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ORIGINAL ARTICLE

Leaf traits and fog harvest potential in xerophytic plants

Rasgos de las hojas y potencial de cosecha de niebla en plantas xerófitas

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ABSTRACT

Fog is an important water resource for ecosystems in arid zones, where plants play a key role in fog harvest. Studies on adaptive traits for fog interception have been addressed mainly in terms of forest tree species, considering stand distribution, shoot architecture, and leaf inclination angle, with less emphasis on leaf surface traits. Moreover, xerophytic shrubs, whose role in fog capture is only recently being recognized, have been barely studied in this regard. We analyzed leaf traits, and fog throughfall in 11 and 12 xerophytic species of two sites (xeric and mesic) in semi-arid northern-central Chile, with a combination of laboratory and field experiments. According to principal component analyses, in the xeric site, leaf water retention capacity was positively associated with fog drip. In the mesic site, hydrophobic leaves dripped less fog water than the hydrophilic ones. The magnitude of the variability depended on the xeric or mesic nature of sites, suggesting a differential adaptation to fog abundance on these sites. Overall, our results show leaf functional traits of xerophytic plants associated to the capacity of fog water capture and retention. The relation between leaf traits and fog harvest is species-specific, since every species is a mixture of different traits that do not necessarily optimize fog harvest. This research opens prospects for the screening of mechanisms and ecosystem services of xerophytes as natural fog catchers.

Keywords: cloud forests, natural fog catchers, shrublands, succulent plants, xerophytes.

RESUMEN

La niebla es un recurso hídrico importante para los ecosistemas de zonas áridas, donde las plantas desempeñan un papel clave en la recolección de niebla. Los estudios sobre los rasgos adaptativos para su intercepción se han realizado principalmente en especies de árboles en bosques, considerando la distribución del rodal, la arquitectura del vástago, y el ángulo de inclinación de las hojas, con menos énfasis en los rasgos de la superficie de las hojas. Además, los arbustos xerófitos, cuyo papel en la captura de niebla está recientemente siendo reconocido, han sido apenas estudiados a este respecto. Analizamos los rasgos foliares y el goteo de niebla en 11 y 12 especies xerofíticas en dos sitios (xérico y mésico) en el semiárido del centro-norte de Chile, con una combinación de experimentos de laboratorio y de campo. De acuerdo al análisis de componentes principales, en el sitio xérico, la capacidad de retención de agua de la hoja se relacionó positivamente con el goteo de niebla. En el sitio mésico, las hojas hidrofóbicas gotearon menos agua de niebla que las hidrofílicas. La magnitud de la variabilidad dependió de la naturaleza xérica o mésica de los sitios, lo que sugiere una adaptación diferencial a la abundancia de niebla de estos sitios. En general, nuestros resultados muestran rasgos funcionales foliares de plantas xerófitas asociados a la captura y retención del agua de niebla. La relación entre los rasgos de las hojas y la recolección de niebla es específica de cada especie, ya que cada una de ellas es una mezcla de diferentes rasgos que no necesariamente optimizan la recolección de niebla. Esta investigación abre perspectivas para la búsqueda de mecanismos y servicios ecosistémicos de las xerófitas como captadoras de niebla naturales.

Palabras clave: atrapanieblas naturales, bosques nubosos, matorrales, plantas suculentas, xerófitas.

INTRODUCTION

Fog is an important water resource for plant communities of cloud ecosystems from arid and semi-arid regions of the world (Aravena *et al.* 1989; Barbosa *et al.* 2010). Fog has also been used by humans to sustain agriculture, livestock, forestry, and human consumption (Leiva & Hernández 2014). Usually, fog is collected via fog catchers, special meshes that trap fog droplets (Rivera & Holmes 2014). Plants in cloud ecosystems can act as living fog catchers (Vogelmann 1973, Fischer *et al.* 2009, Hildebrandt & Eltahir 2006). Plants play important roles in most hydrological flows in terrestrial ecosystems, including precipitation interception, retention, spatial redistribution of water above and below the ground, as well as water loss through evaporation and transpiration (Huber *et al*. 2008, Lazo *et al.* 2019). The water intercepted by plants can follow different routes, such as free fall (Bellot *et al.* 1999), evaporation from leaf surface, intrafoliar uptake (Bryant *et al.* 2021), and drainage via branches and stems (stem flow; Sadeghi *et al.* 2020).

Large-scale approaches partially explain the different pathways through which fog precipitation reaches the soil. Attributes such as stand area have been found to scale positively with stemflow volume and soil-and-litter water contents (Barbosa *et al.* 2010). Medium scale-approaches have been used to study variations in the canopy structure of tree species (e.g., vertical stratification, branching patterns, crown biomass, canopy roughness; Chung *et al.* 2017). Indeed, canopy structure can significantly alter the water inputs to the system, through the capture and channeling of fog and rain to the soil (Hutley *et al.* 1997, Weathers *et al.* 2006). On a smaller scale, leaf projection and a high leaf inclination angle can significantly affect fog collection (Squeo *et al.* 2004).

Plant fog harvest has typically been studied in cloud forest species (Nagel 1956, Vogelmann 1973, Fischer *et al.* 2009, Hildebrandt & Eltahir 2006). However, recently xerophytic shrubs and cacti scattered among cloud forests or growing peripherally have been found to be fog harvesters (Stanton *et al.* 2014b, Chung *et al.* 2017, Cuevas *et al.* 2023). For example, Cuevas *et al.* (2023) reported that the plant height of xerophytic plants explained *ca.* 60% of the variance in fog harvest. The unexplained variance, though, makes the study of other plant attributes, such as leaf traits necessary. Among key leaf traits that determine water interception on plant surfaces are the leaf area and mass, leaf water retention capacity, leaf hydrophobicity, and water droplet retention (Rosado & Holder 2013, Holder 2012, Ginebra-Solanellas *et al.* 2020). First, the leaf size (mass, area) has been associated with the degree of sclerophylly, hence, it is related to the capacity of plants to save water under arid and semi-arid environmental conditions (Pompelli *et al.* 2019, Alonso-Forn *et al.* 2020). Moreover, large leaves intercept more fog than smaller ones (Martorell & Ezcurra 2007). Second, water retention is understood as the capacity to store water in the leaf, both internally and externally (Holder 2012). Leaf morphology and surface type can significantly affect this capacity, e.g., leaves with curvatures, sharp apices, and trichomes facilitate wettability, interception, and runoff of water captured from fog (Holder 2012). In addition, the presence of salt glands confers leaves with a hygroscopic capacity (Mooney *et al.* 1980, Nguyen *et al.* 2017). Morphological innovations permit the diffusion of water from the leaf surface to its interior, such as the presence of hydathodes, aquaporins, and permeable cuticles, which help maintain leaf turgor and plant water retention when soil water is at extremely negative water potentials (Eller *et al.* 2013). Thirdly, water droplets tend to be repelled when they fall on hydrophobic surfaces with high contact angles, while water spreads across the surface as a film on hydrophilic surfaces with low contact angles (Rosado & Holder 2013). The surface features that most affect wettability include cuticular waxes and trichomes (Holder 2020, Jura-Morawiec & Marcinkiewicz 2020).

