

Revisiting an ecophysiological oddity: hydathode-mediated foliar water uptake in *Crassula* species from southern Africa

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Abstract

Hydathodes are usually associated with water exudation in plants. However, foliar water uptake (FWU) through the hydathodes has long been suspected in the leaf-succulent genus *Crassula* (Crassulaceae), a highly diverse group in southern Africa, and, to our knowledge, no empirical observations exist in the literature that unequivocally link FWU to hydathodes in this genus. FWU is expected to be particularly beneficial on the arid western side of southern Africa, where up to 50% of *Crassula* species occur and where periodically high air humidity leads to fog and/or dew formation. To investigate if FWU is operational in different *Crassula* species we used the apoplastic fluorescent tracer Lucifer Yellow in combination with different imaging techniques. Our images of dye-treated leaves confirm that hydathode-mediated FWU does indeed occur in *Crassula* and that it is probably widespread across the genus. Hydathodes in *Crassula* have been repurposed as moisture-harvesting structures, besides their more common purpose of guttation, an adaptation that has likely played an important role in the evolutionary history of the genus. Our observations suggest that FWU ability is independent of geographical distribution and its associated environmental conditions, as FWU is possible in species occurring within the fog belt of western southern Africa but also in those from the rather humid eastern side. We did not find a strong apparent link between FWU ability and leaf surface wettability. Instead, the hierarchically sculptured leaf surfaces of several *Crassula* species may facilitate FWU due to hydrophilic leaf surface microdomains, even in seemingly hydrophobic species. Overall, these results confirm the ecophysiological relevance of FWU in *Crassula* and reassert the importance of atmospheric humidity for some arid-adapted plant groups.

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Keywords

arid environments; atmospheric water; *Crassula* ; foliar water uptake; hydathodes; southern Africa; succulent plants; wettability

Abstract

Hydathodes are usually associated with water exudation in plants. However, foliar water uptake (FWU) through the hydathodes has long been suspected in the leaf-succulent genus *Crassula* (Crassulaceae), a highly diverse group in southern Africa, and, to our knowledge, no empirical observations exist in the literature that unequivocally link FWU to hydathodes in this genus. FWU is expected to be particularly beneficial on the arid western side of southern Africa, where up to 50% of *Crassula* species occur and where periodically high air humidity leads to fog and/or dew formation. To investigate if FWU is operational in different *Crassula* species we used the apoplastic fluorescent tracer Lucifer Yellow in combination with different imaging techniques. Our images of dye-treated leaves confirm that hydathode-mediated FWU does indeed occur in *Crassula* and that it is probably widespread across the genus. Hydathodes in *Crassula* have been repurposed as moisture-harvesting structures, besides their more common purpose of guttation, an adaptation that has likely played an important role in the evolutionary history of the genus. Our observations suggest that FWU ability is independent of geographical distribution and its associated environmental conditions, as FWU is possible in species occurring within the fog belt of western southern Africa but also in those from the rather humid eastern side. We did not find a strong apparent link between FWU ability and leaf surface wettability. Instead, the hierarchically sculptured leaf surfaces of several *Crassula* species may facilitate FWU due to hydrophilic leaf surface microdomains, even in seemingly hydrophobic species. Overall, these results confirm the ecophysiological relevance of FWU in *Crassula* and reassert the importance of atmospheric humidity for some arid-adapted plant groups.

Abbreviations

<i>C</i>	Hydraulic capacitance
ESEM	Environmental scanning electron microscopy
FWU	Foliar water uptake
GCFR	Greater Cape Floristic Region
LYCH	Lucifer Yellow carbohydrazide
θ_C	Contact angle
Ψ	Water potential

1 INTRODUCTION

Uptake of atmospheric water by plant organs other than roots has been a long-standing debate, yet it is currently believed to be more widespread than previously thought. Foliar water uptake (FWU; Rundel 1982; Dawson and Goldsmith 2018; Berry et al. 2019) and stem water uptake (Oliveira et al. 2005; Earles et al. 2016) have been reported in many plant families and across most biomes. A decreasing water potential (Ψ) gradient from water on the leaf surface into the mesophyll is presumed to be a basic requirement for FWU (Goldsmith 2013; Oliveira et al. 2014), so it is a presumably common phenomenon in habitats with generally high atmospheric humidity (Binks et al. 2019; Boanares et al. 2019; Regalado and Ritter 2021; Chin et al. 2022). However, steep Ψ gradients leading to efficient FWU are more likely to occur in (semi-)arid and saline habitats that experience seasonal rainfall or periodically high air humidity (Rundel 1982; von Willert et al. 1992; Reef and Lovelock 2015), in which FWU is expected to be a highly favourable strategy. Accordingly,

FWU has been reported in mangrove species (Fuenzalida et al. 2019; Hayes et al. 2020; Coopman et al. 2021), in several drought-tolerant shrubs and trees (Breshears et al. 2008; Yan et al. 2015; Hill et al. 2021), and in epiphytes growing in xeric microhabitats (Reyes-García et al. 2012; Gotsch et al. 2015; Pan et al. 2021).

Deposition of liquid water on leaf surfaces is governed by their wettability, which in turn is determined by features such as trichomes, hygroscopic salts and epicuticular waxes (Konrad et al. 2015; Barthlott et al. 2017), and water entering the leaves through FWU must overcome a series of hydraulic resistances until it reaches the cells or the vasculature (Buckley 2015; Boanares et al. 2020). Several entry points into the leaf have been proposed, such as the cuticle and stomata (Fernández et al. 2021; Guzmán-Delgado et al. 2021; Chin et al. 2023), but also specialized trichomes and scales (Fernández et al. 2014; Eller et al. 2016; Pina et al. 2016; Raux et al. 2020; Prats and Brodersen 2021), which may facilitate FWU by relaxing some of the hydraulic resistances. Even more specialized leaf surface structures, usually found in arid- and saline-adapted plants, can be coupled with structures within the mesophyll which may enhance FWU even further and aid in water distribution. Notable examples include the peltate hairs associated with thick-walled idioblasts in the xerophyte *Capparis odoratissima* (Capparaceae; Losada et al. 2021) and the cork warts associated with sclerified idioblasts in species of the mangrove *Sonneratia* (Lythraceae; Bryant et al. 2021). However, linking leaf morpho-anatomical traits to FWU remains challenging, given that different and apparently opposite trait syndromes that support FWU have been reported among different plant groups (dos Santos Garcia et al. 2022; Chin et al. 2023).

Many drought-avoiding succulent plants (for review see Ogburn and Edwards 2010 and Males 2017) occur in habitats with extremely low soil moisture yet with periodically high air humidity due to a strong oceanic influence resulting in fog and/or dew formation, such as the Atacama desert and the Baja California desert (part of the Sonoran Desert) in the Americas (Rundel et al. 1991; Webb and Turner 2015), and the Succulent Karoo in southern Africa (Desmet and Cowling 1999; Matimati et al. 2010). Indeed, fog-harvesting strategies and fog drip have been widely reported among succulents (Mooney et al. 1977; Martorell and Ezcurra 2002; Schulz et al. 2011; Matimati et al. 2013; Kundanati et al. 2022), and water uptake by aerial parts has often been suggested. In the Americas, stem water uptake through the areoles has been long suspected in many Cactaceae (Schill and Barthlott 1973; Barthlott and Capesius 1974; Porembski 1994), likely facilitated by fog-harvesting properties of spines and trichomes (Ju et al. 2012; Liu et al. 2015; Kim et al. 2017). In southern Africa, FWU has been suggested for succulent species of Anacampserotaceae and Aizoaceae, most of which possess specialized trichomes or scales (Marloth 1910; Barthlott and Capesius 1974; Seely et al. 1977; Niesler 1997). However, many of these cases lack solid experimental evidence and thus remain speculative.

A particular case that has attracted more attention is that of the genus *Crassula* (Crassulaceae) in southern Africa, in which FWU has long been suspected. Southern Africa comprises several biomes with contrasting environmental conditions, including differences in aridity, rainfall seasonality and fog influence (**Fig. 1**). Along the (semi-)arid western coast of southern Africa, ocean moisture and topographical features give rise to a coastal fog belt extending up to 100 km inland (**Fig. 1C**) (Olivier 1995, 2002; Atlas of Namibia Team 2022), which strongly influences the coastal areas of the floristically megadiverse Succulent Karoo biome, part of the Greater Cape Floristic Region (GCFR; see **Fig. 1A**) (Cowling et al. 1998; Mucina and Rutherford 2006; Snijman 2013). Within this belt, nighttime and early morning fog and dew are more predictable and even more abundant water sources than rainfall, particularly on rock outcrops, ridges and inselbergs (i.e. isolated mountains) that efficiently intercept moisture (Williamson 1997; Cowling et al. 1999; Desmet and Cowling 1999). In contrast, the eastern side of southern Africa exhibits a dry sub-humid to humid climate, with significantly more abundant rainfall (**Fig. 1B**).

