ECOPHYSIOLOGY

The narrow-leaf syndrome: a functional and evolutionary approach to the form of fog-harvesting rosette plants

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Abstract Plants that use fog as an important water-source frequently 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 results were validated using seven species of *Tillandsia* and four species of xerophytic rosettes. The total amount of fog intercepted in rosette plants increased with total leaf area, while narrow leaves maximized interception efficiency (measured as interception per unit area). The number of leaves in the rosettes is physically constrained because wide-leafed plants can only have a few blades. At the limits of this constraint,
net fog interception was independent of leaf form, but interception efficiency was maximized by large numbers of narrow leaves. Atmospheric *Tillandsia* species show the narrow-leaf syndrome. Their fog interception efficiencies were correlated to the ones predicted from aluminum-model data. In the larger xerophytic rosette species, the interception efficiency was greatest in plants showing the narrow-leaf syndrome. The adaptation to fog-harvesting in several narrow-leaved rosettes was tested for evolutionary convergence in 30 xerophytic rosette species using a comparative method. There was a significant evolutionary tendency towards the development of the narrow-leaf syndrome the closer the species grew to areas where fog is frequently available. This study establishes convergence in a very wide group of plants encompassing genera as contrasting as *Tillandsia* and *Agave* as a result of their dependence on fog.

Keywords Comparative method · Epiphyte · Functional morphology · Montane rosette scrub · Xerophyte

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Introduction

While rain provides water for most plants, several species have evolved the capacity to use fog in environments where rainwater is limited (Cavelier and Golstein 1989; Rundel et al. 1991; Martin 1994; Dawson 1998; Martorell and Ezcurra 2002). We have suggested the term *nebulophyte* for species that use fog as an important water source (Martorell 2002), such as epiphytic bromeliads (Mez 1904; Smith and Downs 1974; Martin 1994). Nebulophytes may also be large ground-

living plants, such as the trees, shrubs and columnar cacti from the hyperarid Atacama Desert (Rundel and Mahu 1976; Rundel et al. 1991). Large rosette plants, such as some Agavaceae and Nolinaceae, constitute as much as 88% of the individuals and 54% of the vegetation cover in the montane rosette scrub of arid North-American mountains where fog provides as much water as rainfall. It is likely that these rosettes are also nebulophytes (Martorell and Ezcurra 2002).

Many nebulophytes, both epiphytes and xerophytes, show the same rosette growth habit. The reason for this may be that rosettes resemble funnels that conduct water to the plant's roots or to the central tank in "pitcher plant" bromeliads. The stem flow of some Agavaceae is highly efficient, even during very small (1 mm) rain events (Gentry 1982; Ramírez de Arellano 1996). We have observed that fog may also initiate stem flow in dryland rosettes, and the tanks of some bromeliads are known to be replenished entirely by fog water (Rundel and Dillon 1998).

Several epiphytic Bromeliaceae absorb humidity directly at the leaf surface; these plants have no water tanks, and their roots serve merely as holdfasts (Smith and Downs 1974; Martin 1994). In these "atmospheric" species, conducting water to the plant's base would be futile or even disadvantageous, so water interception – rather than its subsequent conduction – should be optimized. There are some remarkable morphological convergences in nebulophytes that may serve this purpose. Atmospheric bromeliads have very narrow leaves (Benzing 1990), as it also happens in the Agavaceae and Nolinaceae that grow in foggy mountains. Nebulophytic lichens and mosses have narrow thalli, a trait that increases water uptake rates at the organism's surface (Larson 1981). This may also apply to bromeliads, but Agavaceae or Nolinaceae do not absorb water at the leaf surface. Thus, an alternative hypothesis is needed to explain the reiterated convergence of narrow leaves or thalli in nebulophytes. In this paper we suggest that narrow surfaces, in addition to enlarging water-absorption rates, are an adaptation that increases fog interception.

Fog is conveyed to the plant through wind, and wind speed decreases as it gets closer to surfaces, forming an envelope of slow-moving air around objects known as the boundary layer. For a flat surface such as a leaf, the following relationship holds:

$$\delta^{\mathrm{bl}} \propto \sqrt{\frac{l}{v}}, \tag{1}$$

where δ^{bl} is the thickness of the boundary layer, l is the length of the surface in the downwind direction and v is the wind speed. This relationship means that large leaves have thicker boundary layers (Nobel 1991). Fog is composed of water droplets having an average size of 20 μm; as such, they have a large surface:volume ratio compared to larger drops (Jones 1992). When they cross the boundary layer, their large surfaces are subject to strong friction forces, while their reduced mass retains little kinetic energy. As a result, the fog droplets are easily slowed down by the boundary layer, where they are swept away by a slow laminar air stream flowing parallel to the object's surface (Welty 1984). Only a small fraction of the droplets – known as impaction efficiency – has enough energy to follow its original (perpendicular or oblique to the surface) trajectory, ultimately colliding with the plant. The impaction efficiency is inversely proportional to the thickness of the boundary layer, and it is increased in the presence of turbulence. Turbulent eddies may drive droplets that are far from the plant into its surface. Strong turbulence also drags the water into the leeward side of the leaf, where no droplets would normally collide (Jones 1992).