Consequently, we studied the leaf size, leaf water retention capacity, and leaf hydrophobicity of xerophytic plants as possible determinants of fog harvest-and-drip. Thus, by studying the leaf traits of natural communities of xerophytic plants we can learn about adaptations that improve fog collection efficiency. Here, we hypothesized that: i) a leaf with a higher fog retention capacity presents a high resistance to water dripping onto the soil; and ii) hydrophobic leaves capture spherical, low diameter drops that are more easily released than flattened, high diameter drops typical of hydrophilic leaves. Our main goal was to determine leaf properties of xerophytic plants associated with fog harvest to better understand their role and efficiency in fog collection, and improve our current understanding of fog harvest in natural communities of semi-arid ecosystems.

MATERIALS AND METHODS

Study sites

We selected two sites in the Coquimbo Region, Chile, with ~ 5,000 m^2 area, the northernmost Majada Blanca (MB; 30° 03' 52" S, 71° 19' 24" W, 670 m a.s.l., Coquimbo municipality) and the southernmost Los Tomes (LT; 31° 29' 23" S, 71° 31' 50" W, 830 m a.s.l., Canela municipality). They were selected and delimited based on the frequency and intensity of fog occurrence, and the presence of xerophytic shrubland (11-12 species per site). Most species were shrubs, except *Eulychnia breviflora* Phil. and *Echinopsis chiloensis* (Colla) Friedrich & G.D. Rowley subsp. *litoralis* (Johow) Lowry (both cacti), *Bahia ambrosioides* Lag. (sub-shrub), *Escallonia pulverulenta* (Ruiz & Pav.) Pers. var. *pulverulenta* (a small tree), *Lobelia tupa* L. (a large herb), and *Puya chilensis* Molina (a rosette herb) (nomenclature according to Rodríguez *et al.* [2018]).

Both sites are located on the Coastal Range of the Coquimbo Region in semi-arid northern-central Chile. These locations are representative of a north-south gradient from xeric to mesic conditions (Montecinos *et al.* 2016). The interaction of the orographic characteristics of the area and marine air currents from westerlies produces both advection and orographic fog types (see extended details of the study sites in Cuevas *et al.* 2023). Rainfall was estimated as *ca.* 25-35 mm in the year 2021, but even in average years, it does not rain more than 80 mm according to measurements carried out at lowlands (https://www.ceazamet.cl; see Cuevas *et al.* 2023 for meteorological details from these sites). The same authors measured 250 mm of precipitation (mostly fog) in MB, and 1,192 mm in LT through standard fog collectors.

Leaf traits

Branches of each species, with healthy and fully expanded leaves, were randomly sampled within the plots of the two sites. Sampling was carried out in the spring of 2021, 2022, and the autumn of 2022 for the MB site; and in the autumn-winter of 2021 and the spring of 2022 for the LT site. Each branch was carefully cut and immediately wrapped in a wet paper towel and stored in sealed plastic bags in a cooler. Samples were taken to the laboratory for further analyses (see below). For each test, a total of 15 leaves per species were used as replicates (three leaves per individual, five individuals per species). Each experimental test was conducted with a unique set of leaves per species, avoiding the re-use of a leaf in subsequent tests.

Leaf mass and area

First, a photo of each fresh leaf sample was taken and analyzed with the ImageJ software (ImageJ; nih.gov) to calculate leaf area. Then, the leaves were dried at 72 °C for 72 hours to determine leaf mass with a resolution of 0.1 mg (Pérez-Harguindeguy *et al.* 2013). We also calculated the amount of leaf mass contained per leaf area (LMA), as a proxy for sclerophylly (Squeo *et al.* 2004) and leaf longevity (Alonso-Forn *et al.* 2020).

Water retention capacity (WRC)

Each fresh leaf was weighed using an analytical balance. Then, each leaf was placed on a support covered with Parafilm® paper; holes were made to mount the petioles of each leaf after which they were arranged vertically. Then, the leaves were sprayed three times with distilled water to simulate the effect of fog in the field. After 30 seconds of waiting for the excess water to drain, each leaf was weighed to determine its wet weight. The fresh weight (FW) value was subtracted from the wet weight (WW), and the result was divided by the fresh weight, obtaining a delta for each leaf, which was expressed as a percentage, as indicated by the following formula:

$$WRC = ((WW - FW) / FW) * 100$$

Hydrophobicity

Leaf hydrophobicity was determined by analyzing the diameter of a droplet formed on the leaf surface (Fig. 1): the lower the droplet diameter, the more hydrophobic the leaf surface. For this, each leaf was placed under a stereoscopic magnifying glass, and a 6 µL drop of distilled water was applied with a micropipette on the adaxial surface of the leaf. The droplet's size was within the range of previous studies (Azad 2016, Merrium *et al.* 2022). Then, a photograph was taken through the magnifying glass and analyzed using ImageJ software to obtain the diameter of each droplet.

Fog drip from plants

For a detailed database of fog harvest by plants, see Cuevas *et al.* (2023). Briefly, three plants of each species were randomly selected and two to three plastic funnels (14 cm diameter) connected to a 1 L-plastic bottle were placed beneath each plant in the field to collect the fog or rain dripped. The other four funnel-bottle systems were placed randomly in open spaces as a control, without the influence of the plants. Each bottle was filled with a 5 mm layer of petroleum jelly to avoid water evaporation. Overall, 101 and 99 (MB and LT, respectively) sampling units were installed at each site.

Each bottle was sampled monthly. The collected bottles were measured in the laboratory with a combination of extractions with catheters, syringes, and 50-, 100-, or 250-mL measuring cylinders. The amount of water that funnels received (in L) was divided by the funnel cross section (0.0154 m^2) to calculate the equivalent of water collected (mm).

