude, fog occurs only in narrow fringes, or 'cloud belts'. **b**. Succulent plants are expected to show an 'aridity effect', increasing towards the lower, 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).

Methods

Study sites

We chose four different arid zones with steep altitudinal gradients (Fig. 2):

Tehuacán Valley, Puebla; 18°17' N, 97°28' W, 1500 - 2200 m a.s.l.; Barranca de Metztitlán, Hidalgo; 20°34' N 98°42' W, 1400-1900 m; Sierra de El Doctor, Querétaro; 20°53' N 99°39' W, 1700-2400 m; Sierra de San Francisco, central Baja California Peninsula; 27°32' N 113°08' W, 400-1500 m

The Pueblan, Hidalgan and Queretaroan arid zones are small rain-shadow deserts in central-southern Mexico with an extremely high degree of endemic species richness (Bravo-Holis 1978; Sánchez-Mejorada 1978; Zamudio et al. 1992; 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.

In all cases, mountains with similar geology over their entire altitudinal range were selected. The vegetation is composed of deciduous elements in the lowlands, and perennial ones at the highest elevations. 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, except San Francisco, clouds were observed as fog banks both in summer (rainy season) and winter and were often limited to a narrow belt around the mountains. At San Francisco, a layer of thin coastal fogs was observed at 400 m a.s.l. and persisted throughout the survey period.
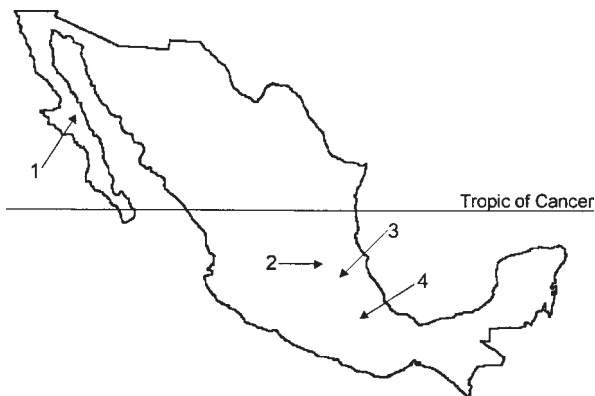

Fig. 2. Study sites. 1. Sierra de San Francisco, Baja California Sur; 2. Sierra de El Doctor, Querétaro; 3. Barranca de Metztitlán, Hidalgo; 4. Tehuacán Valley, Puebla.

Vegetation analysis

The vegetation was sampled every 100 m of altitude through a set of three 50 m × 6 m transects located randomly. We sampled only in zones with approximately the same slope and aspect whenever possible so as to reduce the variation induced by these factors. Along 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 above-ground connection existed. 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: (1) the great number of species and individuals with rosette morphology and (2) the high abundance of rosette plants compared to other life forms. These attributes were measured 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 as the 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, expressed as a proportion, was analysed 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 the 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 (Fig. 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 (Anon. 1992) and Lilliefors tests were run on STATISTICA.

Several factors change together with altitude, soil being one of the most relevant. Elevational position in the geomorphological formations also affects the 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 1989). To control for the possible effect of edaphic 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 constructed. 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 colour (Anon. 1975), depth to rock (if < 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.

To evaluate the relative importance of abiotic factors a multivariate analysis was conducted for the abundance of rosette plants. Since we expected rosette species not to be distributed linearly, but 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 & 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.

Fog measurements

Precipitation measurements were taken along the Tehuacán gradient. We placed six sets of rain gauge/fog catcher pairs (Nagel 1956) were established at different altitudes: at 1450 m (microphyllous scrub), 1800 m (montane rosette scrub) and 2050 m a.s.l. (chaparral), with one replicate at each altitude. The rain gauge collector was a 10.5 mm diameter funnel . 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 comprised 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 m above-ground level. The raingauge/fog catcher pairs were checked monthly during the dry season and fortnightly during the rainy season. Measurements took place between May 1998 and April 1999.