The leaf-succulent genus *Crassula* is a characteristic element of the southern African flora and occurs across all southern African biomes, but its centre of diversity is in the Succulent Karoo and the rest of the predominantly winter-rainfall GCFR, where it has undergone a recent radiation (Manning and Goldblatt 2012; Snijman, 2013; Lu et al. 2022). According to Tölken (1977), the genus can be divided in two subgenera: the paraphyletic subgenus *Disporocarpa* Fisch. & C.A.Mey., which encompasses the two most early-diverging clades, and the

highly diverse monophyletic subgenus *Crassula*, which corresponds to the most speciose clade. The genus displays a high degree of morphological diversity (Dortort 2009a, 2009b), as well as striking variation of leaf surface sculpturing (Jürgens 1985; Whittaker 2015; Fradera-Soler et al. 2021). One of the most defining features of *Crassula* is the presence of marginal and/or laminar hydathodes on the leaves of nearly all species (van Jaarsveld 2003; Thiede and Egli 2007). Hydathodes are often overlooked foliar structures that are relatively common among vascular plants (for review see Cerutti et al. 2019), being responsible for the process of guttation (i.e. the exudation of apoplastic fluid; Bellenot et al. 2022). Marginal and apical hydathodes are the most prevalent (Cerutti et al. 2019; Jauneau et al. 2020; Rios et al. 2020), while laminar hydathodes, which are found over the entire leaf surface, are restricted to Crassulaceae and three other eudicot families, which have very few or no succulent representatives: Moraceae, Urticaceae and Myrothamnaceae (Lersten and Peterson 1974; Lersten and Curtis 1991; Chen and Chen 2005; Drennan et al. 2009). The noteworthy anatomy of hydathodes in *Crassula* and their contrasting foliar distribution among different species have led to several exquisitely illustrated publications through the years (de Bary 1884; Sporer 1915; Rost 1969; Smirnova 1973; Voronin et al. 1976). However, the fact that structures usually associated with excess water and guttation occur so abundantly in arid-adapted *Crassula* species constitutes an ecophysiological enigma. Early studies already speculated that FWU may occur in *Crassula* through trichomes and/or hydathodes (Marloth 1910; Schönland 1910; Sporer 1915), an idea that was revisited and linked more robustly to hydathodes (Barthlott and Capesius 1974; Tölken 1974, 1977; Voronin et al. 1976). The highly variable foliar distribution of hydathodes among *Crassula* species, often occurring on the surfaces most exposed to the atmosphere and thus most likely to experience water deposition, is a compelling indication that FWU may be a widespread adaptation in the genus (Voronin et al. 1976; von Willert et al. 1992). Informal observations by Tölken (1974, 1977) of uptake of a crystal violet solution suggested that nearly all *Crassula* species examined were able to absorb water through the hydathodes if dehydrated enough. This culminated in the most comprehensive work on hydathode ecophysiology in *Crassula* by Martin and von Willert (2000), who demonstrated that FWU is possible in many species by measuring changes in leaf thickness after surface wetting. However, their results did not show a clear distinction between the direct effects of wetting through FWU and the possible indirect effects through transpiration reduction, nor did they empirically link FWU to hydathodes.

Hydathode-mediated FWU in *Crassula* has become a widely assumed phenomenon that often appears in the literature, yet, to our knowledge, no visual proof has been available until now to unequivocally link hydathodes to FWU in this genus. The goal of this study was to corroborate that hydathode-mediated FWU does indeed occur in *Crassula* by using a fluorescent tracer and different imaging techniques. We hypothesized that FWU would occur mostly, if not exclusively, in *Crassula* species occurring in or near the fog belt of western southern Africa. Furthermore, we hypothesized that FWU ability in *Crassula* would be strongly influenced by leaf surface sculpturing and wettability. Finally, we aimed to interpret the results from an evolutionary perspective and assess their ecophysiological relevance.

2 MATERIALS AND METHODS

2.1 *Crassula* species

Nine species of *Crassula* native to southern Africa were used in this study (**Table 1**), spanning the breadth of the most recent phylogeny of the genus (Lu et al. 2022) and different growth forms and habitat preferences in southern Africa (**Figs. 1, 2**). The six species with compact growth forms (*C. ausensis* subsp. *titanopsis*, *C. deceptor*, *C. fragariooides*, *C. plegmatooides*, *C. sericea* var. *sericea*, *C. tecta*) occur along the southwestern and western coasts of southern Africa, mainly within the predominantly winter-rainfall Succulent Karoo biome, whereas the three non-compact species (*C. multicava* subsp. *multicava*, *C. ovata* and *C. perforata* subsp. *perforata*) occur along the southeastern and eastern coasts.

2.2 Plant material

Plants were obtained from specialist nurseries and from the living collections of the Royal Botanic Gardens, Kew (UK) (**Table 1**). All species were potted in a mix of 1:1 pumice:sand, except *C. multicava*, *C. ovata*, *C. perforata* which were potted in a mix of 1:3:3 potting mix:pumice:sand. All plants were grown in a

greenhouse with 12-hour days and 20/17°C day/night temperatures. The methods described below were applied, for each species, to the part of the leaf where water uptake was more likely, due to the presence and/or higher abundance of hydathodes (see **Table 2**).

2.3 Characterization of leaf surfaces and hydathode anatomy

2.3.1 *Sampling and processing of leaf material*

Leaves were carefully excised from the plants and transported in zip-lock bags. The first batch of leaf material was used fresh for a general characterization of leaf surfaces. Additional batches of leaves were collected, and areas of interest (see **Table 2**) isolated using a scalpel, which were then immersed in 4% (w/v) paraformaldehyde in phosphate-buffered saline (PBS) for 1 h under vacuum, and then overnight at 4°C. This fixed leaf material was used for vibratome and ultramicrotome sectioning.

2.3.2 *Visual characterization of leaf surfaces*

Fresh leaves were imaged with a stereo microscope (M205FA, Leica Microsystems) fitted with a digital camera.

2.3.3 *Vibratome sectioning*

Fixed leaf samples were washed twice in PBS and embedded in 8% agarose. The agarose blocks were sectioned using a vibratome (VT1000 S, Leica) to obtain 150 μm -thick sections. These specimens were mounted in 8:2 glycerol:PBS on a microscope slide and imaged with a wide-field microscope (ECLIPSE Ni-U, Nikon) fitted with a digital camera.

2.3.4 *Ultramicrotome sectioning*

Fixed leaf samples were washed twice in PBS and dehydrated through an ethanol graded series (30, 50, 70, 90, 100% EtOH). They were then embedded in medium-grade LR white resin (Agar Scientific), using a 3-step graded series (1:3, 1:1, 3:1 resin:EtOH, 2 h each) and overnight immersion in 100% resin twice. The resin was polymerized at 60°C for 24 h, semi-thin 2 μm -thick sections were obtained using an ultramicrotome (EM-UC7, Leica) fitted with a glass blade, and sections were adhered to glass slides. The sections were stained with 0.5% toluidine blue on a hotplate for 2 min, washed three times in dH₂O, and mounted in 8:2 glycerol:PBS on a microscope slide. Stained specimens were imaged with a wide-field microscope (ECLIPSE Ni-U, Nikon) fitted with a digital camera.

2.3.5 *Environmental scanning electron microscope*

Surface characterization with light microscopy was complemented by environmental scanning electron microscopy (ESEM). ESEM differs from conventional SEM in that only a low vacuum is applied to the chamber, which allows for rather high humidity, while a high vacuum can be maintained in the column (McGregor and Donald 2010; Stabentheiner et al. 2010). Therefore, fully hydrated specimens can be imaged under near-native conditions without the need for sample preparation, which often results in technical artefacts and morphological alterations (Yuan et al. 2020). Fresh leaf samples were imaged using the environmental mode in a SEM (Quanta FEG 3D, FEI) at room temperature, 0.4–0.7 mbar, high voltage of 20 kV, and a working distance of 3–7.5 mm.

2.4 Leaf surface wettability

Three fresh leaves per species were carefully excised from the plants and used as replicates. For each species, the area of interest (see **Table 2**) was isolated using a scalpel so that it would lie as flat as possible on the stage. Leaf surface wettability was assessed by measuring the contact angle (ϑ_C) in a tensiometer fitted with a high-speed camera (Attension Theta optical tensiometer, Biolin Scientific AB), using the sessile drop method. A 5 μl droplet of dH₂O (as suggested by Matos and Rosado 2016) was placed on the leaf surface by the tensiometer and the ϑ_C was recorded for 10 seconds (14 FPS). The resulting static ϑ_C was measured using the Young-Laplace fit.

2.5 Foliar water uptake experiment

Plants were grown in the greenhouse for a year and a half before being transferred to a climate chamber. Conditions in the climate chamber were 12-hour days, with $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ of light, $25/20^\circ\text{C}$ day/night temperatures, and 20–35% relative humidity. Plants were acclimated to these conditions for three months before the start of the experiment. Drought was simulated by withholding water for six weeks in at least two plants per species, while at least two other plants per species were kept under a well-watered regime (i.e. thorough watering every 10 days).

For the FWU experiment, we used Lucifer Yellow carbohydrazide (LYCH), a fluorescent tracer often used to study water transport *in vivo* in plants (Oparka and Prior 1988; Oparka et al. 1988; Farrar et al. 1992; Bederska et al. 2012), including studies focusing on FWU (Burrows et al. 2013; Eller et al. 2013, 2016; Pina et al. 2016; Holanda et al. 2019; Losada et al. 2021). LYCH was used as an apoplastic tracer, as it is unable to cross plasma membranes. A 50mM stock solution of LYCH as dilithium salt (Sigma) was prepared in dH_2O and stored at -18°C . Before use, the stock solution was thawed and diluted in dH_2O to a working solution of 0.5 mM.

