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Idioblasts and peltate hairs as distribution networks for water absorbed by xerophilous leaves

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Abstract

Capparis odoratissima is a tree species native to semi-arid environments of South America where low soil water availability coexists with frequent night-time fog. A previous study showed that water applied to leaf surfaces enhanced leaf hydration, photosynthesis and growth, but the mechanisms of foliar water uptake are unknown. Here, we combine detailed anatomical evaluations with water and dye uptake experiments in the laboratory, and use immunolocalization of pectin and arabinogalactan protein epitopes to characterize water uptake pathways in leaves. Abaxially, the leaves of *C. odoratissima* are covered with peltate hairs, while the adaxial surfaces are glabrous. Both surfaces are able to absorb condensed water, but the abaxial surface has higher rates of water uptake. Thousands of idioblasts per cm^2, a higher density than stomata, connect the adaxial leaf surface and the abaxial peltate hairs, both of which contain hygroscopic substances such as arabinogalactan proteins and pectins. The highly specialized anatomy of the leaves of *C odoratissima* fulfils the dual function of minimizing water loss when stomata are closed, while maintaining the ability to absorb liquid water. Cell-wall related hygroscopic compounds in the peltate hairs and idioblasts create a network of microchannels that maintain leaf hydration and promote water uptake.

KEYWORDS
arabinogalactan proteins (AGPs), foliar water uptake, idioblasts, pectins, peltate hairs, sclerenchyma

1 | INTRODUCTION

Water-energy dynamics drive global patterns of plant diversity (Kreft & Jetz, 2007), with the predicted global increase of aridity likely to make plants more vulnerable to a lack of water in the soil (Choat et al., 2012; Olson et al., 2018). In arid and semi-arid environments, plant productivity is compromised due to prolonged soil drought. Xerophilous plants that thrive in these ecosystems exhibit anatomical adaptations that reduce rates of water loss, such as smaller leaves, lower stomata index and impermeable coating structures, like cuticles (see Shields, 1950). Surprisingly, some of the structures that prevent evaporative water loss may also facilitate the uptake of atmospheric water condensed on the leaf surface, decoupling the water status of the canopy from soil water availability (Benzing, Seemann, & Renfrow, 1978; Gouvra & Grammatikopoulos, 2003; Schreel et al., 2020; Schreel & Steppe, 2019; Schreel, van de Wal, Hervé-Fernandez, Boeckx, & Steppe, 2019; Schreel, von der Crone, Kangur, & Steppe, 2020).

Foliar water uptake is a widespread phenomenon of vascular plants, known for three centuries, and evaluated in at least 53 plant families (Dawson & Goldsmith, 2018). Foliar water uptake has direct consequences on plant function, relaxing tension in the water column of the xylem, enhancing turgor-driven growth and increasing the productivity of agricultural and natural ecosystems (Aguirre-Gutiérrez et al., 2019; Mayr et al., 2014; Steppe et al., 2018). The key conditions for foliar water uptake are met in fog-dominated environments

(Tognetti, 2015; Weathers, Ponette-González, & Dawson, 2019), where high atmospheric humidity enhances night-time dew formation on leaf surfaces, thus increasing the possibility of foliar water absorption. Indeed, studies in montane cloud forests of Brazil (Eller, Lima, & Oliveira, 2016), coastal California redwood forests in the USA (Burgess & Dawson, 2004) and cloud forests in Mexico (Gotsch et al., 2014) have demonstrated that foliar water uptake has an important impact on plant functioning, especially during dry periods (Breshears et al., 2008). Foliar uptake in semi-arid areas of the tropics is less studied, despite reports that it can enhance biomass productivity (Díaz & Granadillo, 2005; Limm, Simonin, Bothman, & Dawson, 2009).

Foliar water uptake occurs through a variety of mechanisms and pathways. Some species absorb water through the natural leaf openings, such as stomata (Berry, White, & Smith, 2014; Burkhardt, Basi, Pariyar, & Hunsche, 2012) or hydathodes (Boanares et al., 2019; Martin & von Willert, 2000). Other structures that are supposedly impermeable to water may participate in water uptake, including cuticles (Fernández et al., 2017; Schuster, Burghardt, & Riederer, 2017; Vaadia & Waisel, 1963; Yates & Hutley, 1995) and trichomes (Franke, 1967; Benzing et al., 1978; reviewed by Berry, Emery, Gotsch, & Goldsmith, 2019). While the use of these wall-thickened, sealing structures appears as a good strategy to capture atmospheric water condensed on leaf surfaces, demonstration of their hygroscopic capacity requires a careful examination of their cell-wall biochemistry, so far lacking for most plant species. Early work in this area showed that the absorptive capacity of leaves is related to the presence of polysaccharides under the cuticle (Kerstiens, 1996). However, the role of ubiquitous compounds of the cell walls, such as pectins and glycoproteins, on foliar water uptake has received little attention (Boanares et al., 2018). It is not known whether trichomes or sclerenchymatous structures display such hygroscopic compounds.

This knowledge gap is particularly severe for xerophilous species, which have leaves with abundant sclerenchymatous tissues, such as idioblasts, highly specialized structures that are understudied from a functional perspective. Idioblasts (Schwendener, 1874) are thick-walled cells typically buried in the mesophyll of vascular plants (Bailey & Nast, 1945; Tomlinson & Fisher, 2005), and commonly found in the leaves of xerophilous species (Foster, 1956; Heide-Jorgensen, 1990). Traditionally, idioblasts have been explored from the perspective of morphology, ontogeny and taxonomic values (Bloch, 1946; Foster, 1944, 1945a, 1945b, 1955a, 1955b; Rao & Mody, 1961). However, important functions attributed to idioblasts are typically inferred from their putative stiffness, such as support and defence (Foster, 1947; Rao & Sharma, 1968; Tucker, 1964), or from their topology, such as a possible role in leaf capacitance (Heide-Jorgensen, 1990) or serving as light guides (Karabourniotis, 1998). The diverse array of anatomies of xerophilous species is exemplified in the genus *Capparis* (Gan et al., 2013; Rao & Mody, 1961). *Capparis odoratissima* is native to the semi-arid tropical environments of the South American continent with a remarkable capacity to produce more biomass in response to canopy irrigation than to surface irrigation at low soil water availability, compared with other species living in the same environment (Díaz & Granadillo, 2005), likely through foliar water uptake as suggested by the authors. However, the mechanism of foliar water uptake in this species is unknown.

C. odoratissima is the most conspicuous evergreen species in xerophytic forests of north-western Venezuela. We focused on this regionally important species with the goal of understanding the relationship between anatomy and function in this extreme ecosystem. We show that the leaves of *C. odoratissima* are highly specialized structures that perform a dual function: minimizing water loss when dry and absorbing water when wet. We examine how an intricate network of hygroscopic pathways within the mesophyll enhances water uptake, thus maintaining leaf hydration upon water condensation on the leaf surface.

2 | MATERIALS AND METHODS

2.1 | Plant material

Leaf material was obtained from *Capparis odoratissima* trees growing near the University of Francisco de Miranda in the state of Falcón, Venezuela. Cut branches with leaves attached were transported to the laboratory (approximately 2–3 days) in tightly sealed plastic bags containing humidified paper to avoid evaporation.

2.2 | Evaluation of the external leaf morphology

Five-to-six fully expanded leaves were scanned (along with a scale) using a CANON CanoScan LiDE 400 scanner, and leaf areas calculated using Image J1.51d software (National Institutes of Health, Bethesda, MD, USA). These same leaves were then used to photograph the details of both adaxial and abaxial surfaces with a Zeiss Discovery v12 Dissecting microscope (objective 0.63x PanApo). Adaxially, the idioblast tips were easily visualized by their translucency, and, abaxially, the peltate hairs were counted using their central parts as references. Both idioblasts and peltate hairs were counted in 1 mm^2 areas at five positions on each leaf surface. To count the number of stomata, five leaves were fixed in FAA (formalin: acetic acid, Johansen, 1940), washed three times in distilled water for 1 h each, stained with Feulgen reaction (modified from Barrell & Grossniklaus, 2005). Then, the leaves were cleared with a solution containing ethanol:benzoyl benzoate 3:1 (v/v) for 6 h, ethanol:benzoyl benzoate 1:3 (v/v) and finally benzoyl benzoate:dibutyl phthalate 1:1 (v/v) for several days (Crane & Carman, 1987). Following the removal of the peltate hairs, 1 mm^2 samples were imaged with a Zeiss LSM700 Confocal Microscope connected to an AxioCam 512 camera and Zen Blue 2.3 software, using a 20x/0.8 M27 Plan-Apochromat objective. Note that the area occupied by the rounded base of the peltate hairs (3.45%) never contained stomata, and hence was subtracted from the total leaf area to get a more accurate estimate of stomatal density.