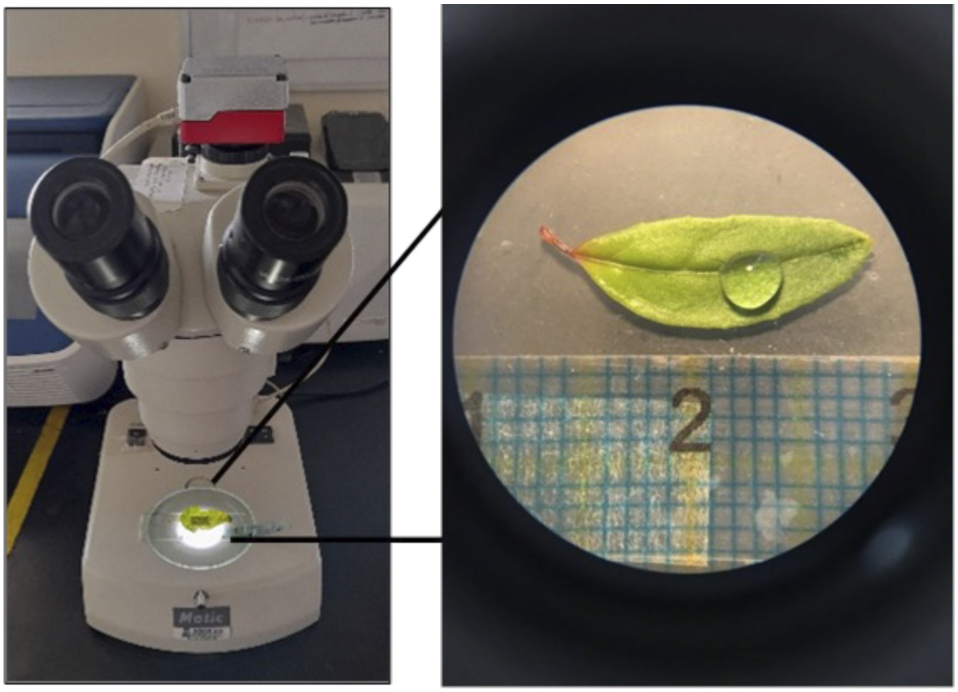

Figure 1. Measurement of the droplet diameter on the leaf surface of *Fuchsia lycioides*. The reference scale to the right corresponds to 1 mm^2 for each square. / Medición del diámetro de gota en la superficie foliar de *Fuchsia lycioides*. La escala de referencia a la derecha corresponde a 1 mm^2 cada cuadrado.

Data analyses

Leaf traits were compared among species through Kruskal-Wallis tests because data were not normally distributed nor they were homoscedastic. To compare the fog drip among species, we used a nested analysis of variance because the field design followed a hierarchical scheme. Data were transformed to satisfy ANOVA assumptions with the Box-Cox function provided by Wessa (2021) at: http://www.wessa.net/rwasp_boxcoxnorm.wasp#output. The *post hoc* tests of Tukey and multiple comparisons of mean ranks were used to identify significant differences among pairs of species.

Principal component analyses (PCA) were used to test the associations among leaf traits and fog drip. First, the variables were checked for normal data distributions. If this assumption was not fulfilled, Log_{10} and arcsin transformations were performed. Second, the Bartlett's test of sphericity was used to prove that the correlation matrix of variables differs significantly from the identity matrix, i.e., there is some degree of correlation among variables. Analyses were done with Statistica 7.0 software (StatSoft Inc., Tulsa, Oklahoma, USA).

RESULTS

Leaf mass and area, LMA

In the MB site, *Senna cumingii* (Hook. & Arn.) H.S. Irwin & Barneby showed the highest value for dry weight (0.11 g), while *Junellia selaginoides* (Kunth ex Walp.) Moldenke var. *illapelina* (Phil.) Botta and *Adesmia microphylla* Hook. & Arn. demonstrated the lowest (0.00108 g and 0.00209 g, respectively) (Fig. 2A). *S. cumingii* had the highest leaf area

($10.38\ cm^2$), whilst *Heliotropium stenophyllum* Hook. & Arn. ($0.33\ cm^2$), *A. microphylla* ($0.25\ cm^2$), and *J. selaginoides* ($0.16\ cm^2$) had the lowest (Fig. 2B). The cactus *E. breviflora* showed the greatest LMA value ($649.29\ g/m^2$) (Fig. 2C). In contrast, *Proustia cuneifolia* D. Don, *Gutierrezia resinosa* (Hook. & Arn.) S.F. Blake, *Baccharis paniculata* DC., and *Fuchsia lycioides* Andrews showed the lowest LMA values ($33.88\ g/m^2$; $23.96\ g/m^2$; $21.22\ g/m^2$; and $14.92\ g/m^2$, respectively).