The evening before the experiment, leaves from both treatments (i.e. drought and well-watered) were carefully excised from the plants and the cut end was sealed with an ethyl cyanoacrylate-based glue (Super Glue, Loctite) to prevent both water loss and tracer uptake during the experiment. Rudimental humidity chambers were assembled by laying out wet paper towels inside plant propagators with transparent covers. The excised leaves were balanced on inverted Petri dishes, so that they would not touch the wet towels. On the day of the experiment, 10–100 μl droplets (depending on the species) of LYCH solution were applied to the area of interest of each leaf (see **Table 2**) at 8:00 a.m. (local time), two hours into the light period ($250 \mu\text{mol m}^{-2}\text{s}^{-1}$, 25°C), to simulate morning fog and dew. Three hours after the application of the tracer, the lamina of the leaves was rinsed thoroughly three times by immersion in dH_2O to remove the residual surface dye and carefully dried with paper towel. Free-hand sections were made of the treated leaf areas and mounted in 9:1 glycerol:PBS to minimize efflux and redistribution of the dyes (Mastroberti and de Araujo Mariath 2008). We made additional free-hand sections of untreated leaves (i.e. controls) to observe the natural autofluorescence of leaf tissues. All leaves were imaged immediately after sectioning and mounting in a fluorescence stereo microscope fitted with a digital camera (M205FA, Leica Microsystems), using both the GFP2 (ex. 480/40 nm; em. 510 nm LP) and the ET GFP (ex. 470/40 nm; em. 525/50 nm) filter sets.

3 RESULTS

3.1 General leaf morphology

Leaf morphology of the *Crassula* species examined ranged from planar and bifacial (e.g. *C. multicava* and *C. ovata*) to subterete and equifacial (e.g. *C. tecta* and *C. ausensis*) (**Figs. 2, 3**). Furthermore, leaf orientation varied: leaves were patent in *C. multicava*, *C. ovata* and *C. perforata*, erecto-patent in *C. sericea*, and erecto-patent to erect in *C. fragarioides*, *C. tecta* and *C. ausensis*. In these three last species, only the distal half of the leaves was exposed to the atmosphere, due to the tight arrangement of the leaves. In the two columnar species, *C. deceptor* and *C. plegmatoides*, leaves were wide and short and tightly arranged, so that the abaxial side of the leaves was predominantly exposed to the atmosphere.

3.2 Leaf surface anatomy

Leaf surface sculpturing was strikingly variable (**Figs. 3–6 ;Table 2**). In *C. multicava* and *C. ovata*, leaf surfaces were glabrous, with white mineral crusts or salt deposits associated with the hydathodes, whereas in *C. perforata* they were glabrous yet with large conical trichomes along the margins. *C. deceptor*, *C. fragarioides* and *C. plegmatoides* had papillate leaf surfaces, while *C. sericea* had long, subulate trichomes. The most spectacular indumenta were those of *C. ausensis* and *C. tecta*, with clavate trichomes and large bladder-cell idioblasts respectively. In some species, the indumentum showed patterning, with clustering of papillae/trichomes/idioblasts, as in *C. fragarioides*, *C. ausensis* and *C. tecta*. Besides the indumentum, in some species the leaf surface was hierarchically sculptured: a series of tubercles (i.e. surface protuberances)

and depressions were present in *C. ausensis*, *C. deceptor* and *C. tecta*. In *C. ausensis* and *C. tecta*, these tubercles coincided with the sites of trichome/idioblast clustering. In the case of *C. tecta*, the tubercles were in turn arranged in bands along the length of the leaf, thus forming regular ridges and grooves. Epicuticular waxes (**Fig. 5**) were particularly prominent in *C. ovata*, in which they formed cracked crusts, in *C. plegmatoides*, in which they formed tubules on top of the papillae, and in *C. deceptor*, in which they formed a flaky cover over the papillae. It is worth noting that the tips of the tubercles in *C. deceptor* were mostly free of these waxes (**Figs. 4G, 5G**).

3.3 Hydathode anatomy and distribution

The anatomy of hydathodes in the *Crassula* species examined was rather conserved (**Fig. 6**). They all displayed the anatomical arrangement typical of epithemal hydathodes, with three main components: water pore(s), epithem and tracheids. The water pores consisted of more or less sunken pairs of guard cells, which were partially concealed by subsidiary cells. The epithem appeared as a mass of small achlorophyllous cells (**Fig. 4**) underneath the water pore(s), with cytoplasmic contents such as nuclei noticeably stained (**Fig. 6**). A loosely arranged array of xylem tracheids irrigated the epithem and connected it to the leaf vasculature. Cells containing tannins were observed in association with the hydathodes (**Figs. 4, 6**), forming a more or less continuous sheath in some species (e.g. *C. ovata*). Anthocyanin contents in hydathode sheath cells were observed in *C. perforata* and *C. ausensis* (**Fig. 4**).

Two types of hydathodes (sensu Martin and von Willert 2000) were observed (**Table 2**). Type I hydathodes, characterized by being larger and having numerous water pores within a more or less circular epidermal area, were observed in *C. multicava* and *C. ovata* (**Figs. 5, 6**). These hydathodes were also associated with a mineral crust, observed with both light and electron microscopes (**Figs. 3–5**). The remaining species exhibited type II hydathodes, which tend to be smaller and with a single large water pore, often with bulging subsidiary cells (**Figs. 4–6**). The water pores of these hydathodes were located, if present, within the aforementioned papillary/trichomic/idioblastic clusters and/or surface tubercles. The foliar distribution of hydathodes varied among species (**Table 2**), yet they always occurred more abundantly, or even exclusively, on the surfaces most exposed to the atmosphere.

3.4 Leaf surface wettability

The results of surface wettability at the area of interest of each species (see **Table 2**) were summarized in **Fig. 7** (see **Fig. S1** for representative images). Leaf surface wettability ranged from highly hydrophobic ($90^\circ < \vartheta_C < 150^\circ$) to superhydrophilic ($\vartheta_C < 10^\circ$). We observed extremely fast hemiwicking (i.e. capillarity-driven spread of liquid on a rough hydrophilic surface) in *C. tecta* (**Video S1**) and, to a much lesser degree, in *C. ausensis* (**Video S2**).

3.5 Hydathode-mediated foliar water uptake

The results of the experiment showed that FWU could be induced in drought-stressed plants of all but one (i.e. *C. perforata*) *Crassula* species examined (**Fig. 8**). In all species in which FWU could be induced, well-watered plants showed no or very little uptake of the tracer compared with drought-stressed plants. In all species that absorbed the tracer, LYCH fluorescence could be detected in the hydathodes of the leaf surface exposed to the tracer, in most vascular bundles within the leaf, and even in the hydathodes of surfaces that were not exposed to the tracer, which indicates efficient redistribution of absorbed water. Varying degrees of tracer fluorescence were also observed in the indumentum of several species. The redistribution of absorbed water within the leaves was most noticeable in the two species with planar leaves, given that they were easier to image (**Fig. 9**).

4 DISCUSSION

4.1 Hydathode-mediated foliar water uptake is probably a widespread phenomenon among *Crassula* species

After decades of speculation, our results reaffirm hydathode-mediated FWU as a common phenomenon in

both subgenera of *Crassula* (i.e. *Disporocarpa* and *Crassula*), regardless of growth form, habitat preference and phylogenetic relationship. Our results unequivocally prove that FWU through hydathodes is possible in all but one of the *Crassula* species examined. The fact that LYCH fluorescence was present throughout the uptake path demonstrates that this is an entirely, or at least predominantly, apoplastic process (**Fig. 8**). The foliar distribution of hydathodes, occurring on the most exposed leaf surfaces (**Table 2** ; Voronin et al. 1976; Martin and von Willert 2000), and the highly developed 3D venation that interconnects them (Rost 1969; Melo-de-Pinna et al. 2016; Fradera-Soler et al. 2021) are anatomical features that further imply that FWU and subsequent redistribution of absorbed water provide an ecophysiological advantage to *Crassula* species. Since succulents experience very little water loss, even small amounts of water from fog and dew can considerably improve their water balance (von Willert et al. 1992). Furthermore, Martin and von Willert (2000) reported that CO₂ uptake rates in *Crassula* increase in response to FWU and that absorbed water can be transferred from wetted older leaves to younger ones, which highlights the far-reaching physiological consequences of this phenomenon.

Other genera in the Crassulaceae, such as *Kalanchoe* , *Aichryson* and *Sedum* , have only marginal hydathodes or a single (sub)apical one (Caballero and Jiménez 1977; ‘t Hart and Bleij 2003; Thiede and Eggli 2007; Moreira et al. 2012), and even though there are reports of laminar hydathodes in some *Cotyledon* species (Weingart 1935), further anatomical investigations are needed to confirm this. This makes *Crassula* one of the few, if not the only, plant group in which laminar hydathodes and leaf succulence converge. Succulent organs are characterized by high values of hydraulic capacitance (C) (i.e. the change in water content relative to the change in Ψ), which reflects their ability to maintain relatively high Ψ values even during periods of net water loss (Ogburn and Edwards 2010; Fradera-Soler et al. 2022; Leverett et al. 2023). As hypothesized by Berry et al. (2019), high values of C should result in lower overall FWU rates that are sustained for longer: an increase in Ψ resulting from FWU will be slower and will take longer to reach equilibrium, so that the Ψ gradients that underlie FWU can persist for longer. Indeed, a trade-off between C and FWU has been postulated, with species with high C exhibiting lower FWU rates and/or capacity (Gotsch et al. 2015; Boanares et al. 2018). Moreover, higher C means that succulents capable of FWU such as *Crassula* will be able to absorb greater amounts of atmospheric water, thus buffering declines in Ψ during drought. This suggests that the ecophysiological implications of hydathode-mediated FWU have likely played an important role in the diversification of *Crassula* , particularly in (semi-)arid habitats with periodically high air humidity in western southern Africa, such as the Succulent Karoo.