2.3 | Evaluation of the internal leaf anatomy: Idioblast characterization

To better understand the structure of the idioblasts in the mesophyll, hand-cut transverse thin sections (perpendicular to the leaf surface) were made and stained with a solution of 0.01% w/v calcofluor white in 10 mM CHES buffer with 100 mM KCl (pH = 10) (Hughes & McCully, 1975), to identify cellulose-rich walls, and then with auramine O in 0.05 M Tris/HCl buffer, (pH = 7.2), to detect cutinized lipids (Heslop-Harrison & Shivanna, 1977). These sections were visualized with a Zeiss Axioskop microscope equipped with epifluorescence, and imaged with an AxioCam HRc camera, operated by Zen Blue software with multichannel wavelength detection. For calcofluor white, we used a DAPI narrow (Zeiss 48,702) excitation G 365, bandpass 12 nm; dichroic mirror FT 395; barrier filter LP397; for auramine O, we used an AF488/FITC/GFP (Zeiss Filter set 9) excitation 450–490; dichroic mirror 510; emission filter LP515. We isolated the idioblasts by macerating 1 mm^2 leaf pieces in a solution containing acetic acid:hydrogen peroxide 1:1 (v/v) at 60°C for 2 days. The debris of these samples was then mounted in distilled water or glycerol and visualized with a Zeiss LSM700 Confocal Microscope. 3D images were obtained without staining with the objective: 63x/1.40 Oil DIC M27 Plan-Apochromat.

Samples obtained from five previously fixed leaves in FAA were washed in distilled water three times, 1 h each, and dehydrated with an increasing gradient of aqueous ethanol concentrations (10%, 30%, 50%, 70% and 100% [x3]). They were then soaked in the infiltration solution of Technovit7100 (Electron Microscopy Sciences, Hetfield, PA, USA) for several weeks, and polymerized under anoxic conditions. Blocks with samples oriented parallel to the leaf surface (paradermal) were serially sectioned at 4 μm with a Leica RM2155 rotary microtome (Leica Microsystems, Wetlar, Germany). Sections were then stained with an aqueous solution of 0.025% toluidine blue for general structure of the leaf tissues (Feder & O'brien, 1968), and finally imaged with a Zeiss AxioImager A2 Upright microscope equipped with an AxioCam 512 camera and Zen Blue Pro with multichannel software.

2.4 | Water and dye uptake experiments

We first monitored epidermal transpiration in 10 fully expanded leaves by letting them dry with their petiole covered with parafilm at room temperature (average 23 ± 3°C) and 30 ± 3% of relative humidity (RH), which is a value that approximates daytime RH in the field. We weighed them every 2 h with a four-digit precision scale, and then divided the weights by the leaf projected area (x2), fitted the temporal loss of each leaf weight to a linear regression function for the initial 10 h and averaged the slopes. This value served as a reference of epidermal evaporation from both leaf sides (slope = −0.041 mg cm^{-2} h^{-1}, average r^2 = 0.95). After that, we calculated the relative leaf water content (RWC) using the formula RWC = [(FW_t-DW)/(FW_0-DW)], where FW_t is the fresh weight at time t, DW is the dry weight and FW_0 is the fresh weight at time 0 (Figure S1). We further calculated the initial water content of the leaves (Wi) as the difference between the fresh weight minus the dry weight per unit leaf area.

To estimate maximum rates of foliar uptake and the strength of water retention, five leaves were weighed (Wt_0) before being submerged in distilled water, with the petiole sealed, but not submerged, for 15 min (*wet cycle*). To better estimate the water retained within leaves, we eliminated any surface water; leaves were centrifuged at 1800 rpm for 2 min using a Sorvall RC6 Ultracentrifuge, and immediately weighed with a precision scale (Wt_1). Leaves were left to dry at room temperature for 15 min (*dry cycle*) and weighed again before immersion (Wt_2). The cycle was repeated five times.

Given the sharp day-to-night temperature variation (42°C at midday to 26°C at midnight) and RH (from 48% to 92%), water condensation can occur on both leaf surfaces in the field. To understand the possible contribution of each surface to foliar water uptake, we simulated water condensation on both leaf surfaces. Ten leaves were loaded with 350 μL of distilled water (350 mg) evenly distributed in 35 droplets (10 μL each), covering roughly 25–30% of one surface, five leaves loaded on the abaxial side and five loaded on the adaxial surface. When the droplets disappeared from the surfaces, the leaves were weighed with a precision scale, loaded again with the same amount of water, and this cycle repeated. Droplet disappearance was faster from the abaxial leaf surface, resulting in more time points during the 10 h of the experiment, which is an approximation of the persistence of dew on the leaf surfaces under field conditions.

To calculate water absorbed by each surface, we used the following formula for each cycle.

$$ABS_t = \left[(W_t - W_{t0}) - (EP_t\, L_{A^*}[t - t_0])\right]/L_A, \quad (1)$$

where ABS_t is the water absorbed, measured in mg cm^{-2}, at time t (after droplet disappearance from the surfaces), W_t is the weight of the leaves in mg, L_{A^*} the leaf exposed area (the projected area of the unloaded surface plus 70% of the loaded one), L_A is the projected leaf area (only one surface) measured in cm^2 and W_{t0} the initial weight of the leaves in mg. EP_t is the epidermal transpiration rate of the leaf surface not covered by droplets (one side plus 70% of the other), which assumes that water loss from the two sides occurs at the same rate: EP_t = −0.035 mg cm^{-2} h^{-1}. We further assumed that the stomata are closed.

To understand the pathways of water uptake, we used a 1% aqueous solution of the apoplastic fluorescent dye tracer Lucifer Yellow (LY; CH dilithium salt; Sigma). Dye (10 μL droplets) was applied to either the adaxial or the abaxial surfaces within a humidified chamber. We waited until the droplets disappeared from the surface, and then used a paper tissue to wipe any traces of the dye from the leaf surface prior to making transverse sections with a double edge razor blade. Sections were mounted in an aqueous solution of 70% glycerol, and immediately observed with a Zeiss LSM700 Confocal Microscope (wavelength 488 nm). Similar sections of the same leaves, but in areas without the dye, were used as negative controls, using the same exposure settings.

We further evaluated the rate of water and dye uptake by each leaf side *in vivo*, applying 5 μL droplets to the leaves of a seedling, and then taking images every five seconds (Videos S1-S4).

2.5 | Immunolocalization of pectin and arabinogalactan glycoprotein epitopes

A preliminary test with the general dye ruthenium red was used in freshly dissected leaves (Figure S2) to evaluate the presence of neutral pectins (Colombo & Rascio, 1977). Similarly, a preliminary test for arabinogalactan protein (AGP) presence was applied to cleared leaves with a 2% solution of the chemical reagent beta-glucosyl Yariv reagent in 0.15 M NaCl (Yariv, Lis, & Katchalski, 1967). The β-GlcYR reacts with AGP_S giving a red colour upon precipitation (Figure S3).

To identify the presence of pectic and AGP epitopes in the leaves of *Capparis odoratissima*, two monoclonal antibodies that detect highly un-esterified homogalacturonans (JIM5) and AGPs (JIM8) (Carbosource services, Georgia, USA) were used. Transverse and paradermal sections (4 μm thick) of embedded leaves were incubated with 1XPBS 3x for 5 min each, followed by 5% bovine albumin serum (BSA) for five more minutes and finally the undiluted primary monoclonal antibody for 45 min. The sections were then washed three times in 1XPBS, 5 min each, and incubated again with an anti-Rat secondary antibody Alexa 488 conjugated with a fluorescent compound fluorescein isothiocyanate for 1 h. Three final washes with 1XPBS preceded observations with a confocal microscope. Negative controls were treated in the same way, but substituting the primary antibody with a solution of 1% BSA in PBS.

3 | RESULTS

3.1 | External leaf morphology of *Capparis odoratissima*

Detailed evaluations of the oblong, hypostomatous leaves of *C. odoratissima* showed a dark green colour of the adaxial surface (Figure 1a). Numerous translucent spots were located in concave areas of the surface, which corresponded with the tips of individual idioblasts (Figure 1b). Idioblast tips were interspersed between epidermal cells and, after staining and clearing the tissue, displayed a star-like shape when observed from above (Figure 1c). At higher magnification, each idioblast projected a narrow pore towards the adaxial surface of the leaf (Figure 1d). Abaxially, the leaves exhibited a pale green colour (Figure 1e), which resulted from the total coverage of the lamina by an imbricate carpet of peltate hairs (Figure 1f). These non-glandular hairs were variable in size, but each contains a uniform multicellular, umbrella-like base, with thick-walled filiform cells (Figure 1g), and a central domed shield on top that protrudes to the exterior. Despite having very thick walls, there are interconnections between the central channels of the cells (Figure 1h).