Therefore, three factors may facilitate fog-water transfer to the plants. (1) Small or narrow leaves result in thin boundary layers. Leaf form is variable in rosettes, and the length:width ratio of the nearly triangular leaves of xerophytes ranges from 2 (*Agave potatorum*) to 265 (*Dasylirion longissimum*), possibly reaching above 450 in some *Tillandsia*. (2) Fast winds reduce boundary layers and provide sufficient kinetic energy to droplets. Since wind-speed increases with distance from the ground, rosettes should be placed high above the soil. This may be achieved either by having a stem or caudex, as in some *Yucca* and *Nolina*, or by being an epiphyte. (3) Turbulence is induced by complex surfaces (Jones 1992), such as many-leafed rosettes, or by flexible leaves that whisk in the wind. Therefore, narrow leaves, together with some ancillary traits (leaf distance from the ground and flexible leaves in large numbers), should characterize efficient fog harvesters. These co-occurring traits would then constitute what we have named the narrow-leaf syndrome.

Two complementary approaches may be used to test the adaptive value of the syndrome (Harvey and Pagel 1991; Coddington 1994; Pagel 1994; Wenzel and Carpenter 1994). According to the homology approach, a trait can be proved to be adaptive if it increases the performance of the organisms that possess it. Detailed studies on the evolution of the trait are often needed that lack generality because the evolution of a trait on any species is a "historical unique" (Coddington 1994). The convergence approach states that adaptation may be shown through the repeated evolution of the same

trait in different taxa as a result of the same evolutionary pressures. This approach has the advantage of generality and provides strong evidence to discard alternative explanatory factors (Coddington 1994; Wenzel and Carpenter 1994). A highly widespread convergence rules out exaptation and, therefore, evinces adaptation rather than mere adaptive value (Harvey and Pagel 1991; Pagel 1994). However, being correlative, the convergence method cannot resolve a causal relation between the traits and the hypothetical pressures that shaped them.

In this study we use both approaches. The homologist's data on performance is needed to discriminate between Larson's hypothesis (high water-uptake rate) and ours (high fog interception efficiency). Convergence, on the other hand, would establish the narrow-leaf syndrome as an evolutionary trend, allowing us to understand phenomena such as the high diversity of rosettes in cloud belts (Martorell and Ezcurra 2002). Performance was defined in terms of fog interception as the net amount of water gained per time unit. However, the amount of water that suffices for a small plant may not be enough for a large one. Thus, we defined a second measure of performance, interception efficiency, as fog interception in relation to total leaf area. Leaf area estimates plant size and the amount of resources (plant surface) invested in fog-catchment. Performance was measured for plants with different morphologies. Once the adaptive value of the narrow-leaf syndrome was established, its generality was tested by means of a comparative analysis (Harvey and Pagel 1991) using xerophytic rosettes, because these are found in a larger set of families than only epiphytes, thereby allowing us to achieve a greater level of generality.

Methods

Fog-interception modeling

Aluminum models

To test the hypothesis that rosettes with many thin leaves are the best fog interceptors, we used aluminum models of rosettes exposed to artificial fog in order to evaluate the effect of length, width and number of leaves. The use of models overcomes the difficulty of finding different plant species that differ only 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 amount of water intercepted to be measured precisely by weighing. Because of the non-linear effect that size was expected to have on water interception (Eq. 1), it was important to use models of at least three different sizes. The leaves of the models were triangular, with lengths of 12, 18 and 24 cm, and there were three leaf-form variants. Leaf form was defined as the ratio of length to width, and set to values of 2.67, 4 and 8. Models with larger form indices had more leaves, so the overall area was the same for all models of the same size. Finally, for each combination of leaf length and form, two variants were assembled, one with twice as many leaves as the other (Table 1). Leaves were inserted at the base of the models in verticils of six, and the angle between them was obtained by dividing 60° (=360/6) by the number of verticils, so the density of leaves pointing to any direction was the same. The leaves were then folded upwards. The angle of each was obtained by dividing 90° by the number of leaves, so the uppermost leaf was vertical, the lowermost one was horizontal and the remainder of the leaves covered homogeneously the range between both extremes. Folding was performed in a spiraling order in an attempt to simulate real phylotaxis. The model's surface was flat, with no pubescence or ornamentation.

The models were weighed and exposed to an artificial fog stream for 1 min [see Electronic Supplementary Material (ESM), Appendix A, for details). The change in the model's weight due to intercepted water was measured. To avoid the effects of potential changes in the relative humidity or temperature over time, the models were exposed to fog in a quasi-latin square sequence (Cochran and Cox 1957). The design was randomized and replicated four times. Any potential effects that the accumulation of water on the model's surface may have on the fog interception dynamics were avoided by allowing all of the models to dry off completely before the replications were conducted.

Data on the total amount of water captured was regressed on morphological variables using GLIM ver.

Table 1 Number of leaves in the 18 aluminum models used in fog simulations

Leaf density	Leaf length (cm)	Leaf form index[a]		
		2.67 (wide leaves)	4	8 (narrow leaves)
Low	12	12	18	36
	18	12	18	36
	24	12	18	36
High	12	24	36	72
	18	24	36	72
	24	24	36	72

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

4.0 (release 1992) (Numerical Algorithms Group), and ANOVA assumptions were tested using STATISTICA ver. 4.0 (release 1993) (StatSoft, Tulsa, Okla.). Since the relationship was expected to follow a power law (Eq. 1) the data were log–log transformed. The resulting equation was divided by total leaf area to produce a model for interception efficiency. We will refer to both equations as the mathematical model.