However, not all *Crassula* species seem to be capable of hydathode-mediated FWU. In this study FWU could not be induced in *C. perforata* (**Fig. 8**), which agrees with the observations by Martin and von Willert (2000). Tölken (1974, 1977) did not observe signs of FWU in *C. rupestris* , *C. macowaniana* or *C. brevifolia* either. In contrast with most *Crassula* species, these four species share some commonalities: belonging to subgenus *Crassula* , a mostly glabrous leaf surface with a hydrophobic waxy bloom, a relatively large shrubby growth form, and the ability to dominate in exposed zonal habitats under considerable aridity (Jürgens 1995; Bruyns et al. 2019; Lu et al. 2022). It has been hypothesized that, since these larger species have more extensive root systems, high leaf hydrophobicity may increase water throughfall during precipitation events and provide more water to the roots (Rosado and Holder 2013; Fradera-Soler et al. 2021), which may render FWU less essential for their survival. This may also explain the loss of hydathodes in *C. brevifolia* (von Willert et al. 1992; Martin and von Willert 2000).

4.2 Foliar water uptake ability in *Crassula* is independent of geographical distribution

Our observations suggest that FWU ability in *Crassula* is independent of geographical distribution and the associated environmental conditions, thus challenging our initial assumptions. The coastal areas of the (semi-)arid western and southwestern sides of southern Africa, which fall under the influence of the fog belt, comprise most of the species diversity of *Crassula* (Jürgens 1995), particularly in subgenus *Crassula* (Bruyns et al. 2019; Lu et al. 2022). In the Succulent Karoo, nighttime and early morning fog and dew are more reliable and even more abundant water sources than the overall low rainfall (Williamson 1997; Cowling et al. 1999; Desmet and Cowling 1999). There, shallow-rooted dwarf *Crassula* species usually grow in extremely

xeric microhabitats on rock outcrops, which makes them highly dependent on regular water supply (Esler and Rundel 1999). Accordingly, most of these species grow on south- and west-facing slopes that face the ocean, where interception of wind-driven advective fog is more efficient (Tölken 1974, 1977; Jürgens 1995). Previous studies of FWU in *Crassula* have focused on these species occurring within the fog belt, as the combination of extremely low soil moisture and periodically high air humidity makes them an ideal case study (von Willert et al. 1992; Martin and von Willert 2000). Even in the slightly less arid Little Karoo, the southernmost region of the Succulent Karoo and habitat to *C. tecta*, dew can contribute to significant water deposition despite less fog influence (Weiss and Yapp 1906; Desmet and Cowling 1999).

Overall, these are compelling arguments in support of hydathode-mediated FWU as an ecophysiological strategy that allows dwarf *Crassula* species to exploit even tiny amounts of atmospheric water during long droughts. This may be even more crucial for species occurring within the hyper-arid Gariep centre (sensu van Wyk and Smith 2001), the northernmost region of the Succulent Karoo biome and habitat to *C. ausensis*, *C. deceptor*, *C. plegmatoides* and *C. sericea* (**Fig. 1**). Besides *Crassula*, other plants that occur sympatrically in western southern Africa are also believed to benefit from frequent fog and dew through fog drip, self-irrigation and maybe even FWU (Snow 1985; Andrews et al. 2011; Vogel and Müller-Doblies 2011; Roth-Nebelsick et al. 2012), including leaf succulents in the Aizoaceae (Niesler 1997; Matimati et al. 2013) and the desiccation-tolerant resurrection plant *Myrothamnus flabellifolius* (Myrothamnaceae; Drennan et al. 2009). Interestingly, *Myrothamnus* is also one of the rare cases in which laminar hydathodes occur, suggesting the possibility of FWU.

Far from the influence of the fog belt, *Crassula* species occurring on the southeastern and eastern sides of southern Africa experience overall higher relative humidity and year-round to summer rainfall (**Fig. 1B**; van Wyk and Smith 2001; Mucina and Rutherford 2006). Most of the species in this geographical range belong to subgenus *Disporocarpa*, which tends to extend beyond the GCFR (Bruyns et al. 2019). In *C. multicava* and *C. ovata*, a white mineral crust forms on the hydathodes (**Figs. 3–5**), which has also been noted in other species of subgenus *Disporocarpa*, such as *C. lactea* (Whittaker 2015). This crust has generally been regarded as a sign of frequent guttation (Tölken 1974; Chen and Chen 2005; Michavila et al. 2021; Mehlreter et al. 2022). Thus, under conditions of high soil moisture and low transpiration, these *Crassula* species most likely experience guttation. Guttation through the hydathodes can promote water flux and xylem transport of nutrients when transpiration is limited, while preventing excessive water accumulation and detrimental mesophyll flooding (Feild et al. 2005; Cerutti et al. 2019; Bellenot et al. 2022). Nevertheless, our results show that *C. multicava* and *C. ovata* are also as capable of FWU as the *Crassula* species from within the fog belt, and they are able to quickly redistribute the absorbed water within the leaf (**Fig. 9**). Even though droughts are less severe on the eastern side of southern Africa and fog has minimal, if any, influence, FWU may allow them to utilize any available water from dew formation or brief rainfall events that can wet the leaves, even if they do not lead to significant soil wetting.

4.3 Foliar water uptake in *Crassula* is likely facilitated by hierarchical leaf surface sculpturing

Leaf surfaces exhibit notoriously diverse wettability across the plant kingdom, governed by features such as surface sculpturing and the chemical properties of epicuticular waxes (Prüm et al. 2012; Barthlott et al. 2017). In the *Crassula* species examined we observed a wide range of leaf wettability (**Fig. 7**) that did not seem to be clearly linked to the leaf indumentum. The highly diverse hierarchical sculpturing of the leaf surfaces (Barthlott et al. 2017; Riglet et al. 2021) among the studied *Crassula* species ranged from glabrous to different types of indumentum (**Figs. 3–5**; **Table 2**). Besides its long-established functions in reflecting excessive insolation and limiting transpirational water loss (Bickford 2016; Karabourniotis et al. 2021; Buckley et al. 2022), the indumentum has been implicated in initiating dew formation (von Willert et al. 1992; Burkhardt and Hunsche 2013; Konrad et al. 2015) and collecting fog droplets (Andrews et al. 2011; Ju et al. 2012). However, even among the *Crassula* species with indumentum, leaf wettability ranged widely, from superhydrophilic to highly hydrophobic (**Fig. 7**). We observed hemiwicking (i.e. capillarity-driven spread of liquid on a rough hydrophilic surface; Quéré 2008; Kim et al. 2016; Telecka et al. 2018) in the two *Crassula* species with the most hydrophilic leaf surfaces. This phenomenon occurred very rapidly on the

asymmetrically sculptured leaf surface of *C. tecta* and led to efficient spread of the water film (**Video S1**) (Shin et al. 2016; Jiang et al. 2022), as previously reported (Tölken 1974, 1977; Fradera-Soler et al. 2021), while it was rather slow and barely noticeable in *C. ausensis* (**Video S2**). At the other end of the spectrum, we observed near superhydrophobicity in *C. deceptor* and *C. plegmatoides*, known as the ‘lotus effect’ (i.e. high ϑ_C and low ϑ_C hysteresis, see Bhushan and Nosonovsky 2010; Schneider et al. 2016; Okulova et al. 2018), which is likely caused by the highly hierarchical sculpturing of leaf surfaces, involving the epicuticular waxes (**Fig. 5**) (Barthlott et al. 2017; Riglet et al. 2021).

The interplay of leaf surface wettability and FWU is not strictly relational. Although higher wettability has often been linked to increased FWU capacity or rate (Pan et al. 2021; Tianshi and Chau 2022), and species with hydrophobic leaves are assumed to be less likely to benefit from water deposition from fog and dew, other studies have noted no significant relationship between FWU and leaf surface wettability (Matos and Rosado 2016). This also reflects the diversity of strategies underlying FWU among different plant groups (dos Santos Garcia et al. 2022; Chin et al. 2023). In *Crassula*, even species with seemingly hydrophobic leaves are capable of FWU. Our experimental ϑ_C measurements are based on a water droplet size typical of large raindrops (i.e. 5 μl volume, ~ 2 mm diameter) (Glickman 2000), so wetting behaviours that deviate from our observations are plausible under natural conditions with different droplet sizes, such as those from fog deposition (< 200 μm droplet diameter) and rainfall (> 500 μm droplet diameter). As seen in other plant groups (Pierce et al. 2001), *Crassula* species with seemingly hydrophobic leaf surfaces may still be able to induce condensation or collect fog droplets within hydrophilic leaf surface microdomains. For instance, the wax-free epidermal tubercle tips and hydathode water pores in *C. deceptor* (**Figs. 4G, 5G**) (Barthlott and Capesius 1974; Jürgens 1985) may be able to experience condensation and droplet coalescence (Narhe and Beysens 2006; Sharma et al. 2019; Xing et al. 2020). Abrasion of these waxes may also explain why older leaves of some *Crassula* species, such as *C. plegmatoides*, can be more wettable than young ones (pers. obs.) (Ensikat et al. 2011; Rosado and Holder 2013). Furthermore, higher hydrophobicity of the indumentum compared to the surface underneath, coupled with relatively low trichome density (Brewer et al. 1991; Brewer and Smith 1997; Bhushan and Jung 2008), can lead to changes in overall wettability if water droplets exceed a critical size that allows them to sink between the trichomes and spread along the surface, as in some hairy-leaved species of *Echeveria* (Crassulaceae) (Godeau et al. 2017). This may explain similar observations in some *Crassula* species, such as *C. sericea*, in which leaf surface wettability can range from highly hydrophobic to nearly hydrophilic (**Fig. 7**). All things considered, the complex leaf surface sculpturing in *Crassula* and the existence of leaf surface microdomains resulting in differential wettability may facilitate water deposition and/or channelling towards hydathode water pores, thus facilitating FWU even in seemingly hydrophobic species.