3.2 | Leaf anatomy of *Capparis odoratissima*: cuticles, peltate hairs and idioblasts

Leaf cross-sections revealed that the idioblasts are thick-walled columnar structures (average length 252.0 μm ± 18.9SE) that connect the adaxial and the abaxial surfaces (Figure 2a, drawn by Metcalfe & Chalk, 1950). Idioblasts did not stain for lipids, but auramine O staining revealed a thick cuticle layer on the adaxial surfaces of the leaves (Figure 2b), which were thinner in the concave depressions on top of the idioblasts. In contrast, the thick columnar walls of the idioblasts (average diameter 23.6 μm ± 0.5SE) stained intensely with calcofluor white (Figure 2c), indicating the presence of cellulose in the thick walls, while staining with phloroglucinol indicated partial lignification. The abaxial surface of the leaf showed a thinner but rugose cuticle under the peltate hairs (Figure 2d). At the anchoring areas of the peltate hairs, the abaxial epidermis accumulated thick lipidic deposits (Figure 2e).

Idioblasts exhibited a bipolar pattern from the adaxial to the abaxial side of the leaf (Figure 3a). A thin projection that protruded apoplastically between the cells of the adaxial epidermis connected with the surface, and was sustained underneath with four-to-five filiform anchors attached to the base of the epidermal cells (Figure 3b). In the area of the palisade parenchyma, the idioblasts had a columnar shape, with a thick wall, narrow lumen (average diameter 3.9 μm ± 0.3SE) and crenations that connected the lumen with the palisade parenchyma (Figure 3c). In the spongy mesophyll, the irregular shape of idioblasts was characterized by numerous protuberances and crenations that connected the lumen of the idioblasts with adjacent mesophyll cells (Figure 3d). Closer to the abaxial side of the leaf, the idioblasts became thinner, as well as anastomosed and converged towards the base of the peltate hairs, maintaining narrow channels that connected the lumen of the idioblast with the lumen of the peltate hair (Figure 3e). On average, four idioblasts were connected to each peltate hair (Figure 4), whereas the frequency of abaxial stomata under the peltate hairs was significantly lower than that of idioblasts.

3.3 | Leaf water uptake in *Capparis odoratissima*

The initial water content of detached leaves was approximately 9.5 mg cm^{-2}. Weight loss of leaves exposed to lab conditions was used to understand epidermal evapotranspiration (Figure S1). Leaf water content remained higher than 80% during the first 21 h of exposure at low humidity, but then decreased sharply, with leaves becoming brittle 143 h after the initial measurements. The epidermal water loss rate over the first 10 h was 0.041 mg cm^{-2} h^{-1}.

To understand the speed and extent of water retention in a saturated environment, leaves of *Capparis odoratissima* were intermittently

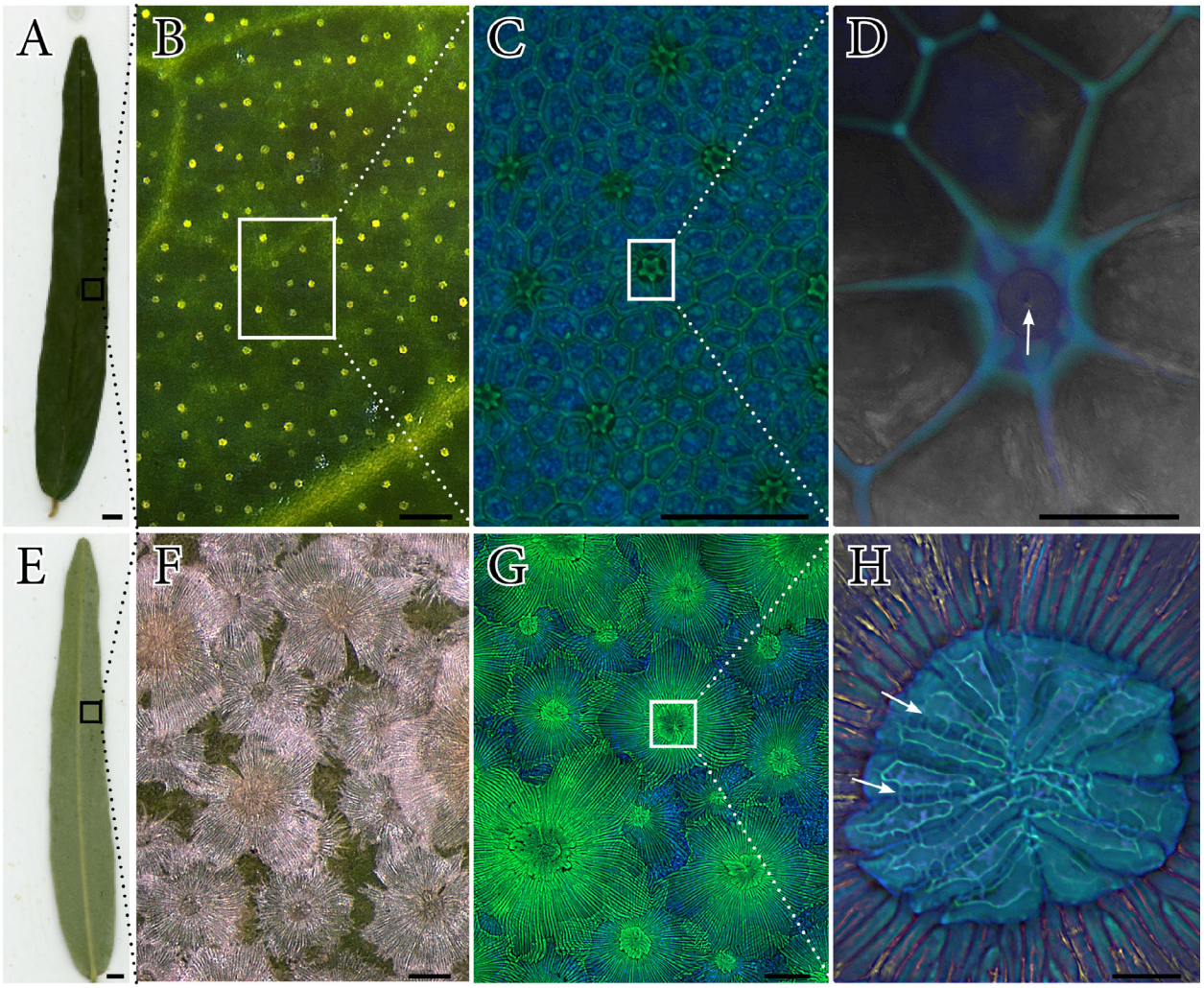

FIGURE 1 Leaf surface anatomy of *Capparis odoratissima*. (a) Elongated leaf shape with a dark green adaxial colour. (b) Conspicuous pattern of translucent idioblast tips on adaxial leaf surface. (c) Cleared tissue showing a star-like appearance at the tip of these structures. (d) Closer view, showing a narrow pore (arrow) in the centre of an idioblast. (e) Abaxial surface of the leaves with a pale green colour. (f) A continuous layer of imbricate peltate hairs covers the abaxial surface. (g) Peltate hairs are composed of two parts: a central stalk surrounded by filiform projections. (h) In the centre of each peltate hair, a compact dome of thick-walled filiform structures further showed connections between their lumens (arrows). Dissecting scope images (a-d, adaxial; e-h, abaxial), and confocal images of cleared leaves stained with the Feulgen reaction (c,d, adaxial; g,h, abaxial). Scale bars: a,e = 500 μm; b,f = 200 μm; c,g = 100 μm; d,h = 20 μm [Colour figure can be viewed at wileyonlinelibrary.com]

submerged for 15 min (wet cycle), when they absorbed water at a rate of 0.30 mg cm^{-2} h^{-1}. Rates of water loss during the dry cycle averaged 0.27 mg cm^{-2} h^{-1}, approximately seven times larger than epidermal water loss rates of leaves allowed to dry over a period of many hours. The water retained following each dry cycle (i.e., not evaporated) increased at a rate of 0.013 mg cm^{-2} h^{-1} (Figure 5a), suggesting that evaporative losses became smaller with each cycle (r^2 = 0.97).