The number of leaves that a rosette may accommodate on its reduced stem may be limited, especially if the leaves are broad. Evolution should maximize interception within the limits imposed by this physical constraint. To assess if this were the case, we performed a stochastic frontier regression using the program FRONTIER ver. 4.1 (Coelli 1996) on data for 32 species of xerophytic and epiphytic rosette plants (see below for the list of species). This method fits a line at the maximum number of leaves that a plant may have given its leaf form, thus detecting the limit imposed by the physical constraint (Aigner et al. 1977). Arecaceae were not included, because folioles are not directly inserted to the stem and, therefore, may experience a different constraint.

Model validation

The previous results were validated by comparing them with living plants of the genus *Tillandsia* (Bromeliaceae), which were chosen for their wide differences in morphology and water usage. For example, we studied *T. imperialis*, a tank bromeliad with very broad leaves (leaf form index = 2.8) that depends on stem flow, and the "atmospheric" *T. chaetophylla*, which displays a few thread-like leaves (leaf form index = 400) that absorb water. 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 that of Smith and Downs (1974).

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 one ramet from different individuals of each species. Following the experiments, the length and width of three fully-developed leaves 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 (*T. plumosa, T. butzii* and *T. chaetophylla*) the leaves had a wide sheath forming a tight bundle similar to the tank of other *Tillandsia* or to the basal stem of xerophytic rosettes; in these cases, only the exposed leaf blade was measured.

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 ramet. As a measure of accuracy, we used the percentage of the variation in *Tillandsia* interception efficiency explained by the model:

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

where O_i is the Ith observed interception efficiency, E_i is the corresponding expected datum calculated from the mathematical model and $\overline{O}$ is the mean of all observed values.

The expected data should only account for the effects of leaf size, form and number because they were based upon aluminum models that only differed in those attributes. The observed data reflected those same effects plus the effects of other traits, whose effect on interception efficiency may then be assessed through the residuals ($O_i - E_i$). Thus, we tested the role of the rosette morphology per se on fog interception by applying a Mann-Whitney test to the residuals, comparing *T. usneoides* and *T. recurvata* against the rest of the species. The same test was carried out for glabrescent and pubescent species. To evaluate if the interception efficiency of these groups was appropriately predicted by the mathematical model, we conducted *t*-tests on the residuals in order to assess if they differed from zero.

Model validation with xerophytic plants was performed on four species with contrasting morphologies:

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

Species	Leaf form index[a]	Number of leaves	Other traits
T. butzii	79.0	8.3	Bulbous sheaths; very sparse trichomes
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

[a] The leaf form index is the ratio of leaf length to width

Agave kerchovei, *Agave salmiana*, *Agave stricta* and *Brahea nitida*. Five plants from each species were selected at random from an area near Tehuacán, Mexico. Since water uptake in these species occurs at the roots, we simulated fog with a backpack sprayer and collected all of the water that flowed into the soil in a waterproof sheet sealed against the plant's stem. To reduce variability in the experiment, as much air as possible was first pumped into the apparatus by the same person every time, and no more pumping was performed while aspersing. The flux of the sprayer was not uniform, but we determined that a continuous circular movement damped a flat area uniformly. Fog was simulated for 15 s at a distance of 2 m from the plant, moving the nozzle as described. The water on the plants was left to flow for 1 min, and the total water volume collected was measured.

As was the case with the aluminum models, we were interested in measuring efficiencies relative to plant sizes. However, the total leaf area of the selected plants could not be accurately estimated because of the difficulty imposed by the sheer size and bulky form of the large succulent leaves. Since the fog flux was horizontal, interception efficiency was standardized by the area exposed to the flow estimated as the product of the height and width of the whole plant. The observed efficiencies were compared to the expected ones in the same manner as for the *Tillandsia* species. Interception efficiency was also compared with a plant form index derived from a principal components analysis (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

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 where rosette montane scrub is found (Sierra de San Francisco, Baja California Sur, Sierra del Doctor, Querétaro, Barranca de Metztitlán, Hidalgo and Tehuacán Valley, Puebla). In each zone, one mountain was sampled along its whole altitudinal gradient, and the density and species of all the rosette plants in three replicate transects placed at 100-m altitude intervals were recorded (see Martorell and Ezcurra 2002 for details). The morphology was measured in 15 individual plants of each of 30 species. Eleven characters that accounted for the narrow-leaf syndrome (Table 3) were used for this purpose, summarizing them by means of PCA into one value per species along only one or a few synthetic

Table 3 Morphological attributes of xerophytic rosettes used to calculate the multivariate form index and their principal component loadings

Trait	Variable measured[a]	Loading[b]
Leaf form	Leaf length	0.25
	Leaf width	**–0.59**
	Leaf thickness	**–0.75**
Distance from soil	Presence of caudex	**0.85**
	Presence of collar[d]	**0.74**
Aerodynamic roughness	Leaf number[e]	**0.55**
	Leaf density[f]	**0.57**
	Mean leaf angle[e]	0.12
	Leaf angle variance[e]	0.36
	Leaf ornamentation[g]	–0.33
Funnel morphology[c]	Leaf curvature[e]	–0.42

[a] For the Arecaceae, leaf length, width, thickness and number were measured using the leaflets because they are the main fog-catching areas. All other traits refer to the petiole

[b] The numbers in bold indicate the traits that are more associated to the narrow-leaf syndrome. The (–) sign indicates that the character negatively associated with the syndrome; the absence of a sign indicates it is positively associated with the syndrome

[c] Not considered to be part of the narrow-leaf syndrome, but related to stem flow

[d] Which also serves as a fog collector (Mabberley 1986; Mandujano 2001)

[e] Measured from photographs using IMAGETOOL 2.00 [developed by C.D. Wilcox et al. (1995) Department of Dental Diagnostic Science, The University of Texas Health Science Center, San Antonio, Tex.]