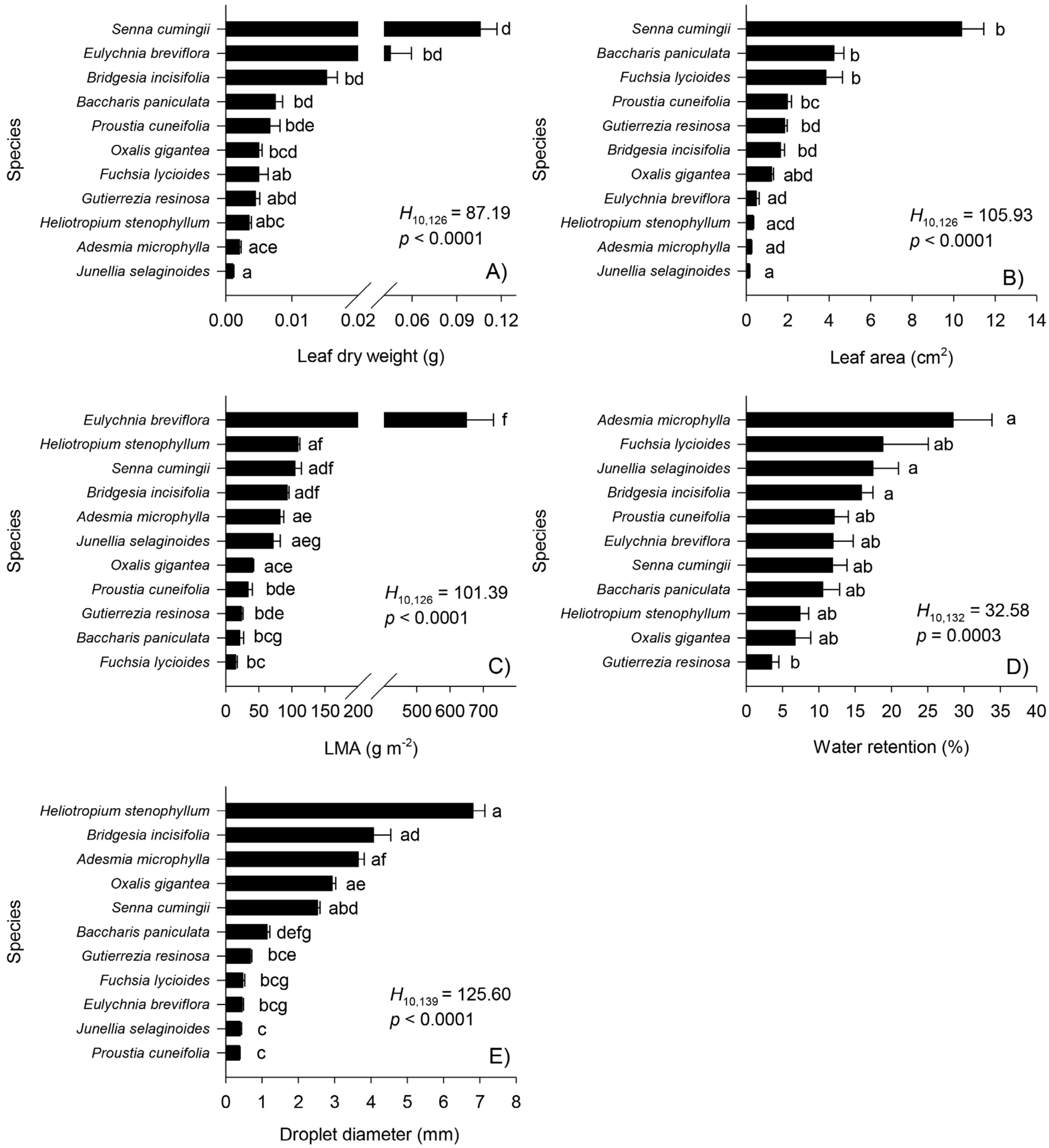

Figure 2. Leaf traits: leaf dry mass (A), leaf area (B), leaf mass/ area ratio (LMA) (C), water retention (D), and droplet diameter (E), for the species studied in the Majada Blanca (MB) site, arranged in decreasing order. Values represent means ± standard error. The letters indicate the difference between the means by non-parametric Kruskal-Wallis (*H*) analyses with a *post hoc* test for multiple comparisons. *p* = probability for the test. / Rasgos de hoja: peso seco foliar (A), área foliar (B), proporción peso/área foliar (LMA) (C), retención de agua (D), y diámetro de la gota (E), para las especies estudiadas en el sitio Majada Blanca (MB), acomodadas en orden decreciente. Los valores representan promedios ± error estándar. Las letras indican la diferencia entre medias en los análisis no paramétricos de Kruskal-Wallis (*H*), con pruebas *post hoc* de comparaciones múltiples. *p* = probabilidad de la prueba.

In the LT site, the greatest value of leaf dry weight was found for *P. chilensis* (0.50 g), and the lowest for *Muehlenbeckia hastulata* (Sm.) I.M. Johnst. var. *hastulata* and *B. ambrosioides* (*ca.* 0.005 g each) (Fig. 3A). *P. chilensis* showed the greatest leaf area (108.88 cm^2), as opposed to *E. chiloensis* (cactus) (0.14 cm^2) (Fig. 3B). Finally, *E. chiloensis* demonstrated the highest LMA value (654.30 g/m^2), while *L. tupa* (10.05 g/m^2) showed the lowest (Fig. 3C).

WATER RETENTION CAPACITY (WRC)

In the MB site, *A. microphylla*, *F. lycioides*, and *J. selaginoides* were found to retain a high amount of water (28.49%, 18.82%, and 17.45%, respectively). On the other hand, the species *G. resinosa* showed the lowest water retention capacity (3.52%) (Fig. 2D).

In the LT site, *Gochnatia foliolosa* (D. Don) D. Don ex Hook. & Arn. var. *foliolosa* showed the highest water retention capacity (13.55%), as opposed to *Lobelia polyphylla* Hook. & Arn. (1.76%) (Fig. 3D).

HYDROPHOBICITY

In MB, the smallest droplet diameters were found on *J. selaginoides* and *P. cuneifolia* (0.40 mm and 0.38 mm, respectively). On the contrary, the largest water droplet was recorded on *H. stenophyllum* (6.81 mm), categorizing this species as hydrophilic (Fig. 2E).

In LT, the smallest droplet diameter was observed on *A. microphylla* (0.19 mm), while *E. chiloensis* showed the greatest droplet diameter (2.15 mm) (Fig. 3E).

FOG DRIP FROM PLANTS

Based on twelve months of cumulative data in MB, *E. breviflora* was the best fog collector, with 182 mm, followed by *A. microphylla* (95 mm), and *B. paniculata* (68 mm). Controls harvested 60 mm. Three additional species (*Oxalis gigantea* Barnéoud, *F. lycioides*, and *S. cumingii*) also dripped more water than the control, while others such as *G. resinosa* showed less fog drip than the control (Fig. 4A), but these differences were not significant. *E. breviflora* statistically differed from all species except *A. microphylla* and *B. paniculata*. Moreover, *A. microphylla* significantly differed from *Bridgesia incisifolia* Bertero ex Cambess.

In LT, the amount of water collected was higher than in MB, as revealed by control data (118.6 mm). Accumulatively, *E. pulverulenta* (145 mm) and *E. chiloensis* (123 mm) collected more than the control, though this difference was not significant (Fig. 4B). Nonetheless, most species accumulated less than the control (e.g., *Baccharis vernalis* F.H. Hellwig, *L. tupa*). Overall, significant differences were found when comparing *E. pulverulenta* with *B. vernalis*, *B. ambrosioides*, *Berberis actinacantha* Mart., *M. hastulata*, and *P. chilensis*. Moreover, *B. actinacantha* differed significantly from *E. chiloensis*.

PCA ANALYSIS: MAJADA BLANCA

In a first analysis, LMA appears to be a main leaf trait associated positively with fog drip (data not shown). However, since the *E. breviflora* (*Eb*) datum is markedly higher than the other species data (i.e., it could be an outlier, Fig. 2C), we checked if this pattern could be influencing the strength of the relationship. Accordingly, we repeated the analysis without including the *Eb* datum. In Fig. 5A, only two axes were extracted (explaining 38.8 and 29.8% of the variance, summing up to 68.6%), while the third axis was not considered because it did not show a clear contribution of any predominant variable. The first one was related mostly to WRC in the positive side, and area in the negative side. *Am* and *Js* effectively were high WRC species, and they were located in the positive side of Axis 1 in Fig. 5B, according to the expected. Leaf area in Fig. 5A predicts that *Sc*, *Gr*, *Bp* should have larger leaves (Fig. 5B), which is finely met (Fig. 2B).

The second axis separates droplet diameter, LMA towards the positive side, and fog drip to the negative side (Fig. 5A). *Sc*, *Bi*, *Hs* are predicted correctly as having high LMA or relatively high diameter (Figs. 5B, 2C, E). Regarding fog drip, *Fl*, *Bp*, *Js*, *Am* were in the negative side of Axis 2 (i.e., they should have a high fog drip) (Fig. 5B). These predictions are closely supported by Fig. 4A, except for *Js*.

In summary, Fig. 5A shows a positive association of fog drip with WRC, and negative with leaf mass. The effect of LMA on fog drip detected in the first analysis seems to be only a coincidence between the highest fog collector species *E. breviflora* and its high LMA.