Results

In all, 34 rosette species were found, belonging to six families. The most diverse and widespread rosette family was the Agavaceae, followed by the Nolinaceae. *Agave* and *Yucca* were the most important genera (Table 1). The Bromeliaceae were important because of their large abundance at El Doctor, Metztitlán and Tehuacán. These three zones showed a very high species richness, with 11 to 14 rosette taxa. San Francisco was relatively species poor, with only six taxa. This site was different from the other three, not just in relative scarcity and low diversity of rosettes, but also in the overall elevational patterns of rosette distribution. The taxonomic similarity among sites was low except for El Doctor and Metztitlán, with a Sørensen index of 64.0%. Tehuacán clearly constituted a different floristic unit with a similarity of only 14.8% to El Doctor and 8.3% to Metztitlán. San Francisco shared no species with the other study sites (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 at 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 a.s.l. of altitude respectively (Figs. 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 a.s.l. (Fig. 3.3). Only at El Doctor was there a significant aridity effect for rosettes, with increased

richness, abundance and diversity in the lower zones of the gradient (Fig. 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 towards increased 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, probably due 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, at Tehuacán and El Doctor, the dominance of

Table 1. Species found at the study sites and densities shown as the mean number of individuals ha^{-1} over the entire elevational range of each site. ED = El Doctor; M = Metztitlán; T = Tehuacán; SF = San Francisco.

Family, Species	ED	T	M	SF
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 spp.	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 spp.	166.7			
Tillandsia albida			577.8	
Arecaceae				
Brahea nitida		1.4		
Erythea brandegeei				6.5
Hyacinthaceae				
Hemiphylacus alatostylus	12.5		337.0	
Crassulaceae				
Dudleya acuminata				111.9
Echeverria subsesilis		34.7		
Echeverria spec. 1	4.2			
Echeverria spec. 2			27.8	

rosettes relative to cacti tended to increase with altitude (Figs. 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 a.s.l. The largest abundance occurred at 600 m and the dominance relative to cacti was greater at 800 m a.s.l. The dominance over shrubs did not show any significant trend with altitude (Fig. 3.4).

At 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 13 variables were irrelevant, except for aspect ($r = 0.803$ in El Doctor), slope and soil colour value ($r = 0.811$ and 0.723 respectively, both in Metztitlán). However, not one of these factors was significant at more than one site.

The study period (April 1998 - March 1999) was during one of the most dramatic El Niño years in Mexico. The rainy season was severely delayed in 1998 and a harsh drought caused several wild fires at the Tehuacán Valley. Even in these dry conditions an important amount of fog was recorded at an altitude of 1800 m a.s.l. 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 a.s.l. (Fig. 4). Very little fog occurred at the other altitudes, although similar rainfall occurred everywhere (Fig. 5), with an overall mean of 200.9 mm for the study period (except 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 a.s.l., 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 2 m. Thus at a height of 2 m above the ground in the montane rosette scrub, nearly the same quantity of water is available as fog as is available in the form of rain (Fig. 5).
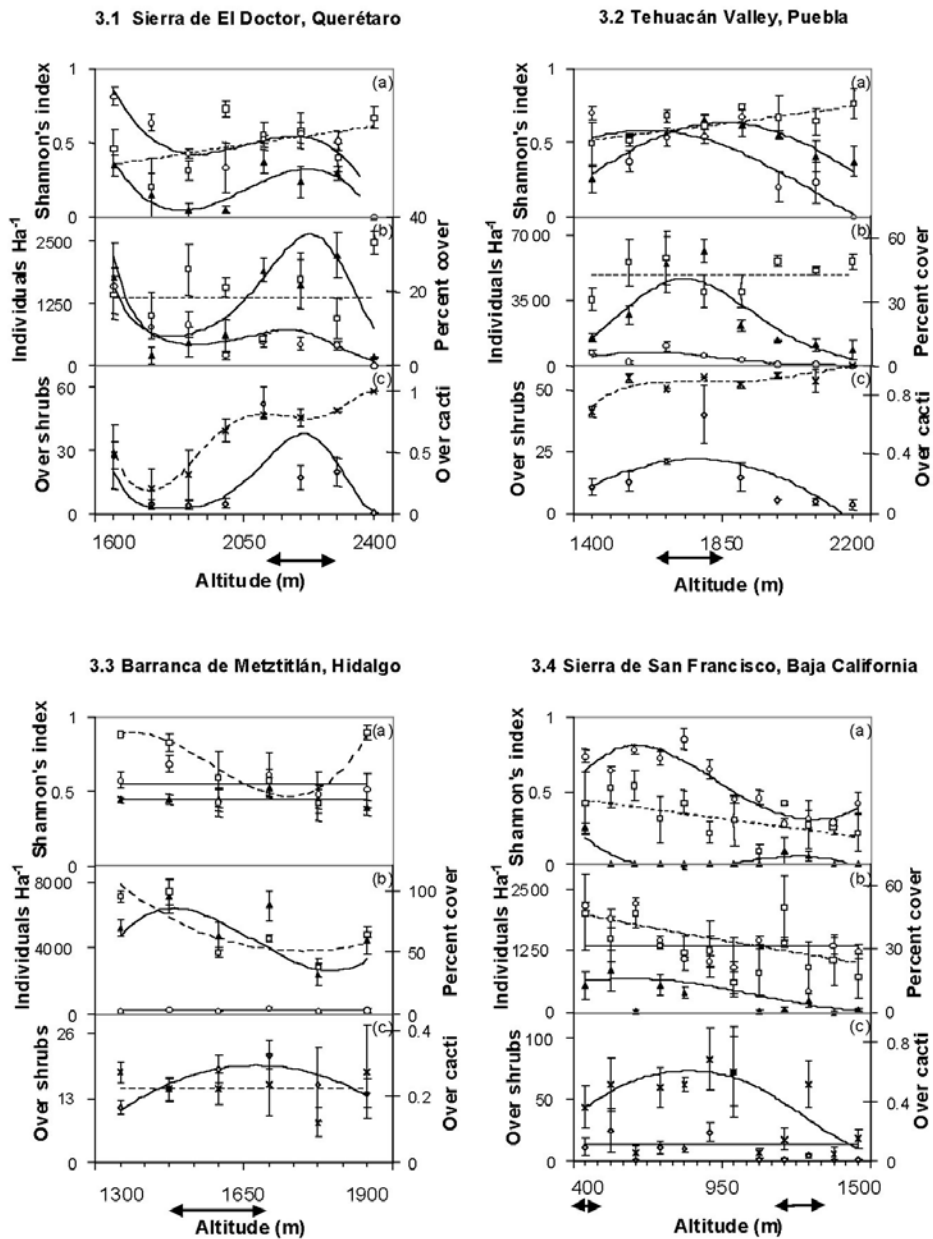
Fig. 3. Richness, diversity, abundance and dominance of three life forms at four Mexican drylands.
a. Diversity of rosettes (——▲——), shrubs (- - -□- - -) and cacti (——○——); **b.** Abundance of the three life forms, measured as density for rosettes and cacti and as cover for shrubs; **c.** Dominance indices 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 the Sierra de El Doctor. Two altitudinal belts with significant fog input and high rosette diversity are believed to be present in the Sierra de San Francisco and are indicated by the arrows at the bottom.