The contribution of adaxial and abaxial leaf surfaces to water uptake was evaluated by loading each surface individually with water droplets (Figure 5b). Comparing the proportional weight variation over time revealed that even though only 30% of one surface was covered with water, the leaves significantly reduced their evaporative losses. However, there was a clear asymmetry: leaves loaded on the adaxial surface reduced their proportional water losses twofold with respect to the unloaded leaves, whereas leaves loaded on the abaxial surface reduced their evaporative losses almost six times. While this indicates that both surfaces can absorb water, water uptake by the abaxial surface was approximately three times larger (0.033 mg cm^{-2} h^{-1}, r^2 = 0.84) relative to water absorption by the adaxial surface, suggesting that the two surfaces have different absorption capacities. To confirm this, the assumption of equal rates of epidermal evaporation from each surface should be tested.

3.4 | The pathways of leaf water uptake in *Capparis odoratissima*

Dye loading onto the abaxial surface resulted in uptake that we believe was mediated by the central anchoring area of the peltate

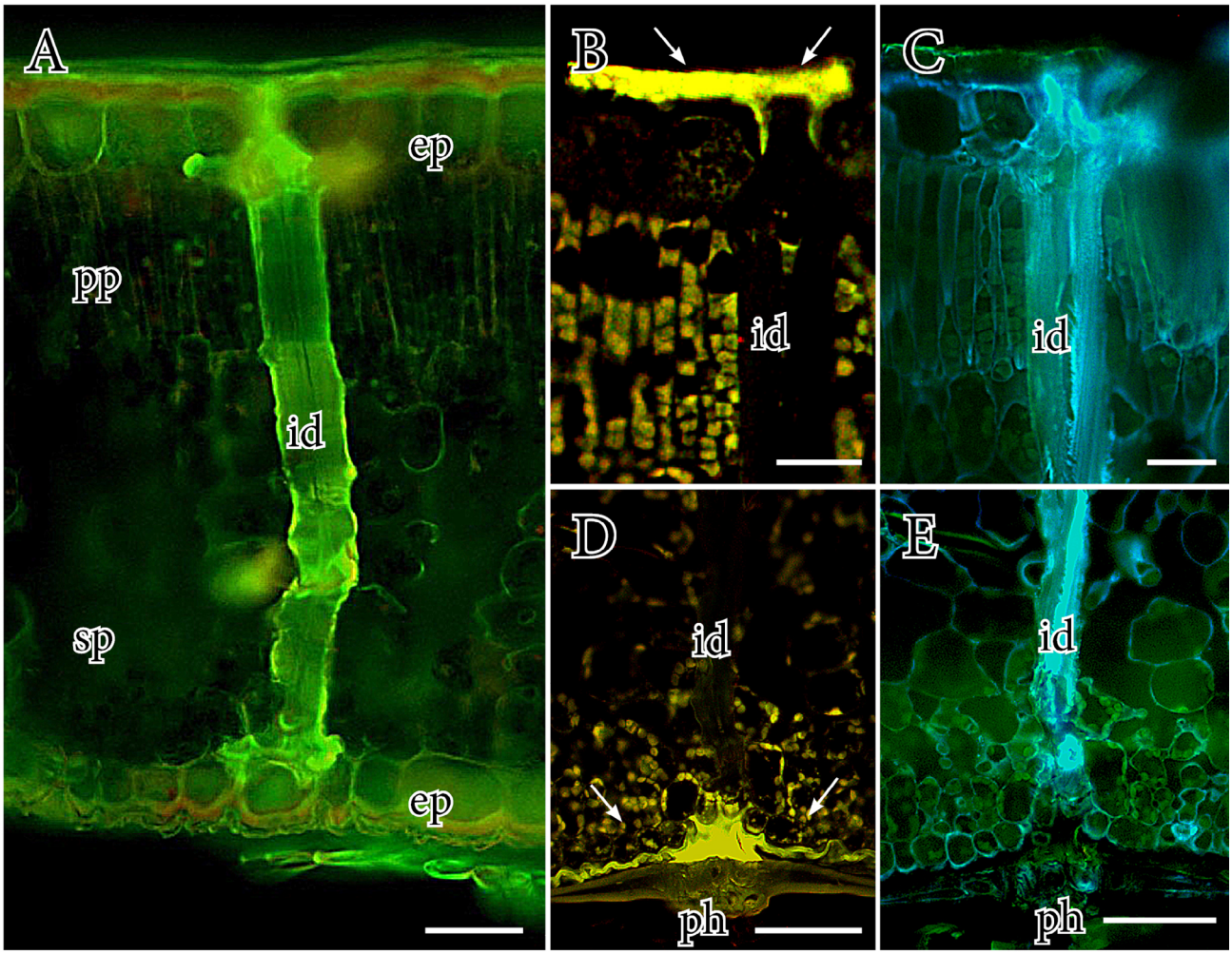

FIGURE 2 Internal anatomy of the leaves in *Capparis odoratissima*. (a) Cross-section of the leaf displaying autofluorescence of the numerous idioblasts that traverse the mesophyll and connect the adaxial and abaxial leaf surfaces. (b) Thick cuticle layer (white arrowheads) on the adaxial epidermis of the leaf, but notably thinner above the idioblasts, stained with auramine O for cutin and lipids (yellow, arrows). (c) The thick walls of the idioblasts contain massive cellulose (stained with calcofluor white, blue colour). (d) The cuticle of the abaxial surface (arrows) is thinner, rugose and accumulates massively at the base of the peltate hairs. (e) Idioblasts directly connect with the centre of the peltate hairs. Ep, epidermis; pp, palisade parenchyma; id, idioblast; sp, spongy parenchyma; ph, peltate hair. Scale bars: a,d,e = 50 μm; b,c = 20 μm [Colour figure can be viewed at wileyonlinelibrary.com]

hairs (Figure 6a) due to the intense staining that remained in the thick walls of this central area of the peltate hairs after dye absorption (Figure 6b, Videos S2-S3). Fluorescence was further observed in the mesophyll of the leaves when dye was loaded onto either the adaxial or the abaxial surface, pointing to the dual role of the leaf surfaces in water uptake. Yet, the dye applied to living seedlings did not travel far from the area of application within the leaf tissues, perhaps because the dye does not move as easily through the tissue as does water (for a discussion see Canny, 1993). Strikingly, the structures that retained the dye the most were the walls of the idioblasts, compared with a lack of fluorescence in these structures at the areas of the leaf without dye, which were used as negative controls (Figure 6c-d). The lumen of the idioblasts also became filled with the fluorescent dye, including the crenations (Figure 6e-f), revealing them as the bridges of water uptake from the leaf surface to the mesophyll.

3.5 | Pectins and arabinogalactan proteins in the leaves of *Capparis odoratissima*

Immunolocalization of pectin and arabinogalactan protein epitopes with monoclonal antibodies showed a dual topological pattern. Pectin epitopes were present in the cell walls of both adaxial and abaxial epidermis (Figure 7a-b), as roughly detected in fresh samples with ruthenium red (Figure S2a), in the external walls of the cells composing the spongy mesophyll (Figure 7c) and the external cell walls of the peltate hairs (Figure 7d; Figure S2b), but not in the idio-