In spite there is an acceptable ordination of species in the PCA space, which is supported by leaf trait and fog drip data (Figs. 2, 4), species do not align perfectly along a low to high magnitude gradient of traits. For instance, *Fl* should be in a middle position in Fig. 5B, given its intermediate fog drip, but it is located in an extreme position instead.

PCA ANALYSIS: LOS TOMES

Following the results obtained for LMA in MB, we chose not to include the highest LMA species (the cactus *E. chiloensis*) in the analysis. In Los Tomes, the three axes extracted from the PCA explained 39.7, 27.2, and 20.2% of the variance, summing up to 87.2%. The first axis had a strong contribution of leaf mass and area in the negative side, which can be associated to *Pch* and *Ep* (Figs. 6A, B), a prediction supported by Figs. 3A, B.

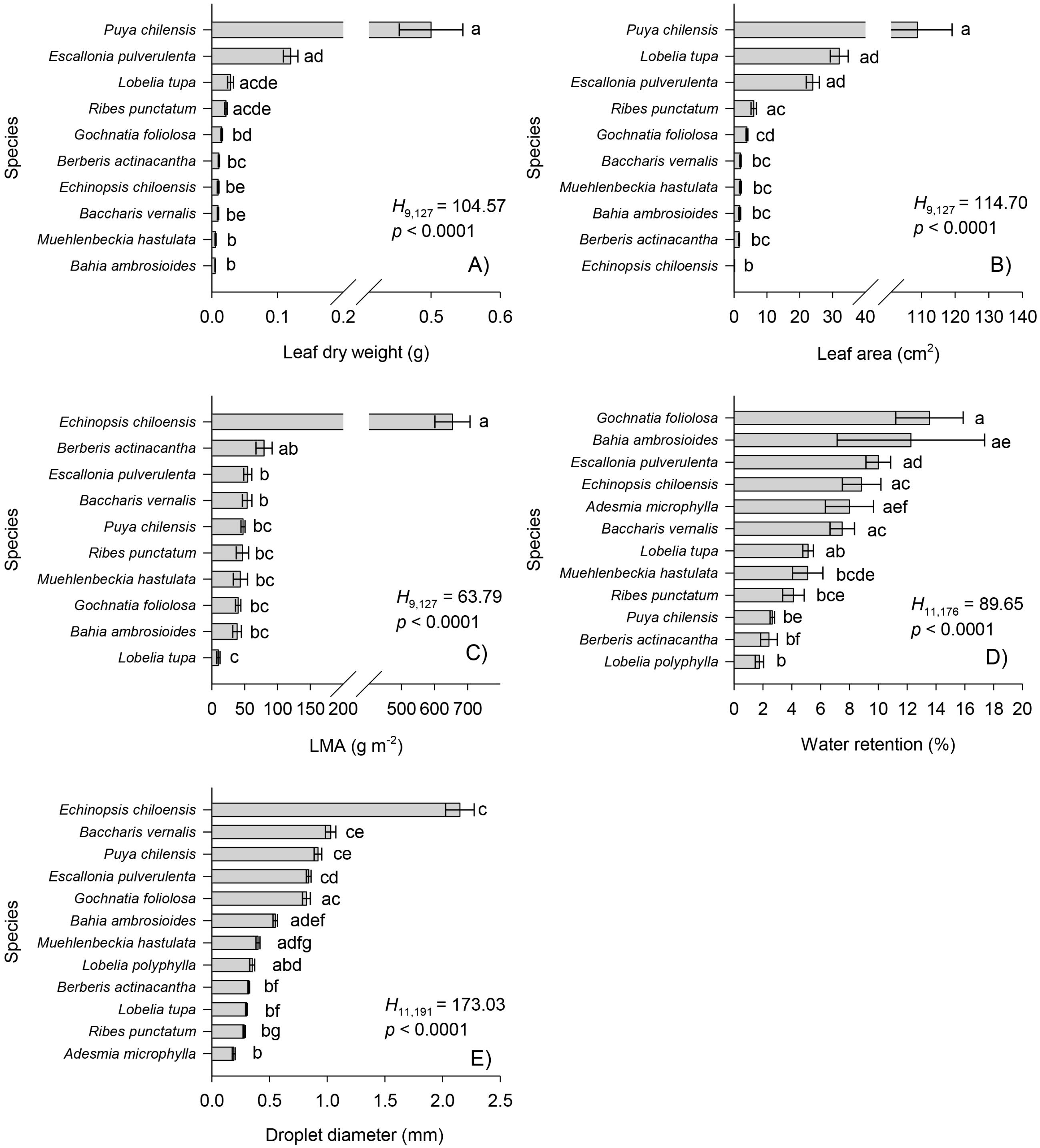

Figure 3. Leaf traits: leaf dry mass (A), leaf area (B), leaf mass/ area ratio (LMA) (C), water retention (D), and droplet diameter (E), for the species studied in the Los Tomes (LT) site, arranged in decreasing order. Values represent means ± standard error. The letters indicate the difference between the means by non-parametric Kruskal-Wallis (H) analyses with a *post hoc* test for multiple comparisons. p = probability for the test. / Rasgos de hoja: peso seco foliar (A), área foliar (B), proporción peso/área foliar (LMA) (C), retención de agua (D), y diámetro de la gota (E), para las especies estudiadas en el sitio Los Tomes (LT), acomodadas en orden decreciente. Los valores representan promedios ± error estándar. Las letras indican la diferencia entre medias en los análisis no paramétricos de Kruskal-Wallis (H), con pruebas *post hoc* de comparaciones múltiples. p = probabilidad de la prueba.

The second axis is mostly determined by WRC in the positive side (Fig. 6A), coinciding with the location of *Gf*, *Ep* and *Ba* in the same side (Fig. 6B), which showed high WRC (Fig. 3D). The third axis had only a strong contribution of LMA in its positive side (Fig. 6A), which should mean a high magnitude for this leaf trait in *Bv* and *Be*. This is in agreement with Fig. 3C.

Fog drip had a stronger association with droplet diameter (positive), which is revealed by the red vector pointing to the direction of both variables that project both in the Axis 1 and 2 (Fig. 6A). This association caused that some species such as *Ech*, *Ep*, and *Gf* (high drip) had a high droplet diameter (Figs. 4B, 3E).