Discussion

The relatively wide range of rosette families (six families in all), as well as the small 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 occurring at a given altitude throughout 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 with similar morphologies at different
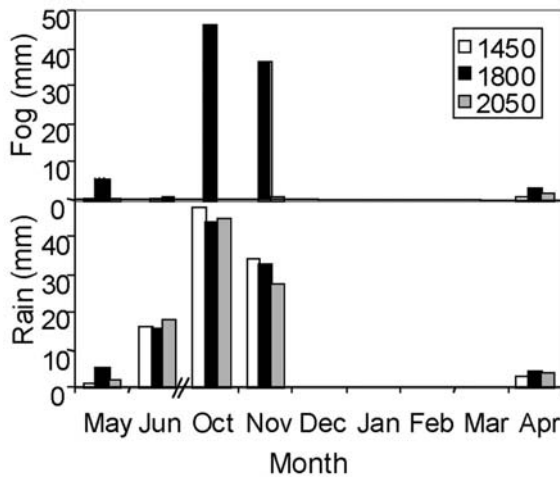
Fig. 4. Fog and rain recorded monthly at three altitudes in the Tehuacán Valley. The 1800 m a.s.l. station was located at the montane rosette scrub, while the other stations were above and below that vegetation belt. Fog measurements are shown for 2 m above the ground.

Fig. 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 a.s.l. Rain is the mean from all rain gauges at each altitude.

sites suggests that there is a strong environmental factor behind rosette dominance (Harvey & Pagel 1991; Ricklefs & Miles 1994; Farnsworth & Niklas 1995).