5 CONCLUSIONS

Although FWU has recently been recognized as a rather common phenomenon among plants (Berry et al. 2019), it remains largely unexplored and thus hampers a comprehensive understanding of plant hydraulic functioning. In arid-adapted lineages such as *Crassula*, FWU is expected to be even more crucial for their survival in severe drought. Our observations clarify previous findings (Martin and von Willert 2000), confirming that hydathode-mediated FWU occurs in *Crassula* and that it is probably widespread across the genus.

From their primordial function of guttation, these hydathodes have been co-opted for water absorption, which has likely had a strong influence in the evolution and diversification of the genus in (semi-)arid environments with periodically high air humidity. However, we suggest that the ability for FWU in *Crassula* is independent of geographical distribution and its associated environmental conditions, as well as phylogenetic relationship. While FWU provides an ecophysiological advantage to *Crassula* species occurring on the (semi-)arid western side of southern Africa, where frequent dew and fog can ameliorate the harsh droughts, FWU is also expected to be beneficial to species occurring on the more humid eastern side, where plants may still be able to exploit dew or brief rainfall events. Furthermore, we did not find a strong link between FWU ability and leaf surface wettability. Instead, FWU in *Crassula* may be facilitated by hierarchically sculptured leaf surfaces and

differential wettability. In highly hydrophilic leaves, such as those of *C. tecta*, hemiwicking spreads the water film over the whole surface, thus leading to efficient FWU. However, even seemingly hydrophobic species such as *C. deceptor* may be able to experience frequent leaf surface wetting and subsequent FWU thanks to hydrophilic leaf surface microdomains.

Several questions remain unanswered regarding FWU in *Crassula*, such as the molecular mechanisms behind it and the possible involvement of the epithem. Moreover, other phylogenetically diverse groups of succulent plants may also be benefiting from this phenomenon for their survival, yet empirical proof is needed. Further exploration of FWU in these plants can advance our understanding of adaptation and ecophysiology of succulents and other arid-adapted plants. Surfaces of *Crassula* and other succulent plants benefiting from atmospheric water could also provide inspiration to improve systems for atmospheric water harvesting, which is becoming an increasingly valuable water resource in many parts of the world (Zhang and Guo 2020; Wang et al. 2021).

AUTHOR CONTRIBUTIONS

MF-S and OMG conceived the study. MF-S, JM, AS, BJ and OMG designed the experiments. MF-S conducted the experiments and wrote the draft of the manuscript. MF-S and RT conducted the contact angle (θ_C) measurements. JM, BJ and OMG supervised the research. All authors contributed to the manuscript and approved the final version.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the **Supporting information** section at the end of the article:

Supplementary figures Figures S1–S3.

Video_S1 Droplet behaviour in *C. tecta*, observed in a tensiometer.

Video_S2 Droplet behaviour in *C. ausensis*, observed in a tensiometer; note slowly advancing contact line

TABLES

Table 1. Nine *Crassula* species examined in this study. Growth form, habitat and habit according to Tölken (1985), Pavelka (1999), van Jaarsveld (2003), van Jaarsveld et al. (2011) and Lu et al. (2022). Biogeography according to van Wyk & Smith (2001), Mucina & Rutherford (2006) and Mucina et al. (2014). Origin of the plant material: (N) specialist nurseries, (K) Royal Botanic Gardens, Kew (UK).

Crassula **taxon**

Subgenus

Growth form

Habit

Habitat

Biome

Bioregion / Domain / District (ecogeographic units)

Origin of plants

C. ausensis subsp. *titanopsis* Pavelka

Crassula

Compact Rosette

Sheltered crevices on quartzite outcrops

Succulent Karoo–Nama-Karoo transition Gariiep centre + extrazonal exclaves inland

N

C. deceptor Schönland & Baker f.

Crassula

Compact Column

Gravel flats or rocky slopes, often in quartz gravel

Succulent Karoo Namaqualand Hardeveld, Namaqualand Sandveld and Richtersveld bioregions

N

C. fragarioides van Jaarsv. & Helme

Crassula

Compact Rosette

Partly shaded sandy microhabitats on sandstone outcrops

Fynbos Bokkeveld plateau

N

C. multicava Lem. subsp. *multicava*

Disporocarpa Fisch. & C.A.Mey.

Non-compact Short shrub

Coastal areas in shaded wooded ravines and valleys

Indian Ocean Coastal Belt, Albany Thicket

K

C. ovata (Mill.) Druce

Disporocarpa Fisch. & C.A.Mey.

Non-compact Tall shrub

Rocky slopes and often associated with scrubland vegetation

Albany Thicket, Fynbos

N

C. perforata Thunb. subsp. *perforata*

Crassula

Non-compact Short shrub

Rock crevices in sheltered localities or associated with scrubland vegetation

Albany Thicket, Fynbos

N

C. plegmatoides Friedrich

Crassula

Compact Column

Sandy/quartz gravel flats and slopes, often on west-facing aspects

Succulent Karoo Namaqualand Sandveld bioregion

N

C. sericea Schönland var. *sericea*

Crassula

Compact Dwarf shrub, tending towards column

Rock crevices and often under overhanging rocks

Succulent Karoo Namaqualand Hardeveld and Richtersveld bioregions, Gariiep centre

N

C. tecta Thunb.

Crassula

Compact Rosette

Gentle lower slopes, often in quartz gravel on north-facing aspects

Succulent Karoo Rainshadow Valley Karoo bioregion (Little Karoo)

N

Table 2. Hydathode distribution in leaves of the nine *Crassula* species examined in this study. Hydathode types according to Martin & von Willert (2000). Asterisks indicate, for each species, on which side the area of interest was found, in which all methods were applied.

<i>Crassula</i> taxon	Leaf indumentum	Hydathode type	Hydathode distribution
<i>C. ausensis</i> subsp. <i>titanopsis</i> §	Clavate trichomes	Type II	++
<i>C. deceptor</i>	Papillae	Type II	+
<i>C. fragarioides</i>	Clavate trichomes	Type II	+
<i>C. multicava</i> subsp. <i>multicava</i>	Glabrous	Type I	++
<i>C. ovata</i>	Glabrous	Type I	+
<i>C. perforata</i> subsp. <i>perforata</i>	Glabrous; conical marginal trichomes	Type II	~
<i>C. plegmatoides</i>	Papillae	Type II	-
<i>C. sericea</i> var. <i>sericea</i>	Subulate trichomes	Type II	+
<i>C. tecta</i>	Bladder-cell idioblasts; marginal trichomes towards the base	Type II	+

Notes

Symbols: “-”, hydathodes absent; “+”, hydathodes present; “~”, submarginal hydathodes only; “++”, hydathodes more abundant than elsewhere.

§ Hydathodes only in the distal half of the leaf.

FIGURE LEGENDS

Figure 1. (A) Biomes of southern Africa (Mucina and Rutherford 2006; Atlas of Namibia Team 2022). The Greater Cape Floristic Region (GCFR) can be divided into the Core Cape Subregion, which corresponds to the Cape Floristic Region (CFR), and the Extra Cape Subregion (ECR), which encompasses the rest of the GCFR (Manning and Goldblatt 2012; Snijman, 2013). (B) Contrasting climatic conditions across southern Africa. Colours indicate the aridity index for the 1970–2000 period (Trabucco and Zomer 2019), with climate classes according to the United Nations Environment Programme (1997). Rainfall seasonality results in a winter-rainfall zone (WRZ), a year-round-rainfall zone (YRZ) and a summer-rainfall zone (SRZ) (Chase and Meadows 2007; Chase et al. 2017). (C) Influence of fog in southern Africa, with shaded areas experiencing [?] 30 days of fog annually (redrawn from Olivier & van Heerden 2003; Bradshaw & Cowling 2014; Atlas of Namibia Team 2022); the Great Escarpment (dashed line) is a major topographical feature that represents the verge of the southern African plateau, with steep slopes down to the coastal areas. Superimposed is the geographical distribution of the nine *Crassula* species examined here; data from GBIF (2022), with manual data cleaning for *C. ovata* and *C. multicava* to approximate it to their native distribution, based on descriptions by Tolken (1985), van Jaarsveld (2003) and Smith, Crouch & Figueiredo (2017). Only one locality is known for *C. ausensis* subsp. *titanopsis*, so all localities for *C. ausensis* were included in the map.