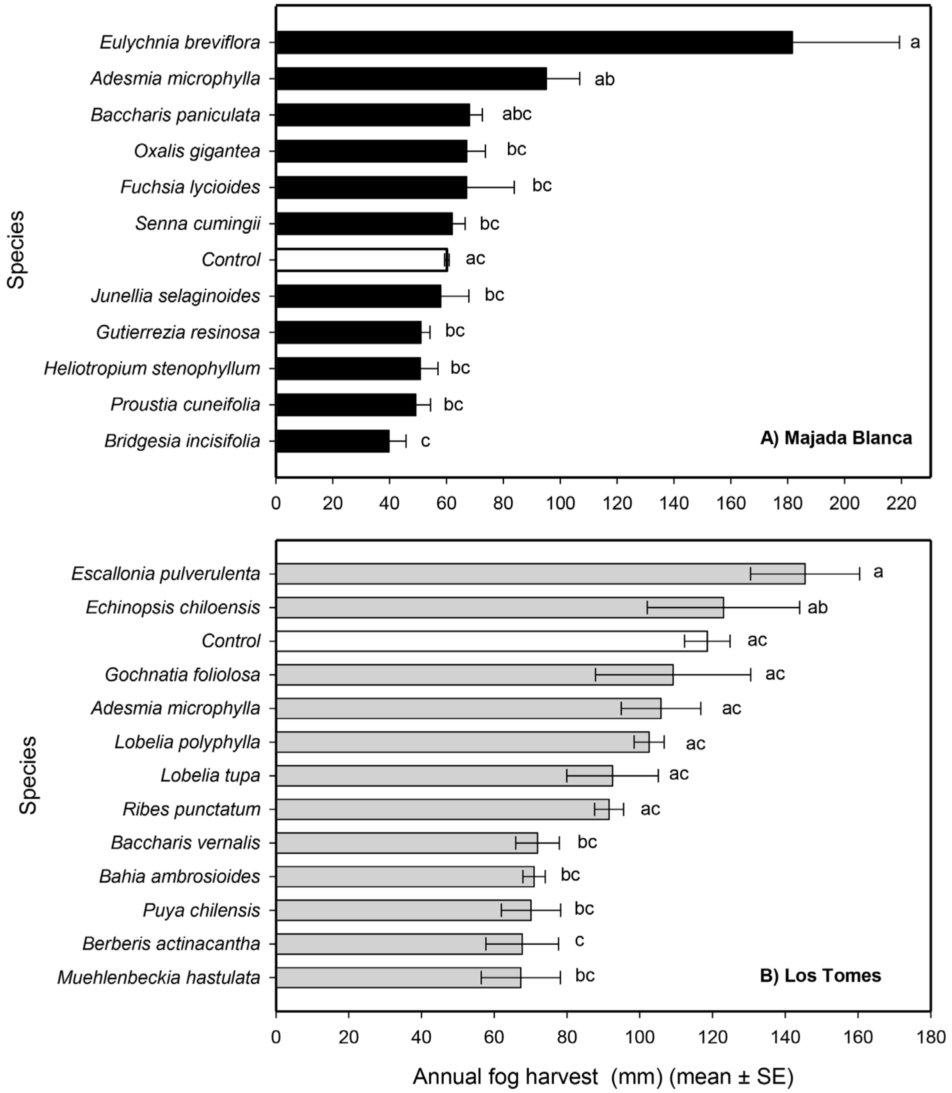

Figure 4. Cumulated water harvest for different xerophytic species at Majada Blanca and Los Tomes sites throughout the years 2021-2022. The control bars correspond to funnels that collected water in open sites. Different superscripts indicate differences at $p \leq 0.044$ (Majada Blanca) and $p < 0.020$ (Los Tomes) (unequal *N* Tukey tests after nested Anovas). / Cosecha de agua acumulada para diferentes especies de xerófitas en los sitios Majada Blanca y Los Tomes en los años 2021-2022. Las barras control corresponden a embudos que colectaron agua en sitios abiertos. Diferentes superíndices indican diferencias a $p \leq 0.044$ (Majada Blanca) y $p < 0.020$ (Los Tomes) (pruebas de Tukey con *N* desigual después de Andevas anidados).

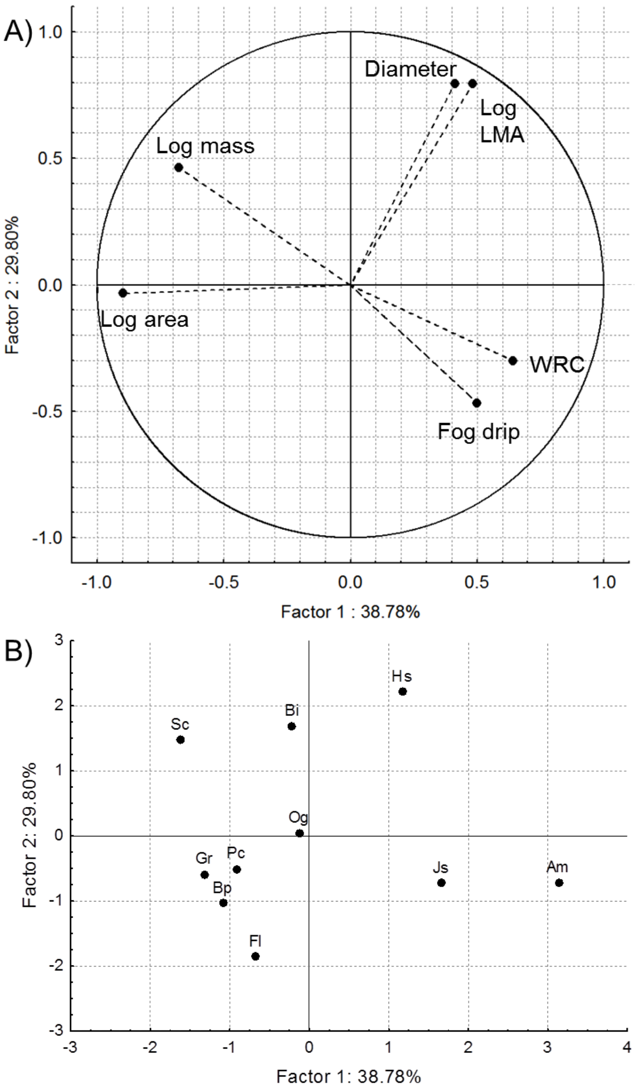

FIGURE 5. Principal components analysis for the site Majada Blanca. The percentages indicate the explained variation by each axis. A) Leaf traits and fog drip. WRC = water retention capacity; LMA = leaf mass:area ratio. Dashed lines are vectors pointing to the variables from the 0,0 coordinate. The circle represents a correlation of radius 1.0 to facilitate point visualization. B) Spatial arrangement of the species analyzed, except for *Eulychnia breviflora*, considered an outlier for LMA. Species code: *Am* = *Adesmia microphylla*, *Bi* = *Bridgesia incisifolia*, *Bp* = *Baccharis paniculata*, *Fl* = *Fuchsia lycioides*, *Gr* = *Gutierrezia resinosa*, *Hs* = *Heliotropium stenophyllum*, *Js* = *Junellia selaginoides*, *Og* = *Oxalis gigantea*, *Pc* = *Proustia cuneifolia*, *Sc* =*Senna cumingii*. / Análisis de componentes principales para el sitio Majada Blanca. Los porcentajes indican la variación explicada por cada eje. A) Rasgos de hoja y goteo de niebla. WRC = capacidad de retención de agua; LMA = cociente masa: área foliar. Las líneas segmentadas son vectores apuntando hacia las variables desde la coordenada 0,0. El círculo representa una correlación de radio 1.0 para facilitar la visualización de los puntos. B) Ordenación en el espacio de las especies analizadas, excepto *Eulychnia breviflora*, que fue considerada un valor extremo para LMA.