[f] Estimated by the number of contact parastichies (or Fibonacci number)

[g] Grooves or striations in the leaf that may increase boundary layer thickness

variables or "axes". The only axis that was found to be significant (following Jackson 1993) was interpreted as a form index.

A phylogenetic hypothesis for all the species was proposed using taxonomic and phylogenetic data in order to conduct a comparative analysis (see ESM, Appendix B). The growth site itself is not a trait of the species, but if its distribution is affected by attributes upon which selection may act, such as morphology (see Wainwright 1994 and references therein for a thorough discussion on the form-environment relationship), then the rosette plants showing the narrow-leaf syndrome should occur preferentially in altitudes of the montane rosette scrub, where fog is available (Martorell and Ezcurra 2002). We calculated the differences between this altitude and the elevational centroid of the distribution of each species. A relationship between this relative position and the form index (species score along the first principal component) was sought by means of independent comparisons (Harvey and Pagel 1991). The required ancestral character states for the

cladogram were calculated using the averaging rule algorithm, which reduces the character differences along the tree so that the evolutionary changes are minimized. This is achieved by iteratively calculating for each node the average of the character states estimated for all the adjacent nodes (Huey and Bennett 1986; Harvey and Pagel 1991). We followed the methodology of Trevelyan et al. (1990) to calculate the comparison corresponding to the only polytomic node. We did not use a phylogeny but a mixture of results from different sources, so the data cannot be controlled for homoscedasticity as required by many independent comparisons methods. Because the assumptions of the model were dubious, a sign test was used to assess the significance of the independent comparisons more reliably (Harvey and Pagel 1991). Iterations, independent comparisons, and P-values were calculated with EXCEL (release 2003).

In order to test the hypothesis that narrow-leafed rosettes should be relatively more abundant near areas with more fog we used data from the Tehuacán Valley where fog condensates at 1800–1900 m a.s.l. (Martorell and Ezcurra 2002). This was assessed by regressing the mean form composition (mean form index of all the plants found at each transect; the same form index was used for all the individuals of each species) against the altitude as independent variable. A quadratic term was tested in the regression analysis because a non-linear trend, with a maximum at the fog belt, was expected.

Results

Fog-interception modeling

Aluminum models

The amount of fog intercepted depended significantly on the length ($F = 165.5$, $P < 0.0001$), width ($F = 37.1$, $P < 0.0001$) and number of leaves ($F = 84.9$, $P < 0.0001$) in the model. No interactions were found to be significant. The equation that best described the relationship between form and fog interception (I) in milliliters was:

$$I = (0.0026 \pm 0.0017)l^{1.48\pm0.27}w^{0.502\pm0.196}n^{0.604\pm0.154}, \tag{2}$$

where l is leaf length in centimeters; w, the leaf width in centimeters; n, the number of leaves. The 95% confidence interval for each regression parameter is reported. Dividing by the total area of the triangular leaves, we obtain the model for the interception efficiency (e) expressed in microliters per square centimeter (μl cm^{-2}):

$$e = \frac{I}{A} = \frac{2I}{lnw}$$
$$= (5.24 \pm 3.53)l^{0.477\pm0.270}w^{-0.498\pm0.196}n^{-0.396\pm0.154}. \tag{3}$$

We expected interception efficiency to be related to square-root functions (powers of 0.5) of the size of the leaves, because impaction efficiency depends on their boundary-layer thickness (Eq. 1). From Eq. 3, this seems to be confirmed for leaf length and width. The regression of fog interception was then repeated, setting the power of length to 1.5 and that of width to 0.5. The resultant increase in deviance 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 interception efficiency were:
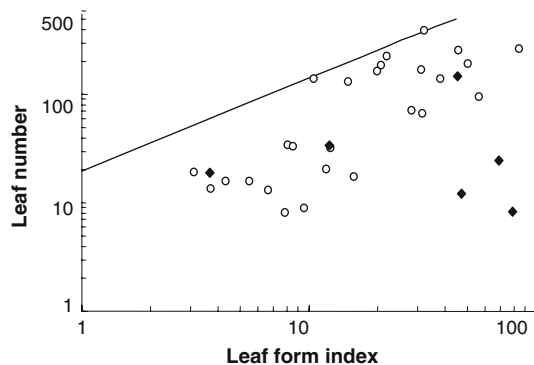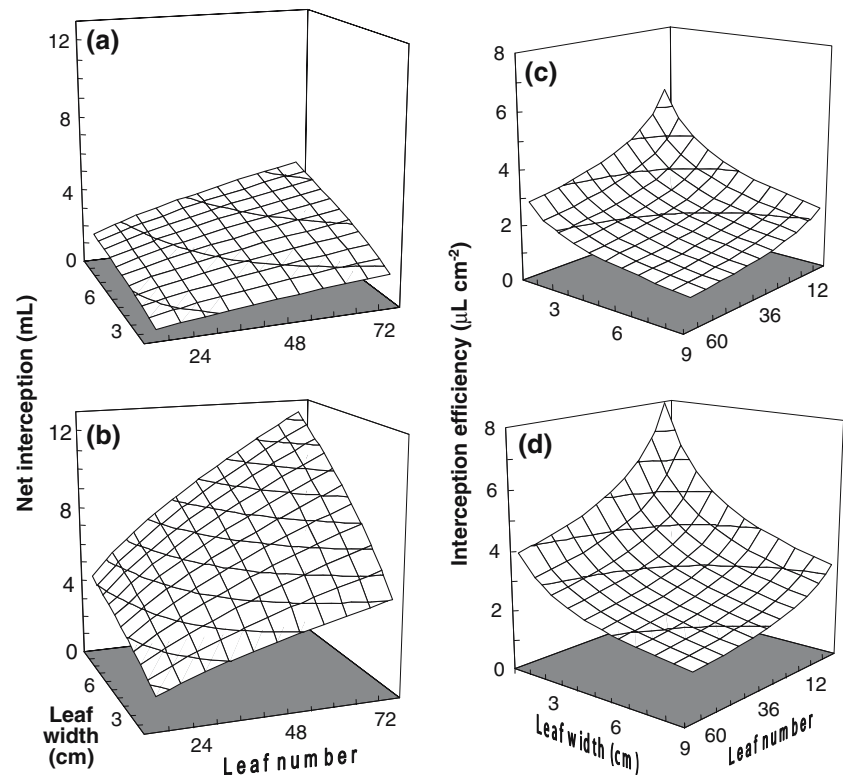
$$I = 0.00266n^{0.602}l\sqrt{lw}, \tag{4}$$