Patterns in the distributions of rosettes and cacti resembling the expected trends shown in Fig. 1, were observed. At all sites there was an intermediate altitudinal belt where rosettes were most abundant and dominant (Fig. 3). At two of the sites, El Doctor and Tehuacán, rosette diversity and richness followed a similar pattern (Fig. 3.1, 3.2). The data from San Francisco require some comments. At this site the curves for abundance, diversity and dominance are not easily interpreted. This occurs because (unlike intertropical deserts) the maxima for each variable occurred at different altitudes (Fig. 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 a.s.l. Our definition of rosette scrub as a formation showing a high diversity and abundance of rosettes which became 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 a.s.l., but it does so in great numbers. This results in this species biasing 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 and 1100-1300 m a.s.l. belts, each with three species. Therefore, we
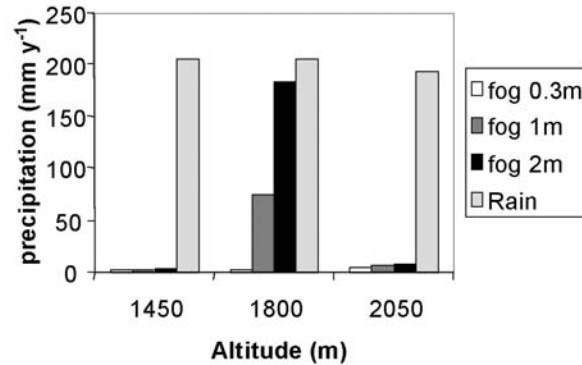
propose that a first montane rosette scrub occurs in San Francisco at 400 m, and a second one in higher areas above 1000 m a.s.l. This seems to correspond with environmental factors.

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 sufficiently great to make them the dominant vegetational elements. Because of the geographic extent, this is a generalized pattern for the Mexican drylands.

At the Sierra de El Doctor, rosettes showed an increase towards the lowlands (Fig. 3.1) similar to the one we expected due to the aridity effect (Fig. 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. *A. marmorata*, *A. xylonacantha* and *A. 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 altitude. This marks a clear distinction between rosette and non-rosette succulent plants. Both are capable of storing water in drylands, may tolerate 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 against 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 did shrub diversity increase with altitude. It should be noted that shrub diversity did not show any significant convexity at intermediate altitudes.

While the increasing trend of vegetation cover with rainfall has been reported in several systems, the same is not necessarily valid for diversity. In several studies of plants and animals all over the world it has been observed 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 & Pacala 1993; Rosenzweig & Abramsky 1993). This phenomenon has been found in several drylands and related to altitude and rainfall (Whittaker & Niering 1975; Tilman & Pacala 1993; Rosenzweig & 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 regions 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 greater 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, are usually present in the intermediate zones of mountains (FitzPatrick 1980; Small 1989) and could account for the occurrence of certain species. If rosette scrub was associated with any such factors we would have seen a consistent correlation between this and rosette distribution. Thus, we may reject factors associated with topographic catenas as being 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 closest sites, El Doctor and Metztitlán, the rosette scrub occurs at 2200 and 1600 m a.s.l. respectively. The closest weather stations (Vizarrón at 1500 m and Metztitlán at 1250 m a.s.l.) show a difference of 4 ºC 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 likely 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 a.s.l. (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 in mountain cloud-belts. At 2 m above the 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 also 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 a notable feature. As we expected, gauges placed at greater heights collected more water. It is noteworthy that at higher altitudes we found more caulescent rosettes and their caudices were longer, so the fog catching leaves are placed higher above the ground and are 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* in 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 in the two altitudinal belts resemble montane rosette scrub. Both correspond to the observed coastal fog belt at 400 m a.s.l., 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 in southern California, where clouds form when moist marine air is trapped against the mountains by an inversion layer (Bailey 1966). These coastal fogs typically reach around 400 m

a.s.l. although the altitude of the inversion may fluctuate. In San Francisco, at 400 m a.s.l. 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 also have 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 & Mahu 1976; Rundel & 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).

There is a 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 & Oxley 1997). The lomas formations of the coast display a high variability in their structure. In some areas they are composed of herbs while other lomas are characterized by trees (Rundel et al. 1991). It has been reported that lomas plants with 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 maintains 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 response of the rosette plants is much stronger, as the dominance indices show.

Rosettes achieve significant 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 of 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 & Mahu 1976; Rundel et al. 1991; Rundel & 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 utilizing shallow fog events that are inaccessible to plants with other architectures.

The present study shows the widespread existence of the montane rosette scrub in Mexican drylands. As is demonstrated from San Francisco, the term 'montane' does not imply high altitude. Rather, it alludes to the topographical relief that plants need to reach the clouds and fogs. 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 & 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. On 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. Species composition varies between sites. Species, are frequently of widely different taxonomic origins, a fact that suggests that the succulent rosette morphology is indeed an adaptive response to environmental conditions prevailing on 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 form. Desert rosettes constitute one of the most common fog-harvesting growth forms.

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