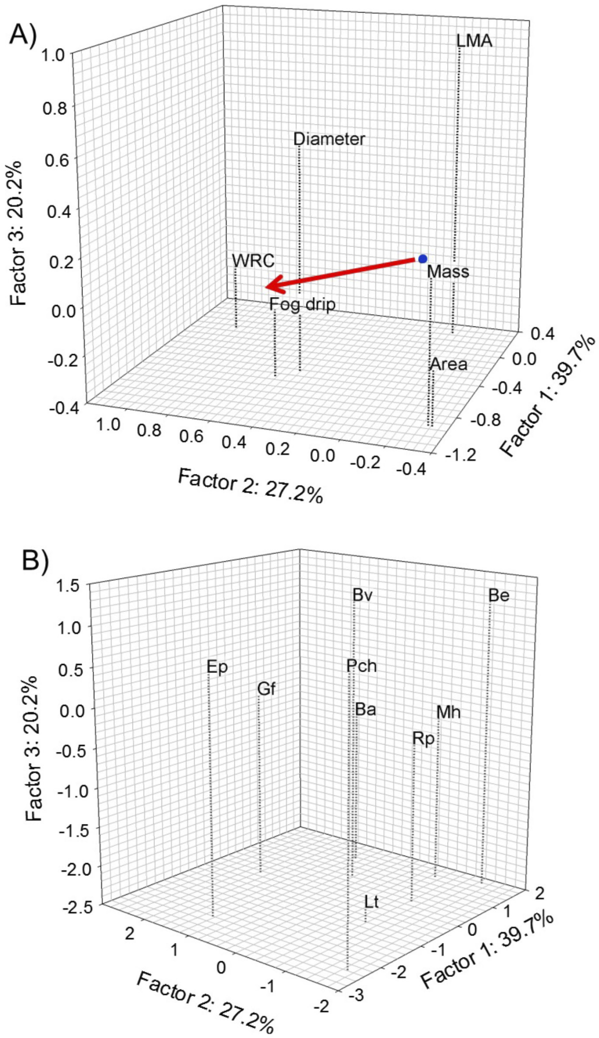

FIGURE 6. Principal component analysis for the site Los Tomes. The percentages indicate the explained variation by each axis. A) Leaf traits and fog drip. WRC = water retention capacity; LMA = leaf mass:area ratio. Mass and area were Log_{10} transformed, while LMA was arcsin transformed. The red vector represents the projection of fog drip and droplet diameter along the axis 1 and 2, starting from the 0,0,0 coordinate indicated by the blue point. B) Spatial arrangement of the species analyzed, except for *Echinopsis chiloensis*, considered an outlier for LMA. Species code: *Ba* = *Bahia ambrosioides*, *Be* = *Berberis actinacantha*, *Bv* = *Baccharis vernalis*, *Ep* = *Escallonia pulverulenta*, *Gf* = *Gochnatia foliolosa*, *Lt* = *Lobelia tupa*, *Mh* = *Muehlenbeckia hastulata*, *Pch* = *Puya chilensis*, *Rp* = *Ribes punctatum*. / Análisis de componentes principales para el sitio Los Tomes. Los porcentajes indican la variación explicada por cada eje. A) Rasgos de hoja y goteo de niebla. WRC = capacidad de retención de agua; LMA = cociente masa: área foliar. La masa y área fueron transformados con la función Log_{10}, mientras que LMA lo fue con la función arcsen. El vector rojo representa la proyección del goteo de niebla y el diámetro de la gota a lo largo de los ejes 1 y 2, comenzando desde la coordenada 0,0,0 indicada por el punto azul. B) Ordenación en el espacio de las especies analizadas, excepto *Echinopsis chiloensis*, que fue considerada un valor extremo para LMA.

DISCUSSION

GENERAL APPROACH

As fog consists of small water droplets deposited on the plant surface through airflow, rather than by gravity, it represents a horizontal type of precipitation. Contrary to rainfall, its interception can be a net gain for the ecosystem since fog does not normally precipitate to the ground unless there is vegetation or an artificial fog catcher (Bruijnzeel *et al.* 2005, Stanton *et al.* 2014a, 2014b). This phenomenon suggests that a tighter relationship should exist between fog offer and the plant strategies for fog capture. In fact, in the present study species were heterogeneous in terms of life form and leaf properties, and thus they should harvest fog differently. Indeed, some xerophytes showed abundant fog capture, supplying more water to the soil through fog precipitation compared to control conditions.

The use of PCAs allowed a representation of different leaf traits and fog drip in a multivariate space, in order to associate plant variables that mostly contribute to fog harvest. In spite of PCAs produced a close approximation to the patterns observed in field and laboratory conditions, there were important exceptions in the relationships predicted by Figs. 5, 6 when applied to a particular species. It is likely that a specific leaf trait may be more important than the others, and they can even cancel their effects upon fog drip. This is expectable because many plant traits can vary in different directions among species, and not all traits with a high development optimize the capture of a given environmental resource, such as fog. In fact, alternative methods to study these issues have used artificial "plant" models constructed with aluminum, successfully testing hypotheses about fog harvest and a particular leaf geometry (Martorell & Ezcurra 2007). Consequently, the relation between leaf traits and fog harvest is expected to be species-specific, and only valid when a particular trait is varying, while all the others kept constant.

LEAF TRAIT EFFECTS ON FOG DRIP

Our analyses of leaf traits clearly approximated the capacity of the studied species to capture fog water in relation to their leaves/spines. Leaf size was smaller in MB plants than in LT. Conversely, MB plants showed higher values for the traits associated with a greater capacity to capture fog water, as well as sclerophylly, compared to plants at the LT site. Since MB plants were less exposed to fog (250 vs. 1,192 mm/yr in LT, standard fog collector data), a plausible explanation could be that the northern plants could have developed adaptive leaf traits to better capture and retain fog than plants in more mesic habitats further south. Hence, in the most xeric habitats (in MB), plants could optimize water capture for their subsistence and vital functions. In addition, the fact that plants in MB were more sclerophyllous coincides with an increased leaf longevity and a greater ability to prevent water loss from leaf cells (Alonso-Forn *et al.* 2020). Cuevas *et al.* (2023) have also found that the species at MB exhibited a stronger correlation of fog harvest with monthly fog occurrence compared to plants from LT. Moreover, the efficiency of fog collection was also higher in MB (72.5 vs. 12% in *E. breviflora* and *E. pulverulenta*, respectively).