$$e = 5.33n^{-0.398}\sqrt{\frac{l}{w}}. \tag{5}$$

Both equations predict that in order to maximize the interception efficiency, leaves should be few and narrow, while the opposite is needed to optimize net interception (Fig. 1). However, stochastic frontier regression shows that the error structure of the data fits a model where there is an upper limit to the number of leaves significantly better than ordinary least-squares regression ($t = 5.64$, $P < 0.0001$) and that broad-leaved rosettes cannot have many leaves ($t = 5.66$, $P < 0.0001$; Fig. 2). Thus, optimality in net interception appears to be unreachable. This confirms the existence of an evolutionary constraint. Using Eqs. 4 and 5, we found that, for rosettes with the maximum possible number of leaves, having several narrow leaves maximizes plant interception efficiency, while net interception remains the same regardless of leaf form (Fig. 3).

Model validation

The interception efficiency of bromeliads as predicted by Eq. 5 was highly correlated with the observed values ($r = 0.82$, $P = 0.0001$; Fig. 4). However, the percentage of the variance explained by the model was quite low (20%). This may be due largely to the inclusion of two non-rosette species. The Mann-Whitney test performed on the residuals showed that non-rosettes were more efficient than rosettes ($U = 9$, $P = 0.020$) and, therefore, that Eq. 5 would not be

Fig. 1 Net interception (**a**, **b**) and interception efficiency (**c**, **d**) of fog in aluminum models with leaf lengths of 12 (**a**, **c**) and 24 cm (**b**, **d**) ($R^2 = 0.926$). Net interception is the total amount of water that was acquired by the model. Interception efficiency is expressed as a function of the total leaf area of the model. Note that the direction of the axes is reversed in the efficiency graphs

Fig. 2 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, *solid diamonds* represent *Tillandsia* spp. The stochastic frontier regression line shows the maximum number of leaves that can be accommodated around the compact stem of rosette plants
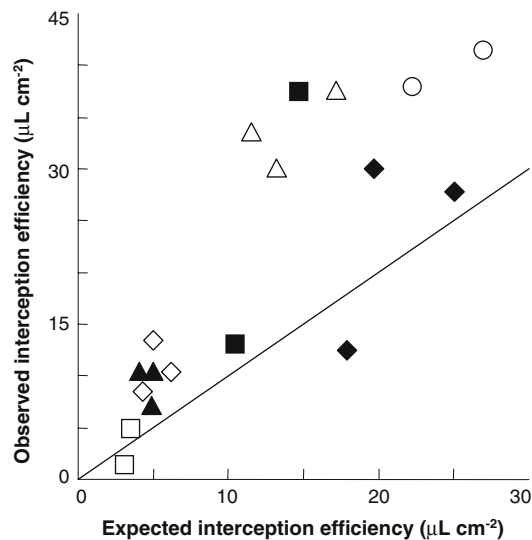
appropriate to predict their efficiencies. After removing *T. usneoides* and *T. recurvata* from the analyses, both the correlation ($r = 0.91$) and the fraction of variance explained by the mathematical model (64.5%) increased substantially. Notwithstanding this, the observed efficiencies of rosette bromeliads alone were still larger than the values predicted by our model ($t = 3.21$, $P = 0.003$), with the exception of the glabrescent species *T. imperialis* and *T. butzii* ($t = 0.59$, NS), which had smaller residuals than the remaining, pubescent species ($U = 9$, $P = 0.019$).