Figure 2. Habit in the wild of the *Crassula* species examined in this study. (A) *C. multicava* subsp. *multicava*, (B) *C. ovata*, (C) *C. perforata* subsp. *perforata*, (D) *C. tecta*, (E) *C. fragarioides*, (F) *C. sericea* var. *sericea*, (G) *C. deceptor*, (H) *C. plegmatoides*, (I) *C. ausensis* subsp. *titanopsis*.

Photo credits: (A) Craig Peter, iNat ID 33843433; (B) Craig Peter, iNat ID 59494774; (C) Luc Strydom, iNat ID 75803984; (D) Di Turner, iNat ID 22557424; (E) Ismail Ebrahim, iNat ID 16279839; (F) Matt Berger, iNat ID 96923577; (G) Andrew Hankey, iNat ID 11038117; (H) Nick Helme, iNat ID 93580736; (I) Petr Pavelka.

Figure 3. Leaf morphology and macroscopic surface details of the *Crassula* species examined. (A) *C. multicava* subsp. *multicava* , (B) *C. ovata* , (C) *C. perforata* subsp. *perforata* , (D) *C. tecta* , (E) *C. fragarioides* , (F) *C. sericea* var. *sericea* , (G) *C. deceptor* , (H) *C. plegmatoides* , (I) *C. ausensis* subsp. *titanopsis* .

Figure 4. Microscopic leaf details of the *Crassula* species examined, showing for each species the leaf surface (left) and a vibratome section (right). Hydathodes can be observed in all species. (A) *C. multicava* subsp. *multicava* ; note the white mineral crust on the hydathodes. (B) *C. ovata* ; note the white mineral crust on the hydathodes. (C) *C. perforata* subsp. *perforata* , margin (top row) and lamina (bottom row); note anthocyanin contents in hydathode sheath cells (top row), and partially removed waxy bloom and absence of hydathodes in the lamina (bottom row). (D) *C. tecta* ; note clustering of bladder-cell idioblasts. (E) *C. fragarioides* ; note clustering of papillae. (F) *C. sericea* var. *sericea* . (G) *C. deceptor* ; note eroded epicuticular waxes at the tip of tubercles. (H) *C. plegmatoides* . (I) *C. ausensis* subsp. *titanopsis* ; note clustering of clavate trichomes and anthocyanin contents in hydathode sheath cells. In all images the adaxial side is towards the top.

Figure 5. Microscopic leaf surface details of *Crassula* species examined with environmental scanning electron microscopy (ESEM). (A) *C. multicava* subsp. *multicava* ; note the presence of a mineral crust on the hydathodes (left), which can be removed revealing the water pores (right). (B) *C. ovata* ; note thick waxy crust on the leaf, which tends to crack (left), and the presence of a mineral crust on and around the hydathodes (right). (C) *C. perforata* subsp. *perforata* . (D) *C. tecta* . (E) *C. fragarioides* . (F) *C. sericea* var. *sericea* . (G) *C. deceptor* . (H) *C. plegmatoides* . (I) *C. ausensis* subsp. *titanopsis* . Arrowheads indicate hydathode water pores, dashed circles indicate water pore epidermal areas of type I hydathodes.

Figure 6. Anatomy of hydathodes of the *Crassula* species examined; semi-thin sections of resin-embedded material, stained with toluidine blue. (A) *C. multicava* subsp. *multicava* , (B) *C. ovata* , (C) *C. perforata* subsp. *perforata* , (D) *C. tecta* , (E) *C. fragarioides* , (F) *C. sericea* var. *sericea* , (G) *C. deceptor* , (H) *C. plegmatoides* , (I) *C. ausensis* subsp. *titanopsis* . Arrowheads indicate hydathode water pores, “E” indicates epithem, “T” indicates tracheids. In all images the adaxial side is towards the top.

Figure 7. Measurements of contact angle (θ_C) in the areas of interest for the *Crassula* species examined (see Table 2) . Mean and \pm standard deviation are plotted for each species. Wettability classes according to Barthlott *et al.* (2017).

Figure 8. Water uptake observed in free-hand sections of leaves from drought-stressed and well-watered plants treated with LYCH. (A) *C. multicava* subsp. *multicava* , (B) *C. ovata* , (C) *C. perforata* subsp. *perforata* , (D) *C. tecta* , (E) *C. fragarioides* , (F) *C. sericea* var. *sericea* , (G) *C. deceptor* , (H) *C. plegmatoides* , (I) *C. ausensis* subsp. *titanopsis* . Same leaf zones imaged with long-pass (ex. 480/40 nm; em. 510 nm LP) and band-pass (ex. 470/40 nm; em. 525/50 nm) filter sets, showing LYCH (green). In all images the adaxial side is orientated upwards. See Figs. S2, S3 for fluorescence in untreated samples (controls).

Figure 9. Water uptake in whole leaves of (A) *C. multicava* subsp. *multicava* and (B) *C. ovata* . Adaxial side shown, leaf margin orientated towards the top of the image. Dashed circles indicate approximate area where the droplet of LYCH was applied.

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Graphical abstract

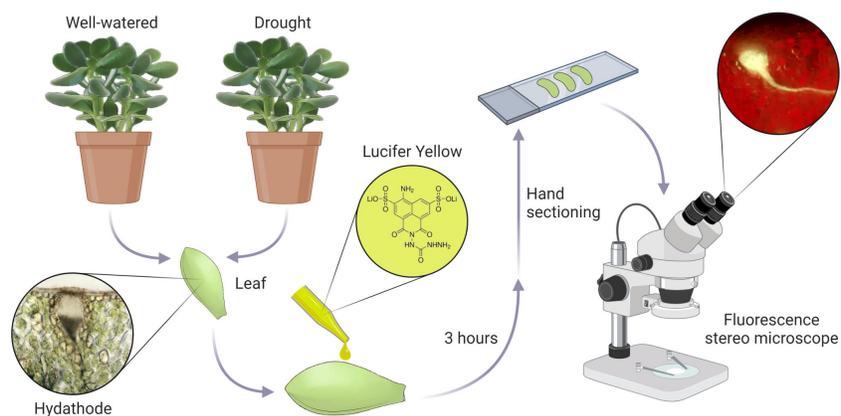


Figure 1

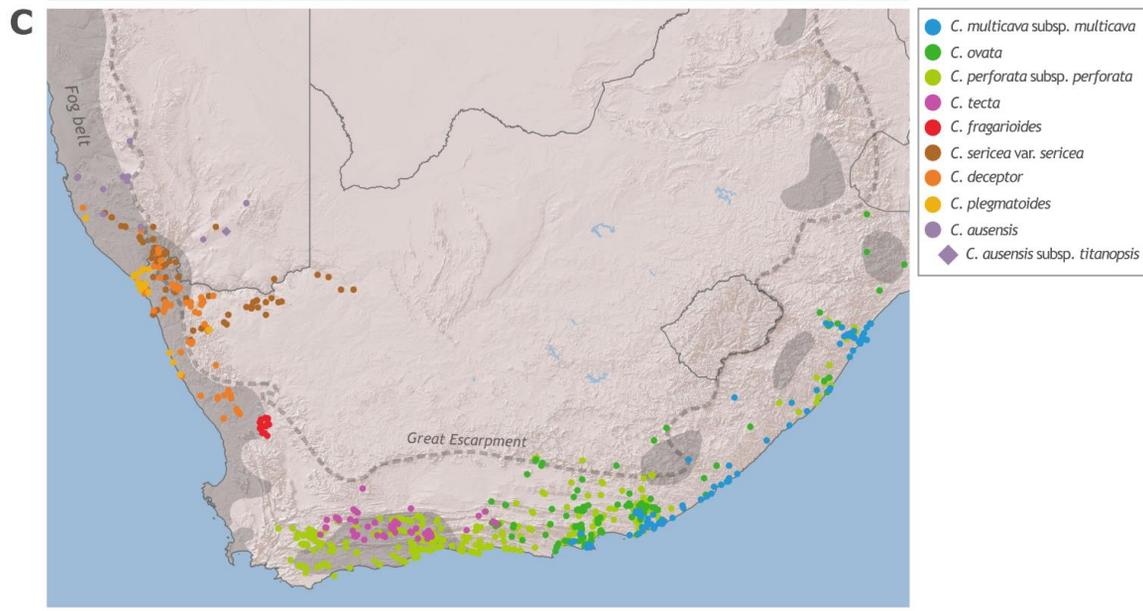
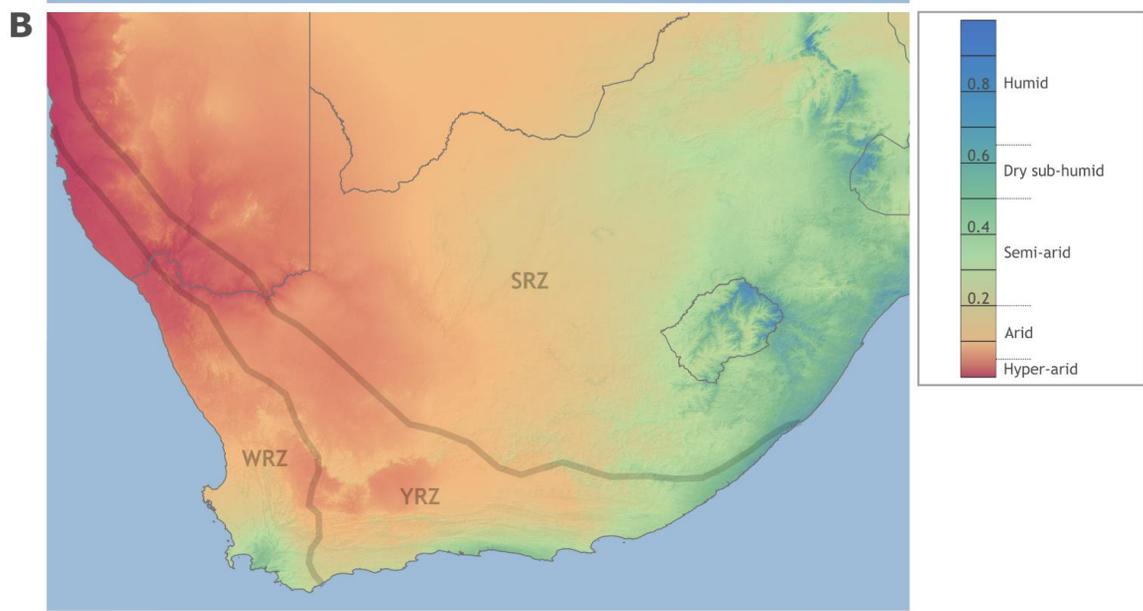
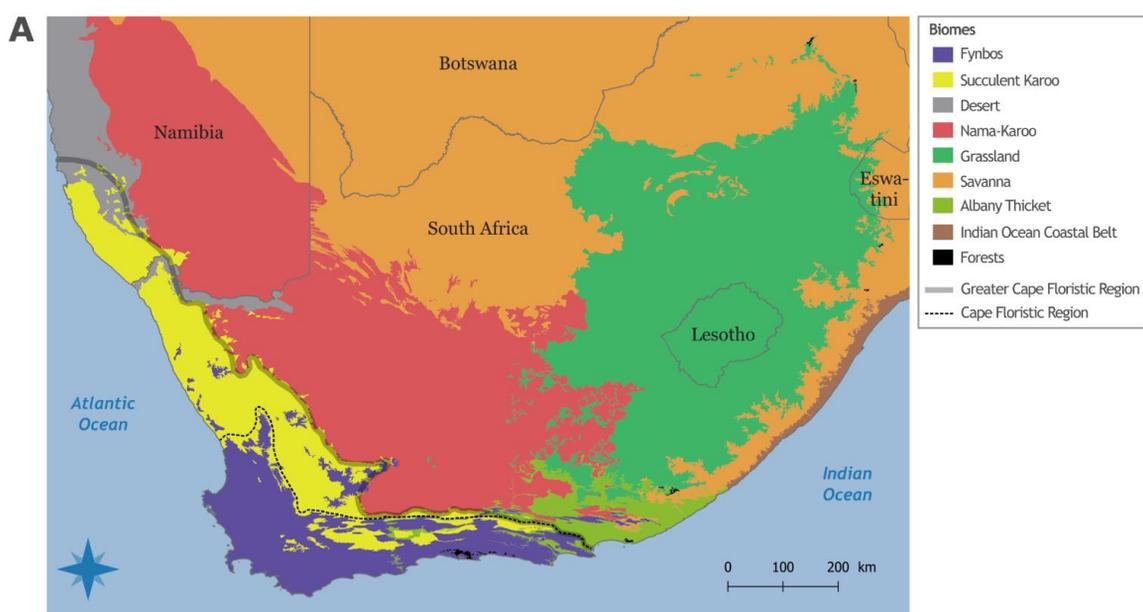