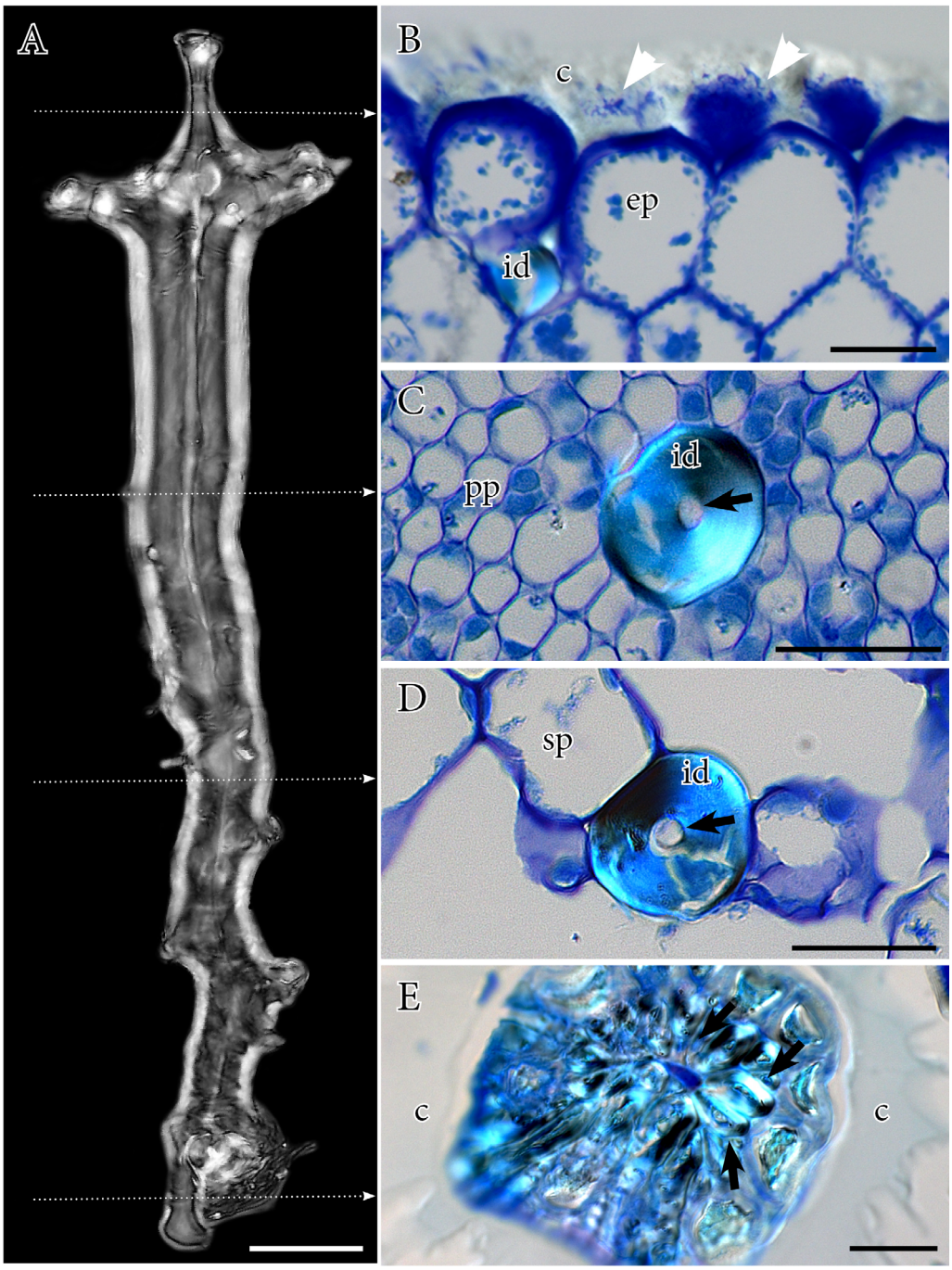

FIGURE 3 Characterization of the idioblasts of *Capparis odoratissima*. (a) Maximum 3D projection of an isolated idioblast showing their typical structure of a small tubular projection towards the adaxial epidermis (top) and irregular walls towards the abaxial surface. (b) Cells of the adaxial epidermis are thick and have substantial extracellular materials (blue colour) that intersperse with the thick adaxial cuticle (white arrowheads). (c) The idioblasts are columnar within the palisade parenchyma, with thick refringent walls and narrow lumens (arrow). (d) At the level of the spongy mesophyll, numerous canals connect the idioblast lumen with the surrounding mesophyll cells. (e) At the abaxial epidermis, adjacent idioblasts anastomose and form an irregular structure that connects with the centre of the peltate hairs. B-D semi-thin sections stained with toluidine blue for general structure. C, cuticle; ep, epidermis; pp, palisade parenchyma; id, idioblast; sp, spongy parenchyma; ph, peltate hair. Dotted arrows in **A** indicate the plane of section of images on the right. Scale bars: 20 μm [Colour figure can be viewed at wileyonlinelibrary.com]

blasts. The presence of arabinogalactan proteins was roughly detected with the beta-glucosyl Yariv reagent, which showed an intense red colour in areas with idioblasts (Figure S3). More specifically, the epitopes recognized by the JIM8 monoclonal antibody labelled a narrow area that corresponded with the lumen of the idioblasts, from their adaxial projection (Figure 7e), through the columnar lumen in the palisade parenchyma (Figure 7f), to the lumens of the anchoring areas of the peltate hairs (Figure 7g). As a result, AGPs coated the continuum of lumens between the peltate hairs and idioblasts.

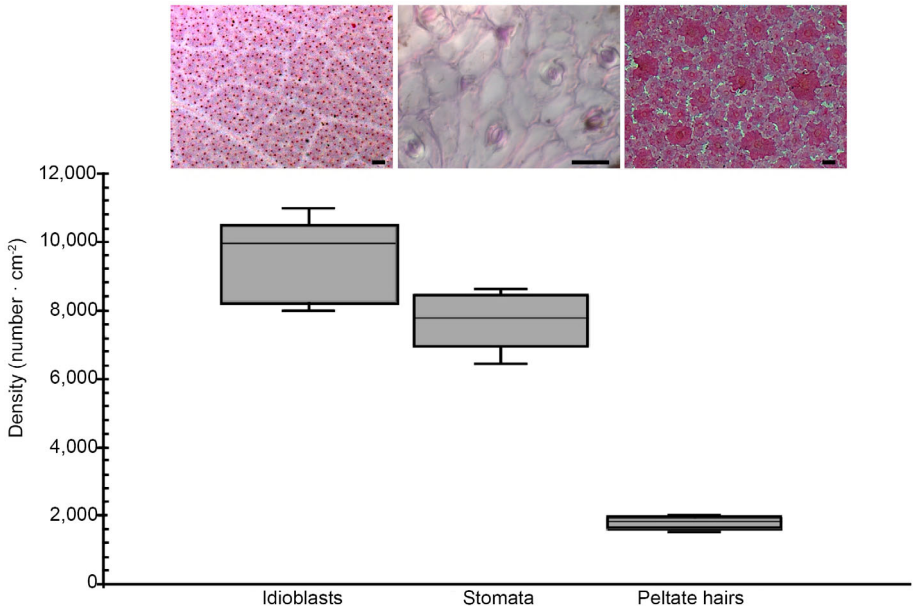

FIGURE 4 Frequency of idioblasts, stomata and peltate hairs in the leaves of *Capparis odoratissima*. Note that idioblasts (red dots in the first image) are more numerous than stomata (middle image). Interestingly, there are, on average, four to six times more idioblasts than peltate hairs (third image). Imaged display parts of the cleared leaves stained with Basic Fuchsin. Scale bars: 200 μm (idioblasts and peltate hairs) and 20 μm (stomata) [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | Water balance and leaf permeability in *Capparis odoratissima*

Previous studies of *C. odoratissima* showed that, unlike other species coexisting in the same environment, *C. odoratissima* increased its biomass when the canopy, but not the soil, was supplied with water (Díaz & Granadillo, 2005). However, the magnitude and pathway of water uptake by individual leaves were not quantified. Our detailed evaluations of water evaporation through time (i.e., epidermal evaporation) and entry of water (measured as the increase of leaf weight) from detached leaves serve to constrain the extreme values of water inputs and outputs. During the initial epidermal evaporation with the petiole sealed, water loss rates of *C. odoratissima* leaves were 0.041 mg cm^{-2} h^{-1}, which results in a permeance (*P*), calculated with the saturation concentration of water vapour at 20°C (according to Kerstiens, 1996), of 0.66 10^{-5} m s^{-1}. Compared with the 85 species for which the permeance was calculated from the mass loss of detached leaves, *C. odoratissima* leaves fall within the lowest ranges observed, similar to the values of other succulent species adapted to xeric environments such as *Opuntia camanchica*, with a *p* value of 0.210^{-5} m s^{-1} (Pisek & Berger, 1938). Recent evaluations critically reviewed the meaning of permeances calculated by Kerstiens, pointing to a high variability of this parameter among species and biomes (Duursma et al., 2019). Our results suggest that the leaves of *C. odoratissima* retain water efficiently, although we could not be entirely sure that our leaves were initially saturated with water (our measurements started sometime after the leaves were detached). Furthermore, the dehydration rate of *C. odoratissima* leaves in natural conditions is likely slower than in our lab conditions, not only because the leaves are not detached, but also because the RH of the atmosphere oscillates between 40% and 95% (Díaz & Granadillo, 2005), which, along with the diurnal variation in temperature, makes water condensation on both leaf surfaces possible.

Capparis odoratissima leaves immersed in water increased in weight at a rate of 0.30 mg cm^{-2} h^{-1}, which is approximately seven times greater than rates of epidermal evaporation. The rate of water absorption by *C. odoratissima* leaves, however, is four times lower than in the pubescent leaves of *Tillandsia mullenbecki*, which grows in the Atacama Desert in Chile, and is entirely dependent on foliar uptake (Raux, Gravelle, & Dumais, 2020). Nevertheless, we estimate that 15 h continuous exposure of the leaves to surface moisture may result in a 50% increase in leaf water content. Unlike in *Tillandsia*, we found that rates of water loss immediately following leaf immersion were large (on average 0.27 mg cm^{-2} h^{-1}), and we interpret this as an evidence that water is weakly retained in the millions of interstices formed by the idioblasts, which were likely responsible for the high initial rate of water loss. The fact that leaves increased in weight over subsequent immersion and drying cycles demonstrates that water was being transferred to the mesophyll.