Fig. 3 Highest net fog interception and 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 *dash-and-dot line* to 12 cm

The interception efficiency of large xerophytic rosettes showed a large variation between species. Our mathematical model (Eq. 5) revealed a low, non-significant correlation ($r = 0.28$, $P = 0.23$) with the
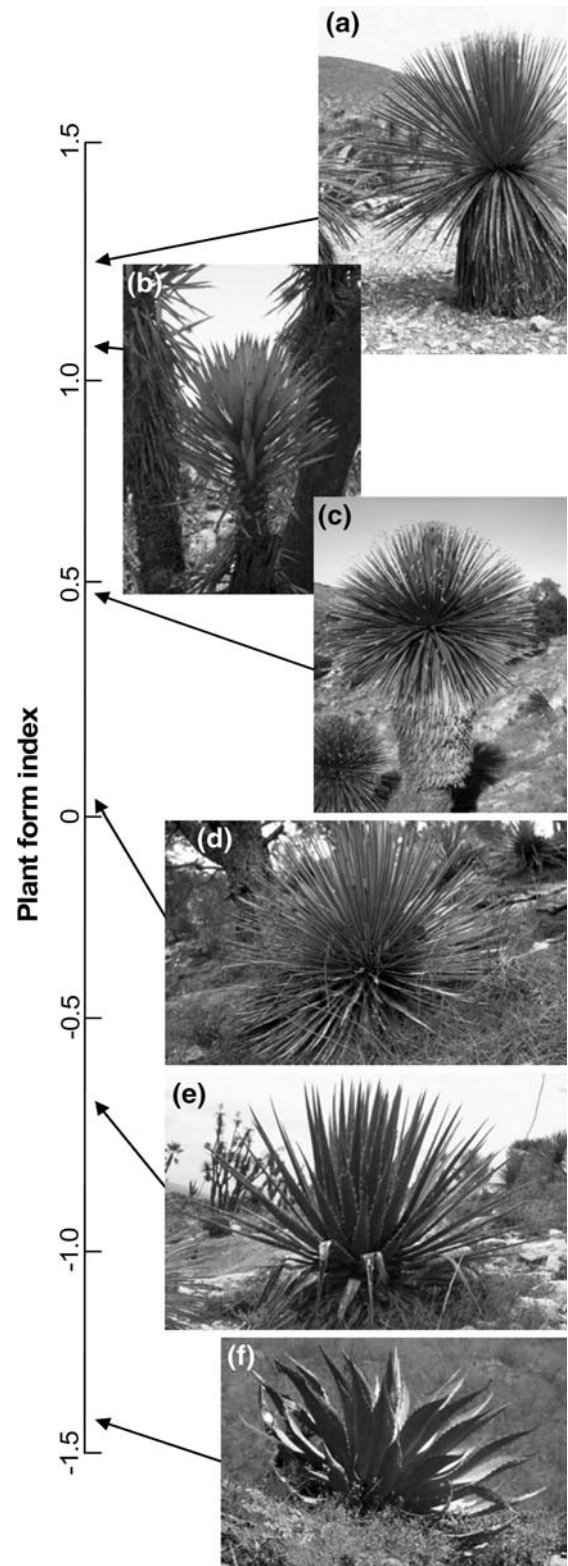
Fig. 4 Observed fog interception efficiencies of seven species of *Tillandsia* and the efficiencies expected for aluminum models having the same leaf number, length and form. The *line* shows the expected relationship if efficiencies were equal. *Filled diamond T. butzii*, *open circle T. chaetophylla*, *filled triangle T. concolor*, *open square T. imperialis*, *open diamond T. plumosa*, *open triangle T. recurvata*, *filled square T. usneoides*

observed fog interception of xerophytes. However, interception efficiency was highly correlated with plant form measured with the multivariate index ($r = 0.76$). Rosettes showing the narrow-leaf syndrome were found to intercept and conduct larger amounts of fog towards their bases ($F = 23.25$, $P = 0.0002$).

Comparative analysis of rosette morphologies

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. It is apparent from the signs of the loadings (Table 3) that high positive values in the index correspond to plants with long, narrow leaves, while low values correspond to plants with wide, thick, fleshy leaves. Other traits that led plants to score high along the PCA axis were longer caudices, many leaves, no ornaments that increase the boundary layer thickness and complex (aerodynamically rough) leaf distributions as measured by the Fibonacci number. Thus, the multivariate axis corresponds largely to the narrow-leaf syndrome (Fig. 5).

The mean form composition of the rosette community at Tehuacán increased with altitude, indicating that slender-leafed rosettes are dominant at higher elevations ($F = 16.9$, $P = 0.0005$). A significant non-linear term was found ($F = 11.94$, $P = 0.0024$), but the
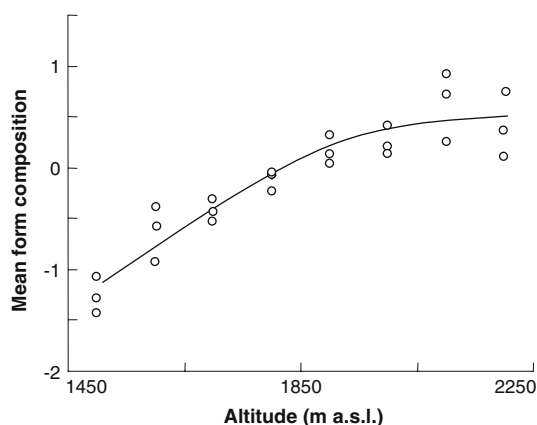

Fig. 5 Xerophytic rosettes having different plant form indices. Plants with larger, positive form indices display all of the traits of the narrow-leaf syndrome. The species depicted are: **a** *Dasylirion acrotriche*, **b** *Yucca valida*, **c** *Nolina parviflora*, **d** *Agave stricta*, **e** *Agave kerchovei*, **f** *Agave salmiana*

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 (Fig. 6). This is not a result of phylogenetic relatedness, as revealed by the method of independent contrasts. After accounting for phylogeny, a significant relationship was found between form and relative altitude (sign test $n = 20$ out of 28 comparisons; $P = 0.027$), indicating that during evolutionary history, shifts in plant form have been accompanied with distributional shifts towards (or away from) the fog belt.