Figure 2



Figure 3

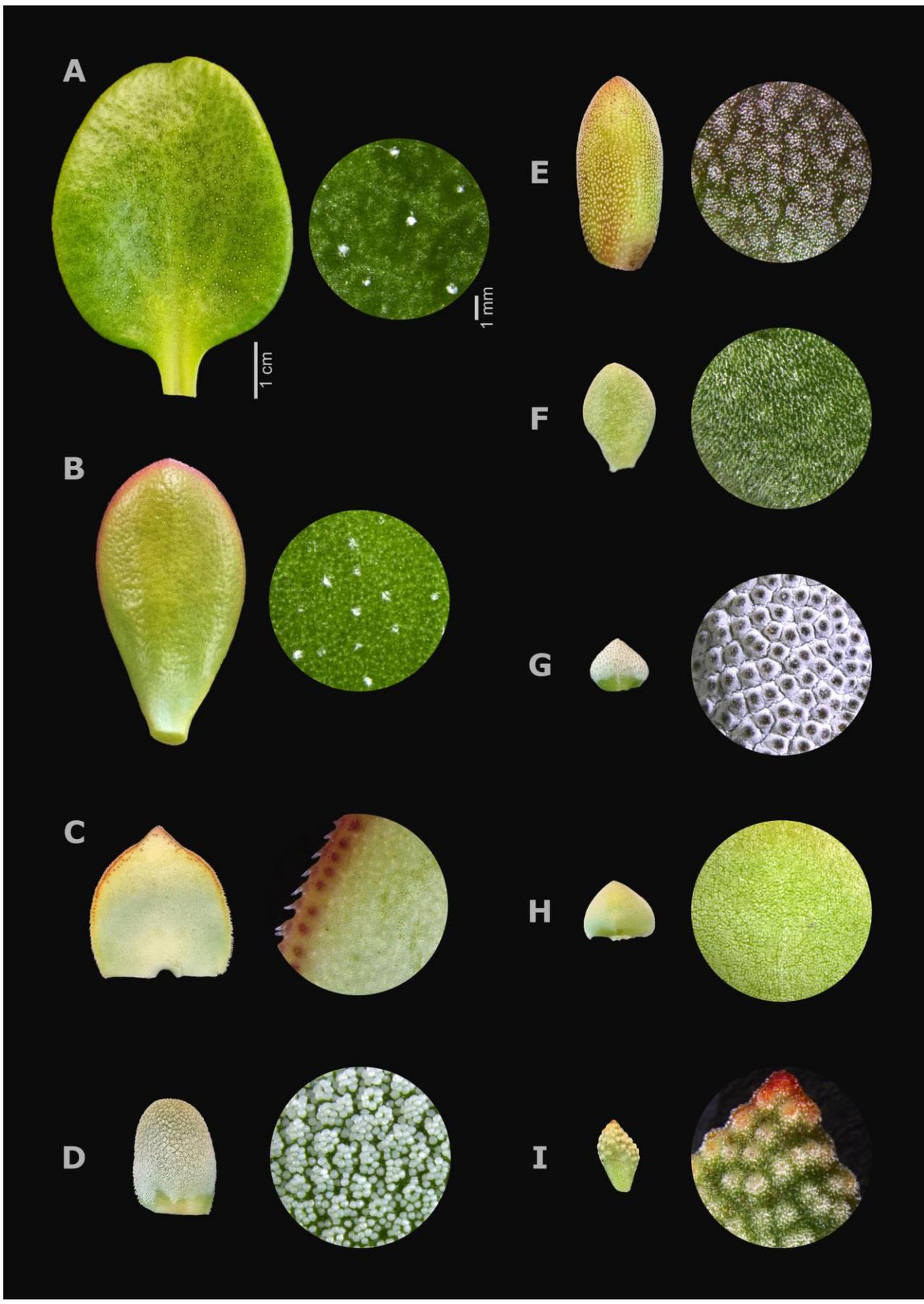


Figure 4

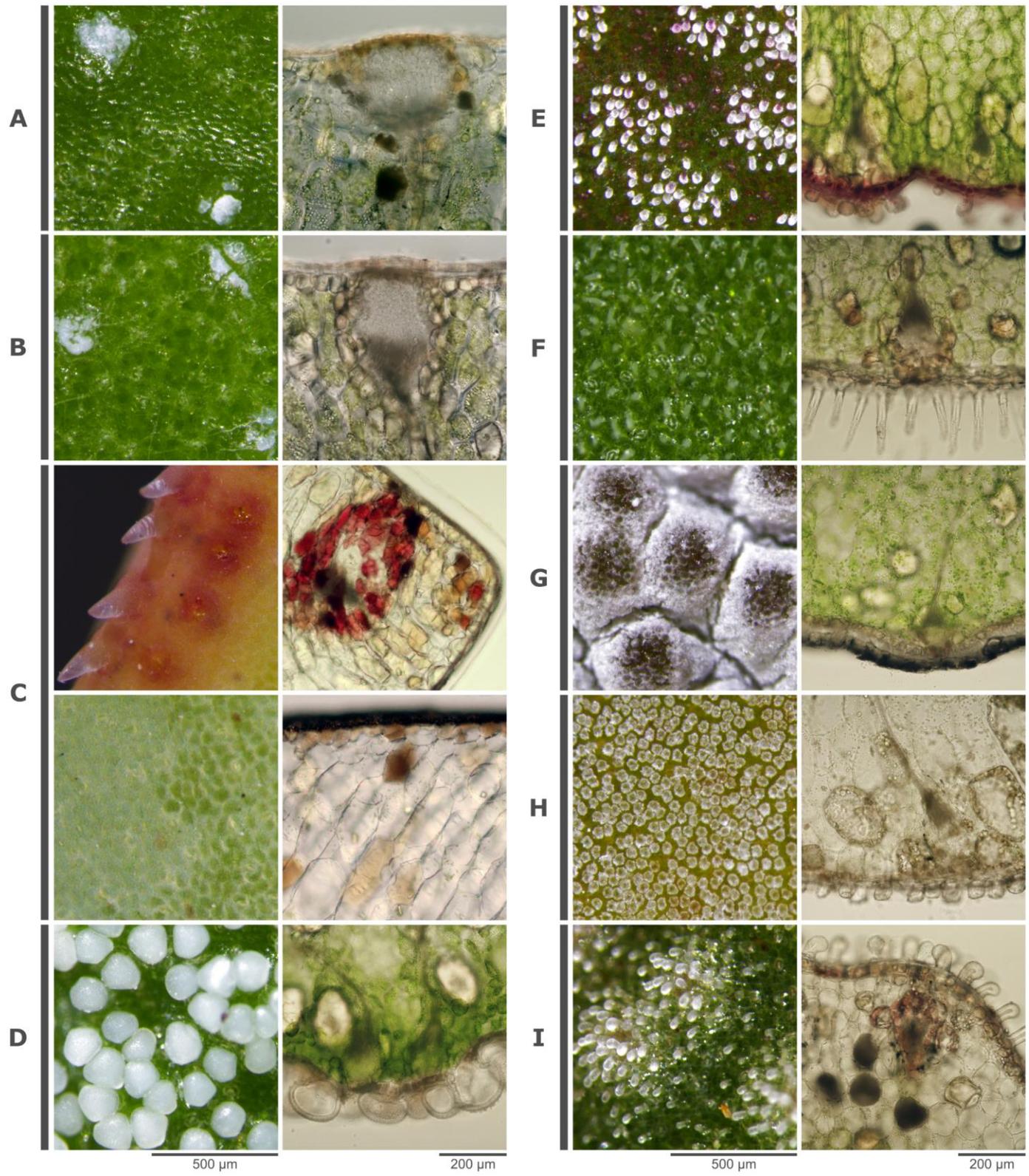