The major barriers for water absorption and/or evaporation are the leaf cuticles. Traditionally, the thicknesses of lipid coatings, such as cuticles, were associated with higher water retention of leaves (Shields, 1950). Yet, the leaf cuticle is gradually revealing as a permeable layer to absorb water and electrolytes (Fernández et al., 2014, 2017). Thus, cuticle thickness may not have a direct relationship with impermeability (Schuster et al., 2017), but rather its biochemistry may be more important for water exchange between the mesophyll and the atmosphere. In our experiments, the leaves loaded adaxially gained less water than the ones loaded abaxially, pointing to a difference in absorption by each surface, and indirectly pointing to their different evaporative losses. The anatomy of leaves further played a role in these capacities, such as the compact and convoluted cuticle in the abaxial side of the leaves of *C. odoratissima*, which is thinner than that of the adaxial surface. Stomata embedded in this cuticle, despite being

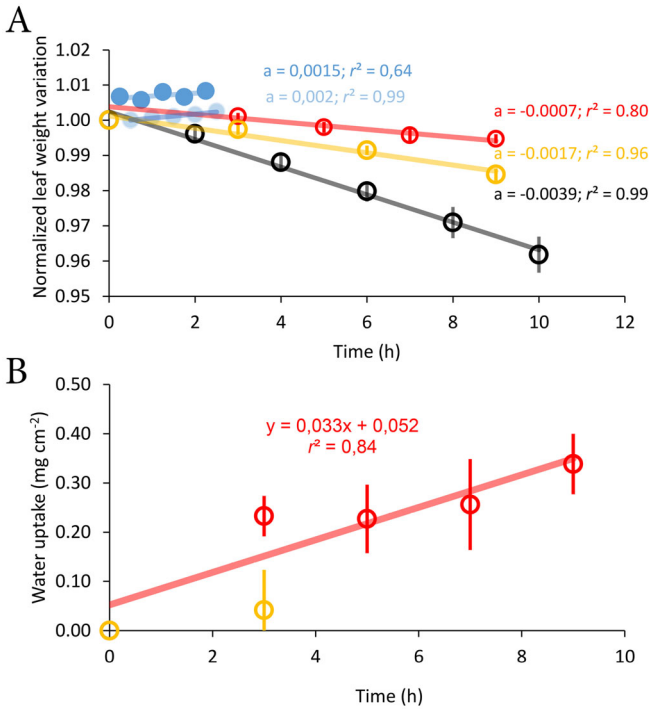

FIGURE 5 Water budgets by leaves of *Capparis odoratissima*. (a) Normalized leaf weight variation (proportional to the initial leaf weight) of the leaves of *Capparis odoratissima* comparing different treatments: blue filled dots represent the maximum weight increase of immersed leaves after the wet cycle (dark blue), and minimum weight variation after the dry cycles (light blue); note that both follow a linear positive rate over time. Empty circles represent weight loss under epidermal evaporation (black), when 30% of the adaxial surface was covered with droplets (yellow), and when 30% of the abaxial surface was covered with droplets (red). Slopes (a) are shown for comparison and have units of h^{-1}. (b) Cumulative water uptake by leaves loaded on the adaxial (yellow) or the abaxial (red) surfaces; note that the r^2 corresponds with the linear fit for the abaxial surface. Bars represent standard errors at a $p \leq .95$ [Colour figure can be viewed at wileyonlinelibrary.com]

covered by a carpet of peltate hairs, which should reduce evapotranspiration, are probably ways of water scape. Pubescence is a typical character of xerophilous species, and functionally related with protection against desiccation and thus temperature regulation (Fahn, 1986; Shields, 1950). Future work is needed to explore the impact of the peltate hairs of the abaxial epidermis on reducing rates of water loss by stomata *in vivo*.

4.2 | Asymmetric foliar water uptake and anatomical specializations in *Capparis odoratissima*

Our experiments with water droplets on each leaf surface revealed an asymmetry in the water uptake. Both surfaces of the *C. odoratissima* leaves loaded with water droplets showed an initial positive gain of water with time. However, when water was applied to the adaxial surface, water gains were only possible for the initial 6 h of exposure, and then water losses occurred. In contrast, when the abaxial surface was loaded, water uptake was linear, and followed a rate of 0.033 mg cm^{-2} h^{-1}, an order or magnitude lower than submerged leaves, due to evaporative losses of the exposed leaf surfaces. Previous work with the Australian subtropical species *Sloanea woollsii* (Yates & Hutley, 1995) showed similar rates for sprayed leaves, although these results were questioned by Kerstiens (1996), who suggested that small cracks in the cuticle could explain the extremely high leaf permeances. Natural openings (i.e., not created by microorganisms) are unusual in the adaxial leaf surface, except in amphistomous leaves, or leaves with hydathodes (Martin & von Willert, 2000). However, we found thousands of micropores per cm area projecting towards concave areas on the adaxial leaf surfaces in *Capparis odoratissima*, which likely correlate with apoplastic water transport from the atmosphere to the leaf. These openings connect with the lumen of columnar idioblasts, pointing to these structures as significant players in the leaf water budgets.

Idioblasts have rarely been demonstrated as contributing to foliar water uptake in angiosperms, with some exceptions such as *Hakea suaveolens* (Heide-Jorgensen, 1990). However, their topology in the numerous forest species where they have been described, including gymnosperms (Hooker, 1864), and more than 80 eudicot families (Foster, 1955a, 1955b; Rao & Mody, 1961; Solereder, 1908; Vitarelli, Riina, Cassino, & Meira, 2016; Zhang, Hu, Li, Wang, & Xu, 2009), suggested a role in the storage of water in leaves. As thick-walled sclerenchymatous tissues (Evert, 2006), idioblasts evolved multiple shapes and dispositions within leaves, but the columnar type of idioblasts displayed in the leaves of *C. odoratissima* have only been described in two species so far, *Hakea suaveolens* (Heide-Jorgensen, 1990) and *Mouriria huberi* (Foster, 1947). These adaptations cannot be related to xeric environments, as other species from the same genus and adapted to dry climates have completely different anatomies, such as the Mediterranean *Capparis spinosa* (Gan et al., 2013; Rhizopoulou, 1990; Rhizopoulou & Psaras, 2003).

In nature, water condenses most likely on the adaxial surface of leaves, and, indeed, most studies of foliar water uptake suggest that the adaxial side is more permeable to water (Fernández et al., 2014; Gardingen & Grace, 1992). In *C. odoratissima*, the reasons behind the asymmetric water uptake correlate with the markedly distinct anatomy between leaf surfaces. Although uptake from the adaxial surface is modest compared with the abaxial one, this dual possibility is unique among flowering plants. Indeed, this correlates with their unique leaf anatomy, in which the lumen of the idioblasts formed a continuum with the peltate hairs located in the abaxial surface, traversing the cross-sectional area of the leaves. As a result, an intricate network of microchannels linked both surfaces with the mesophyll. Trichome–idioblast associations are commonly found in species from arid environments such as those from the family Euphorbiaceae (Metcalfe & Chalk, 1950; Solereder, 1908), *Olea europaea* (Arzeee, 1953) or *Androstachys johnsonii* (Alvin, 1987). The presence of peltate hairs is not indicative of foliar water uptake (Bickford, 2016), since species with peltate hairs such as in *Olea europaea* showed no evidence of water absorption (Arzeee, 1953).