Discussion

In general terms, the hypothesis that the narrow-leaf syndrome is an efficient morphology for fog interception was largely confirmed. We found that aluminum models, *Tillandsia* species and xerophytic rosettes with narrow leaves had the best performances in terms of interception efficiency. However, many plant species throughout the world are rosettes, some of them having slender leaves with pubescence or trichomes. Their form may serve many purposes, and in many cases fog interception may be completely irrelevant. Likewise, the narrow-leaved rosette form of xerophytes and epiphytes may serve other purposes besides fog catchment. Further studies assessing other possible functions of this morphology will be needed to address this problem. However, our results do provide some interesting insights into the adaptive value of fog interception in rosettes.

Fig. 6 Mean form composition of communities at an elevational gradient at Tehuacán Valley, Mexico. The mean form composition of each transect is the average of the form indices for all of the rosette species present in it, weighed by their abundance

Fog-interception modeling

Aluminum models

As expected, interception efficiency was 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. Leaf length had an opposite effect, with the longest leaves showing a better performance. The explanation for this may be that as the wind flow reaches the plants, the windward leaves both deplete its fog-contents and slow down its speed. During the fog simulations it was observed that the leeward leaves intercepted water mainly at the tips, which seem to project beyond the fog-shadow of the windward leaves. Longer leaves are more separated from each other at their apices, thereby avoiding the fog-shadowing and increasing the interception efficiency of the whole plant.

A large size increases both interception and efficiency (Eqs. 4, 5). A plant with few, slender leaves maximizes interception efficiency, while broad, numerous leaves are better to enlarge net interception because they increase the interception surface. The only way for a plant to have a large surface area while keeping to only a few narrow leaves is by having long leaves. Achieving large areas by means of increasing leaf numbers should result in a high pressure to compensate fog-shading. Again, under this scenario the solution is to have long leaves that have access to unshaded, fog-rich air streams.

The manner in which different plants use water appears to influence their morphology. Net interception is of obvious importance for all plants, but in atmospheric bromeliads where water uptake occurs in the leaf itself, interception efficiency is a more appropriate measure of performance since it is a function of the absorptive area. The same may be true for lichens, mosses and pines, where at least part of the fog water is absorbed above ground (Leyton and Armitage 1968; Boucher et al. 1995). There are two other advantages of interception efficiency over net interception as a measure of performance: first, it is related to plant size and, therefore, with the amount of water that the individual may require; second, since gas exchange occurs at the leaf surface, water uptake rates are implicitly compared to potential transpiration loss rates. When water is absorbed at the ground level, as it occurs in xerophytic rosettes living in foggy areas, a high net interception is needed as this will drive a significant quantity of water to the soil. This may be achieved by increasing leaf width, length and number. However, if a rosette evolves towards the maximum

possible number of leaves imposed by the physical constraint, leaf form no longer affects net interception. At this point, developing narrow leaves and therefore increasing interception efficiency may be advantageous, since it would result in a faster saturation of the leaf surface and earlier initiation of the stem flow, thereby allowing access to shorter or lighter fog events. This agrees with the pattern observed in epiphytes that have fewer leaves than xerophytes for any given leaf-form. The maximization of interception efficiency seems to be achieved in atmospheric *Tillandsia* by means of having few leaves (Fig. 1), while xerophytic rosettes optimize net interception and efficiency by having as many narrow leaves as allowed by the physical constraint.

There seems to be an interesting symmetry between fog and light interception. As happens with fog, many-leafed rosettes gain less photosynthetically active radiation (PAR) per unit area due to self-shading while increasing the total amount of PAR received due to a larger area (Woodhouse et al. 1980). However, it remains unclear whether there is a trade-off or a synergism between morphological traits that optimize fog or PAR interception. Apart from leaf number, there are no data available on how the leaf form affects PAR interception. However, it must be noted that instantaneous PAR interception is remarkably similar in three agave species with many narrow leaves or a few wide ones (see Fig. 5.8 in Nobel 1988), suggesting that shading in leafier species may be ameliorated by their narrower leaves. Long caudices may also have a positive effect on light interception. Future research should assess if the narrow-leaf syndrome increases PAR interception in the relatively shady cloud-belts.

Model validation

Both our models and our field measurements show that *Tillandsia* plants 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. Actually, both fog interception and absorption may be two factors acting synergistically in the evolution of bromeliads, leading to the appearance of narrow-leafed *Tillandsia* and *Vriesea*. The same may be concluded for lichens and mosses with narrow thalli, and for the thin, velamentous roots of some Orchidaceae (Benzing 1990).