Leaf mass was negatively associated with the fog harvested. Since a heavier leaf should also be larger (keeping LMA constant), it should capture a large amount of fog given its size. Thus our results disagree with previous findings (Martorell & Ezcurra 2007) that have shown a positive relationship between both variables. According to our observations, lightweight leaves, like those of *A. microphylla*, divide their mass-area in tiny folioles (1-2 mm diameter), which are expected to allow the pass of air free of obstructions, interacting more closely with the small fog droplets and contributing to their capture and later dripping. This may explain the observed relationship. However, if the leaf area index (which was not assessed) differed significantly among species, it could lead to varying fog harvest rates, either higher or lower, depending on the total plant leaf area. Consequently, this topic is worthy of further research.

No relationship of the mass:area ratio (LMA) with the amount of water captured by fog drip was detected, after the exclusion of the outliers attributed to *E. breviflora* and *E. chiloensis* cacti. Despite we do not discard that this effect could exist, there may be other traits for these species that could produce a high fog drip (e.g., its high stature, 2-3 m; Cuevas *et al*. 2023). Moreover, the cacti spines resemble the needles of some conifers, which have previously been described as good fog collectors (Martorell & Ezcurra 2007), following the narrow leaf syndrome. Previous research by Squeo *et al.* (2004) found that tree stands located in areas with less fog delivery have leaves with a greater LMA than those located in more humid areas. LMA therefore appears to be more closely associated with the limitation of evapotranspiration losses rather than the optimization of fog harvest.

In LT, the droplet diameter showed a positive relation with fog harvest, which is counterintuitive considering that a droplet that interacts more fully with the leaf surface (i.e., high diameter) is less likely to be liberated by gravity and wind. However, this result becomes coherent when considering the MB results, which showed that water retention capacity also positively related to fog harvest. Initially, it might be expected that higher water retention by leaves would make it less probable for fog to be collected in the funnels. Instead, the positive association observed between both variables indicates that leaves must retain fog for a certain period of time before it drips to the soil. This finding, combined with the observation that hydrophilic leaves drip more fog water compared to hydrophobic leaves, underscore the importance of the critical processes occurring on the leaf surface to achieve high fog throughfall. Leaves, apparently, must capture a significant amount of fog before this eventually drips. In contrast, leaves with low water retention capacity and small droplet diameter most likely lose water from the leaf surface through different mechanisms such as leaf absorption and evaporation rather than fog drip. Fog droplets might even continue their horizontal trajectory in the air, without interacting with leaves. Our results are in accordance with Merrium *et al.* (2022), who recently found that hydrophobic leaves caused less drip to the soil, while at the same time, several indicators of yield in wheat increased, suggesting that water is channeled via direct stemflow to roots.

Comparison of plant fog drip and control funnel harvest

Unexpectedly, most species in LT harvested less fog water than the control funnels, and about half of the species in MB showed the same pattern. Fog drip is the net result of fog interception (expressed as water retention) plus rainfall, minus the water evaporation from the canopy surface, the water absorption by leaves, and the stemflow (Holwerda *et al.* 2006). Almost none of these variables have been studied in northern-central Chile. In other locations, stemflow has been estimated as 3.4 - 6.2% of the rainfall measured in open areas (Li *et al.* 2009), while Sadeghi *et al*. (2020) showed that shrublands had a median stemflow of 7% (range *ca.* 0-50%). Moreover, since water retention and fog drip were measured under laboratory and field conditions, respectively, a hydrological balance to calculate the other variables would be uncertain. Further research should estimate all these components of the water budget, as carried out by Holwerda *et al.* (2006).

According to our laboratory tests, plants retained water for a period of time before dripping occurred. At the same time, this could increase the amount of water on the leaf surface lost to evaporation. Some species, such as *E. breviflora*, *A. microphylla*, *E. pulverulenta*, and *E. chiloensis*, proved to be good fog collectors, though in other species, the net result was less fog drip than in control funnels. Other traits, besides water retention, could determine the net fog drip. For example, the low fog collection by some species could be partially explained at the shoot scale by a possible "umbrella" effect above the funnels. This is most likely the case of *H. stenophyllum* and *B. incisifolia*, which are low-stature shrubs, with dense stems and foliage. This could make it difficult for water to drip onto the soil. In addition, in the case of stemflow, xerophytic stems that are usually very tortuous, dry, and cracked, could absorb the water or cause it to evaporate before it could fall to the ground.

Prospects for further research

Our research has implications for the provision of water captured by plants for other species that grow underneath them. On the other hand, these patterns could present solutions to optimize the runoff and capture of fog water towards the ground, helping to maintain moisture levels not only for the plant itself but also for species that use water less efficiently. For example, Macek *et al.* (2018) have found that xerophytic species can act as nurses, trapping fog water that is released to smaller plants growing beneath them. The degree of nurse facilitation is expected to be higher in more arid sites. Rigg *et al.* (2002) showed that the tree species *Araucaria laubenfelsii* provides shade and water harvested from clouds directly below its crown, hence, facilitating the regeneration and establishment of shrubs and smaller plants. The foliar traits of the plants in our study most likely have a similar ecological function, helping seedlings and juvenile plants in their regeneration processes, with implications at the ecosystem level. Therefore, the functional criteria analyzed in this paper are key to the adequate choice of nurse plants that can increase the survival of target species in restoration projects.

New research questions arise from the data evaluated for leaf traits, such as whether water captured from fog can enter the leaf interior to be used in physiological processes, such as photosynthesis, or to maintain water relations and avoid/ recover cavitation (Guzmán-Delgado *et al.* 2018, Coopman *et al.* 2021, Fuenzalida *et al.* 2023). Further research should explore even more detailed traits on the leaf surface, such as trichomes, cuticular waxes, and hydathodes, which could be responsible for processes such as water retention, hydrophobicity, and water resistance to flow.

Concluding remarks

The differences in fog harvest among species were mainly correlated with water retention capacity, leaf mass, and droplet diameter. Regarding our hypotheses, we predicted the opposite patterns to those shown by the results, i.e., leaves with a high-water retention capacity (hypothesis i), and hydrophilic leaves (hypothesis ii), proved to be associated with a high fog drip. Differences between the xeric and the mesic sites studied were found, suggesting that plants could have different adaptive strategies for collecting fog at both sites. Moreover, the relation between leaf traits and fog harvest is species-specific, since every species is a mixture of different traits that do not necessarily optimize fog harvest. By studying the leaf traits of natural communities of xerophytic plants we can further understand plant adaptations that improve fog collection efficiency. Finally, it is desirable the study of several scales of analyses (i.e., stand scale, shoot geometry, leaf trait) to have a full understanding of the processes involved in fog capture by xerophytic plants.

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