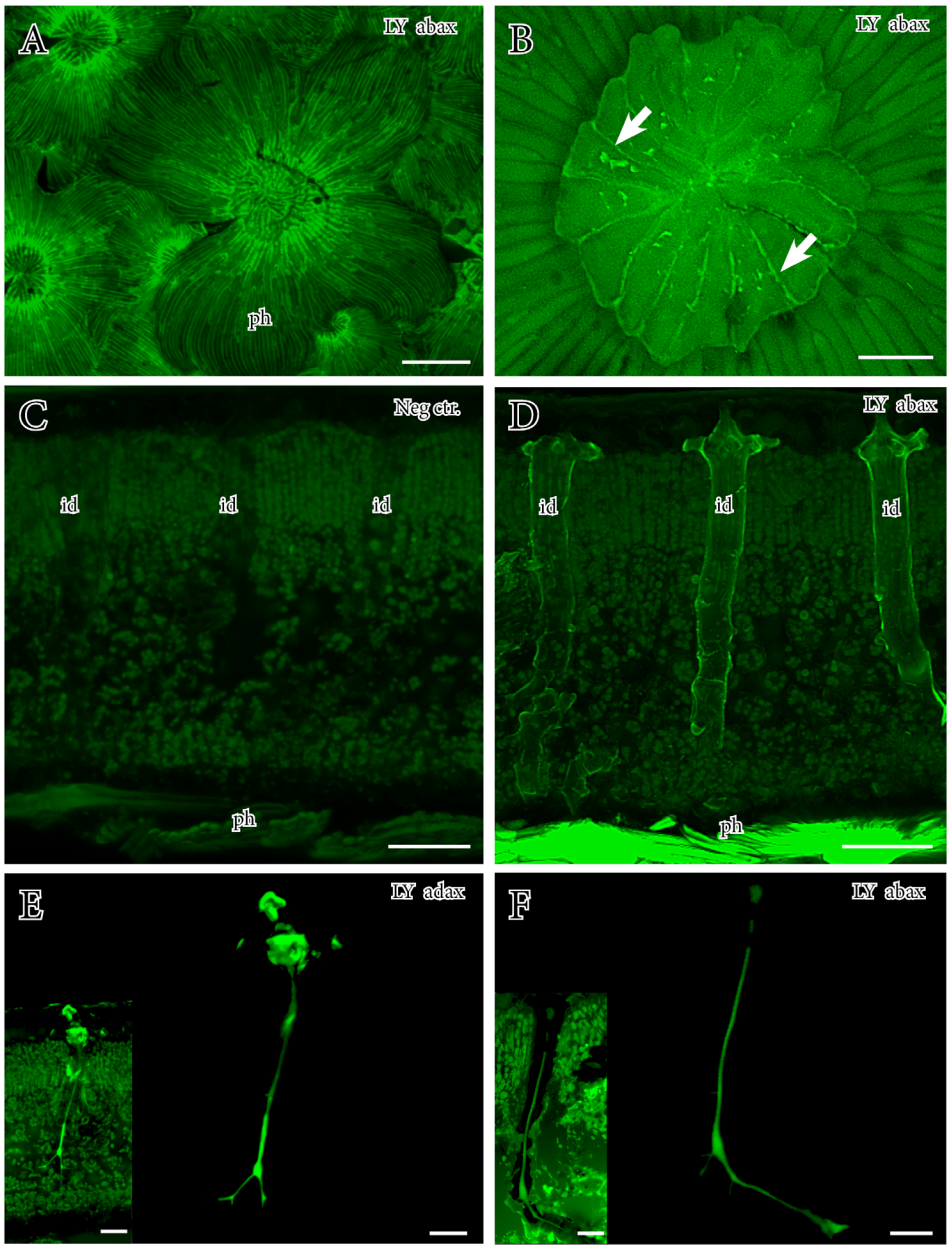

FIGURE 6 Fluorescent dye loading in the leaves of *Capparis odoratissima*. (a) Abaxial deposition of 1 μL droplets LY revealed strong fluorescence towards the centre of the peltate hairs. (b) Detail of the central region of the peltate hairs showing fluorescence in the cell walls (arrows). (c) Negative control showing absence of autofluorescence in the cell walls of the idioblasts with a 488 nm wavelength. (d) Following abaxial loading of the dye, idioblasts showed a strong fluorescence in their walls. (e) Maximum projection of the lumen of an idioblast filled with LY dye after adaxial deposition. (f) Same as E, but with the dye loaded abaxially. Id, idioblast. LY adax, adaxial load of Lucifer yellow; LY abax, abaxial load of Lucifer Yellow. Scale bars: a = 100 μm; b-d = 50 μm; e-f = 20 μm [Colour figure can be viewed at wileyonlinelibrary.com]

Our results revealed a high hygroscopicity of the peltate hairs of *C. odoratissima*. Hygroscopic peltate hairs have been reported in some angiosperm species (Bickford, 2016; Eller et al., 2016; Grammatikopoulos & Manetas, 1994; Pina, Zandavalli, Oliveira, Martins, & Soares, 2016; Vitarelli et al., 2016), with the best studied being epiphytic bromeliads (Benz & Martin, 2006; Benzing, 1976; Benzing et al., 1978; Benzing & Burt, 1970; Ohrui et al., 2007; Raux et al., 2020). While a trade-off between epidermal evaporation and water entrance from the atmosphere might exist, in *C. odoratissima*, this trade-off favours the uptake of water from the trichomes of the abaxial surface, and from the idioblast tips when water condenses in the adaxial surface. Strikingly, loading the leaves of a seedling *in vivo* revealed that the droplet disappearance from the adaxial surface was similar to that of the abaxial surface.

4.3 | The biochemistry of foliar water uptake in *Capparis odoratissima*

The pathway of atmospheric water entry in the leaves of *C. odoratissima* involves hygroscopic materials deposited in the leaf coatings (Gouvra & Grammatikopoulos, 2003). In the current work, we first describe the thick-walled structures composing the multicellular peltate hairs, which project pectins to the external part, suggesting their involvement in the initial water capture when condensation happens in the abaxial side. A few reports have revealed the presence of pectins in trichomes, such as species from semi-arid forests like *Combretum leprosum* (Pina et al., 2016), the tropical species *Drymis brasiliensis* (Eller, Lima, & Oliveira, 2013) or in the trichomes of *Fagus* (Schreel, Leroux, et al., 2020). In addition, we revealed that both