While the narrow-leaf syndrome is largely responsible for the high efficiency of atmospheric epiphytes, most of the species that we studied showed a significantly larger interception than that predicted by the mathematical model. Trichomes may be responsible for this difference, since glabrescent species behaved as expected. As well as *Tillandsia*, other nebulophytes present pubescence or hairs that may increase fog interception. Among the xerophytic rosettes, several Nolinaceae have fibrous tufts at the leaf apices, various *Yucca* have filaments at the leaf margins and a large proportion of the species in the genera *Hechtia* and *Puya* are at least partially pubescent. It has been frequently observed that fruticose lichens have ciliate margins and the fog-absorbing needles of *Pinus radiata* have several tubular waxy outgrows (Leyton and Armitage 1968), both of which that may increase interception efficiency. However, several xerophytic rosettes are completely glabrous. This may suggest that pubescence and interception efficiency are unimportant, but since these species do not take water at the leaf surface (in contrast to lichens, *Tillandsia* and conifers, whodo to some extent), a dense hygroscopic toment may represent an obstacle to water flow to the soil.

It has been considered that a rosulate shoot is required for the evolutionary transference of the absorptive role from the root to the foliage (Benzing 1990). The water impoundment in tank bromeliads – which are among the most primitive *Tillandsia* (Gilmartin 1983; Crayn et al. 2004) – would not occur if the internodes were long, and it would be useless if the leaves could not absorb water directly on their surface. In seven out of the nine subgenera in *Tillandsia*, tank species gave rise to atmospheric taxa (Gilmartin 1983). With the evolutionary disappearance of the tank, and with roots serving only as holdfasts, there is no longer a need to conduct and accumulate water in the base of the plant. Since one of the main functions of the funnel-like rosette morphology is thus lost, increasing the length of the internodes would decrease the fog-shadow effect among leaves without any negative effects for the plant. This is supported by our data: non-rosette species had significantly higher efficiencies than rosette ones. Thus, the rosette habit in atmospheric *Tillandsia* can be considered to be an ancestral trait that has lost its adaptive value and become more of a burden than an asset for the most recently derived nebulophytes.

The equations derived from the aluminum models were not significantly correlated to the efficiencies of xerophytic rosettes. This is most probably the result of the differences in the manner used to measure both area and interception efficiency in the models and in these plants. It may also be an outcome of an invalid extrapolation of the mathematical model to much larger and leafier plants. However, while 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. Other taxonomic groups that rely on fogs seemingly resort to narrow structures to capture water droplets. Lichens and mosses with pendant forms with long internodes are best adapted for fog interception (Kürschner and Parolly 1998; Kürschner and Frey 1999). Cacti on coastal deserts and pines in foggy areas condense large amounts of water on their spines and needles (Mooney et al. 1977; Boucher et al. 1995; Dawson 1998). This may increase interception efficiency while increasing the catchment surface and therefore net interception.

Comparative analysis of morphologies

The distribution of rosette plants in the Tehuacán Valley showed that the broad-leafed rosettes occur in lower zones. The plants that are better fog-interceptors increase rapidly in relative abundance until 1900 m a.s.l., where the mean form composition of the rosette community tends to level off. Although fog is most abundant in a belt around 1800 m, most of the narrow-leafed species characteristic of the montane rosette scrub are also the most frequent ones above it. Nevertheless, the overall abundance of rosettes at higher sites is very reduced, probably because fog is not available there (Martorell and Ezcurra 2002). *Agave salmiana*, the rosette with the second lowest form index, is found at the highest altitudes at two of our other study sites, suggesting that the lack of fog may promote massive succulents at high altitudes just as it does in the lowlands.

The evolutionary processes have produced a wide range of forms in the xerophytic rosettes. At least three families – Nolinaceae, Arecaceae, and a part of the Agavaceae (*Yucca*, subgenus *Yucca*) – form a compact group at one extreme of the PCA ordination. We believe this constitutes evidence for a widespread convergence into a narrow range of morphologies. Several of the attributes of this polyphyletic set are the ones that we expected for nebulophytes: large numbers of narrow, long leaves without ornamentation growing on top of caudices. Leaves are curved towards the apex, so the water intercepted at the tips does not leak outwards (Table 3). Flexible leaves, another trait that is believed to optimize fog interception, was 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.

The independent-contrasts method revealed that the most efficient forms are correlated to areas where fog is most likely to be found. By itself, the analysis does not elucidate the direction in which natural selection has acted. If narrow-leafed ancestors had evolved into large, broad-leafed succulents as they descended to the dry, hot lowlands, then the interception of fogs would not necessarily explain the evolutionary altitude-form correlation. However, montane environments and tree crowns also pose a pressure for water storage. In these environments, rosettes of most of the studied families have also evolved succulence, but not into massive leaf blades. Spongy caudices, enlarged leaf sheaths or several, very narrow but still succulent leaves have solved the problem of water impoundment in montane species and epiphytes without compromising the narrow-leaf syndrome. These species did not become massive leaf succulents because, being nebulophytes, they seemingly evolved under the selective pressure for long, slender leaves and fog capture.

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. The most efficient fog-harvesting rosettes should have a small number of narrow and long leaves.
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 narrow ones. At the limits set by this constraint, net fog interception is independent of leaf-form, but interception efficiency is maximized by having several narrow leaves. These attributes usually occur in nature simultaneously with other ancillary traits (caudices, epiphytism, and/or flexible leaves), thereby constituting a syndrome that characterizes fog-harvesting species.
3. Atmospheric *Tillandsia* species show the narrow-leaf syndrome. Their fog interception efficiencies are correlated to the ones predicted 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 at high altitudes where fog occurs fre-

quently. 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.

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