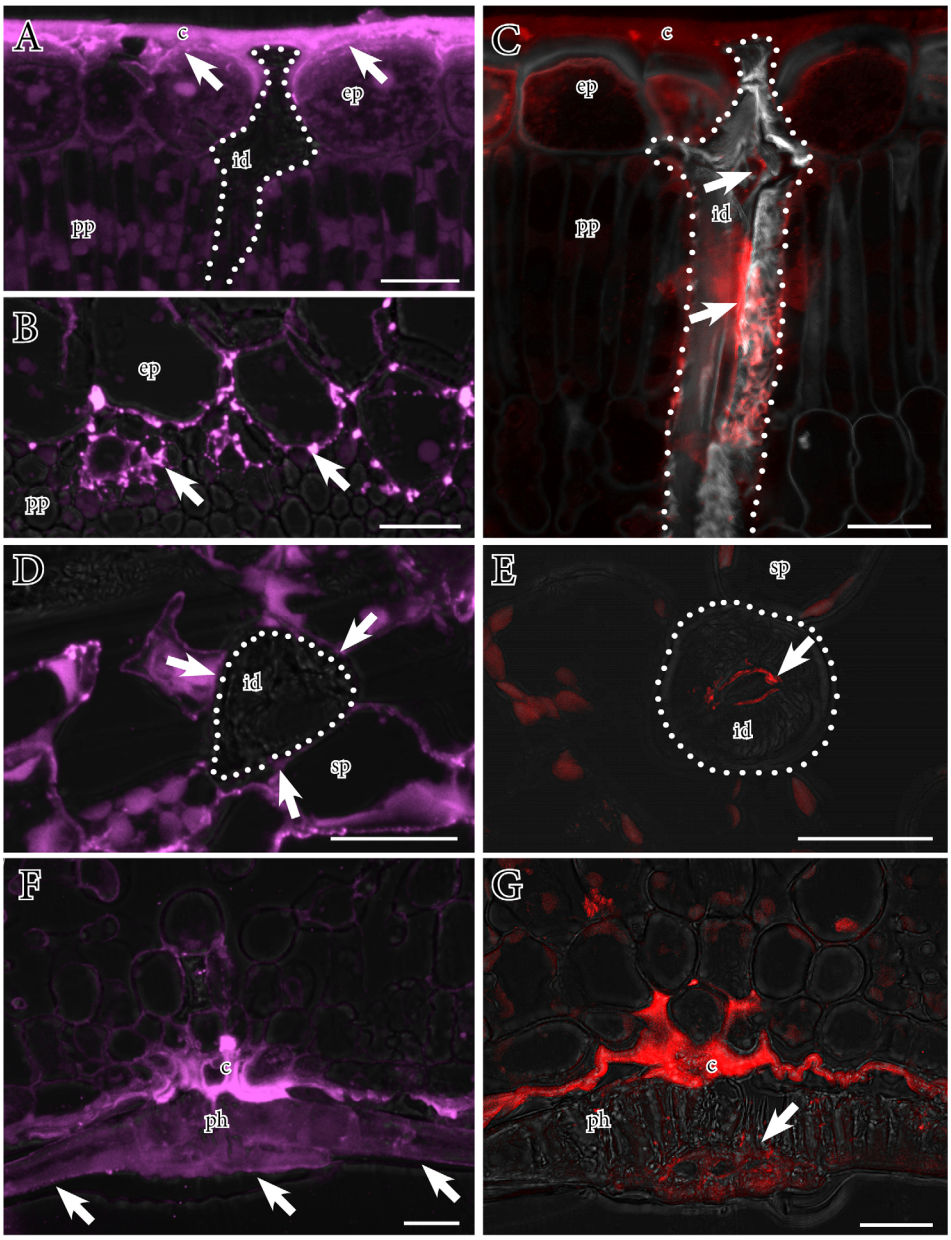

FIGURE 7 Immunolocalization of pectins (JIM7 mAb; purple colour) and arabinogalactan proteins (JIM8 mAb; red colour) in *Capparis odoratissima* leaves in transverse (a, c, f, g) and paradermal (b, d, e) sections. (a, b) High levels of pectins (arrows) were indicated in the apoplast of epidermal cells, particularly between the cuticle and the cell walls of the epidermis (dotted lines indicate the profile of an idioblast). (c) In contrast, AGPs epitopes (arrows) were present in the lumen of the idioblasts (dotted line). (d) Pectins (arrows) were also present in the external cell walls of the spongy mesophyll in contact with the idioblasts (dotted line). (e) Arabinogalactan protein epitopes (arrows) showed a consistent presence along the lumen of idioblasts (dotted line). (f) The external walls of the peltate hairs showed a consistent presence of pectins (arrows). (g) The lumens of the peltate hairs further contained AGPs (arrows), consistent with their presence along the idioblast-hair continuum. C, cuticle; ep, epidermis; pp, palisade parenchyma; id, idioblast; sp, spongy parenchyma; ph, peltate hair. Scale bars: 20 μm [Colour figure can be viewed at wileyonlinelibrary.com]

epidermal and spongy mesophyll cells show a high concentration of un-esterified pectins in their cell walls. This is in line with the ubiquity of pectins within the leaf mesophyll. In the leaves of *C. odoratissima*, the tight association of mesophyll cells and their exposed pectins with the numerous idioblasts may imply a pulling force for water deposited on the leaf surfaces, using idioblasts as carriers.

The idioblasts of *C. odoratissima* are highly hygroscopic, with cellulosic walls that contain polar molecules for water attachment, but also partially lignified, suggesting a secondary role in defence and structural support. A finely tuned water uptake in *C. odoratissima* is revealed by our experiments with the apoplastic dye tracer Lucifer Yellow. Water entering from the surrounding atmosphere to the idioblasts flows through an intricate network of crenations and branches within the idioblasts that connect all leaf tissues and the exterior. Most striking is the fact that epitopes belonging to AGPs are specifically located within these channels. AGPs are highly branched proteins with a short amino acid backbone attached to the plasma membrane of cells, and a large saccharidic part that has been related with nutritive and/or signalling functions between cells (Ellis, Egelund, Schultz, & Bacic, 2010). AGPs play different roles in plant development, including mate recognition and support during reproduction, proper early seedling development and many others (Majewska-Sawka & Nothnagel, 2000; Pereira, Lopes, & Coimbra, 2016; Vaughn, Talbot, Offler, & McCurdy, 2007). However, the role of AGPs in plant hydration has been scarcely studied. Remarkably, works evaluating the composition of the cell walls in the resurrection plant *Craterostigma wilmsii*, which can completely dry out and subsequently regain water, point to the hygroscopic properties of AGPs as critical players in this rapid and effective rehydration (Vicré, Lerouxel, Farrant, Lerouge, & Driouich, 2004). AGP-related proteins have been

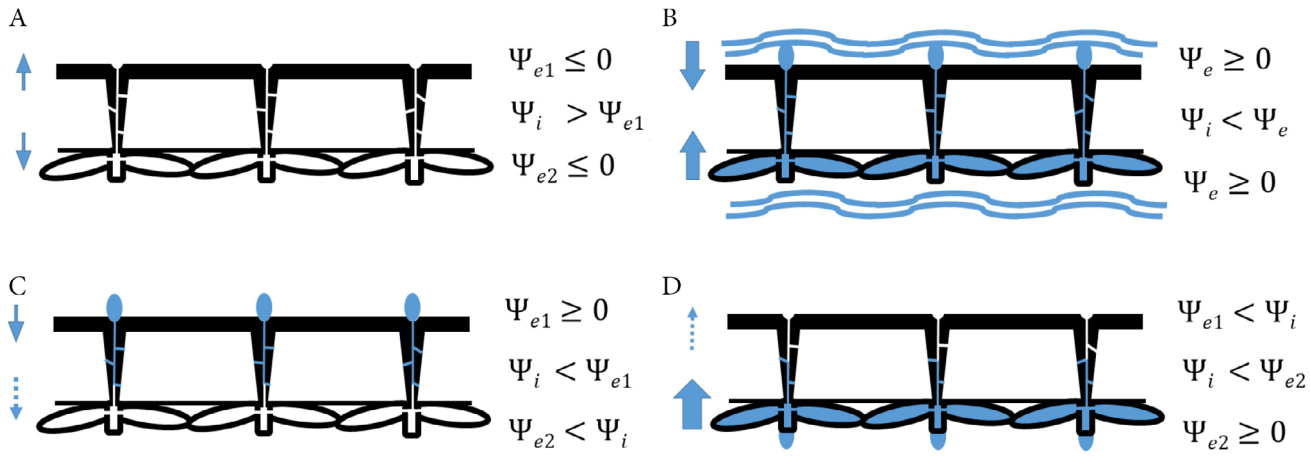

FIGURE 8 Simplified model of water balance in the leaves of *Capparis odoratissima*. (a) In the absence of high humidity of the surrounding atmosphere, the water potential of the leaves is higher than the surrounding environment, thus there is a net loss of water (blue arrows). (b) The opposite situation happens with submerged leaves, which have lower water potentials than the environment, thus gaining water (blue arrows) through the lumen of the continuum peltate hairs-idioblasts. (c) When water condenses in the adaxial surface, the inner leaf potential is lower than this surface, thus allowing water to enter through the lumen of the idioblasts (blue arrow), while water losses from the abaxial surface (assuming a 'dry' environment) may equal water gains (dotted arrows). (d) When water condenses in the abaxial surface, water enters through the lumen of the peltate hairs and the idioblasts (thick blue arrow), but cuticular water loss through the adaxial leaf surface (assuming a 'dry' environment) appears to be lower than water entrance (thin blue arrow). Note that, in scenarios b and c, we did not account for the likely temperature gradient created within the leaf tissues [Colour figure can be viewed at wileyonlinelibrary.com]

previously related with the tensile strength of stems due to their participation in secondary cell-wall composition, such as in the vessels or fibres (Ito, Suzuki, Miyamoto, Ueda, & Yamaguchi, 2005; Liu et al., 2013). But the presence of AGPs has never been reported before in idioblasts with such specific pattern as in the current work. What this reveals is the biochemical complexity of sclerenchymatous tissues, which are possible effectors enabling hydration of tissues during periods where water deficits in the soil combine with water saturation in the atmosphere (Figure 8). Thus, AGPs may be secreted to the lumen of the idioblasts during development, serving as bridges of water uptake between the atmosphere and the leaf mesophyll. Future works should explore the presence of AGPs in sclerenchymatous tissues of other species, as well as their putative role in leaf capacitance.

5 | CONCLUSIONS

Leaf water absorption has been widely studied in the major groups of angiosperms, including magnoliids (eight genera), monocots (seven genera) and eudicots (67 genera) (reviewed by Berry et al., 2019, and by Dawson & Goldsmith, 2018), pointing to foliar water uptake as a key factor affecting plant function in most ecosystems (Weathers et al., 2019). However, the effect of foliar hydration in the overall plant physiology is stronger in dry or semi-dry environments (Schreel et al., 2019), such as the dryland tropical areas where *C. odoratissima* grows, where the water in the soil is often a limiting resource, and foliar water uptake may become pivotal for plant growth and survival.

Our data strongly suggest that the pathway for water uptake in *C. odoratissima* is mediated by the interconnected idioblasts and peltate hairs. We propose a model (Figure 8) that involves apertures of the leaves towards the adaxial surface, which are involved in water uptake, but may facilitate evapotranspiration. Hygroscopic materials belonging to arabinogalactan proteins serve to draw water into the lumen of the idioblasts, while pectins in the mesophyll and the epidermis may further facilitate the incorporation of water into leaf tissues. We believe that this cascade of biochemical and physical events underlies the ability of *Capparis odoratissima* trees to utilize atmospheric water resources.

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CONFLICT OF INTEREST

The authors declare there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available upon request to the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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