Figure 5

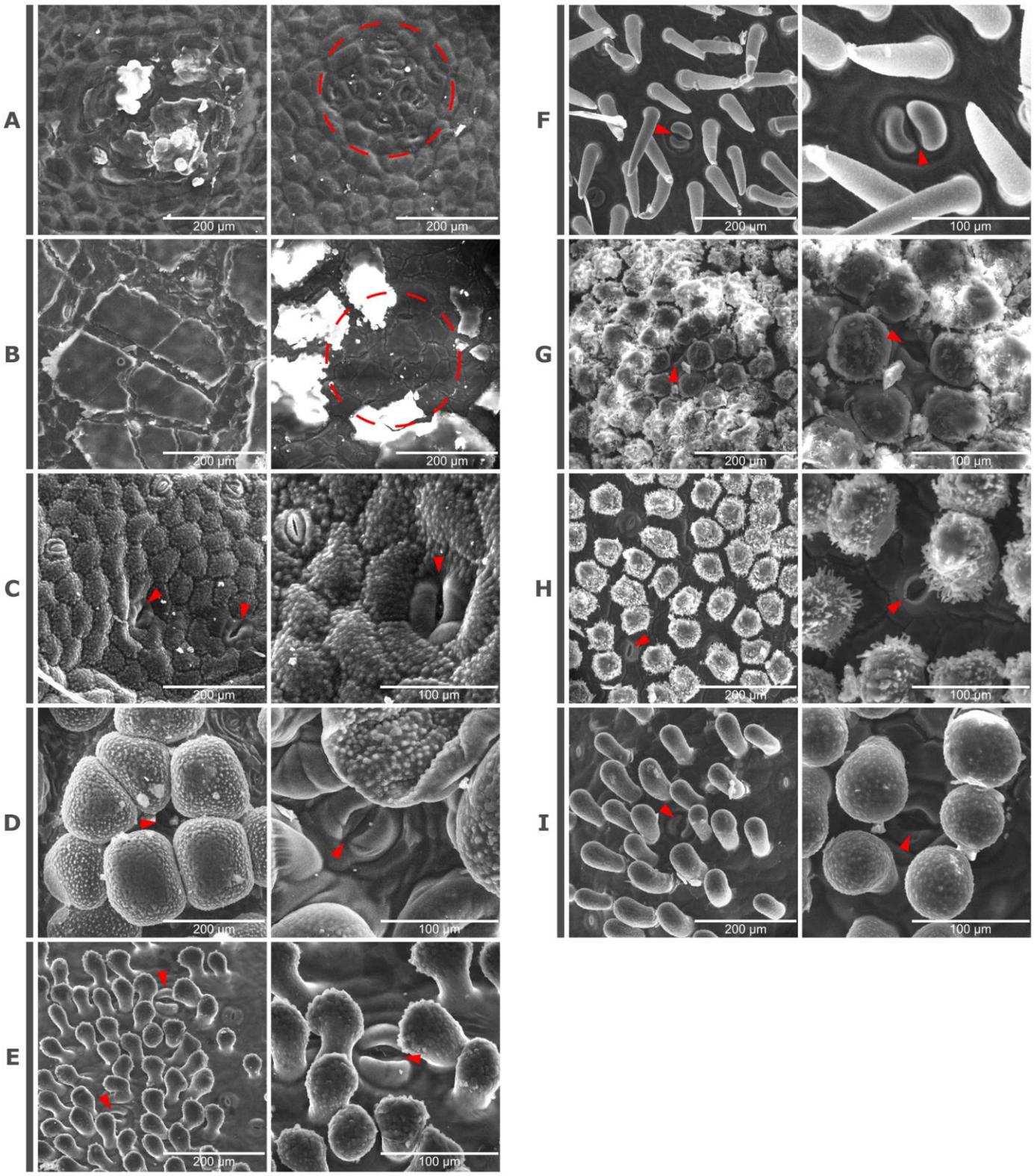


Figure 6

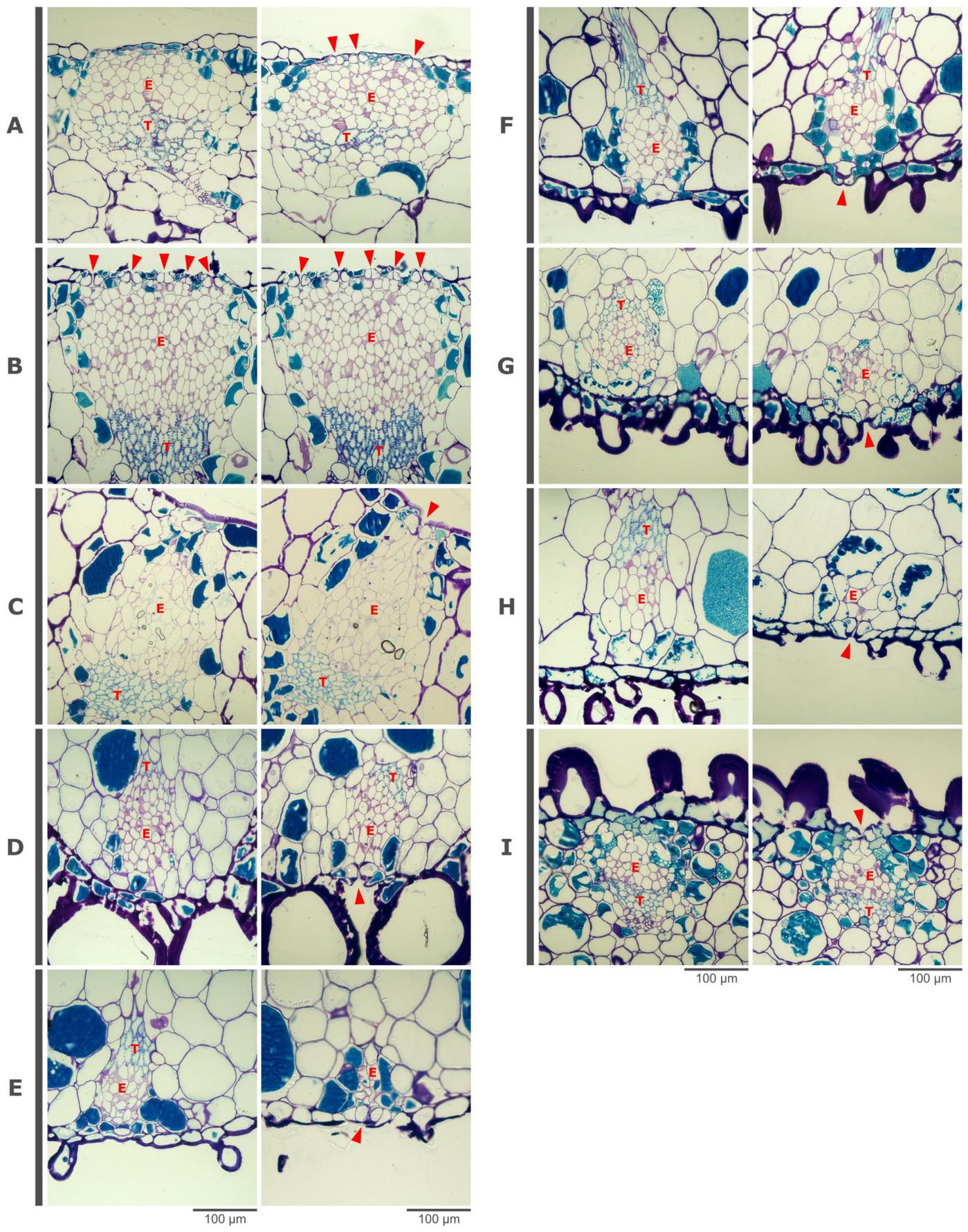


Figure 7

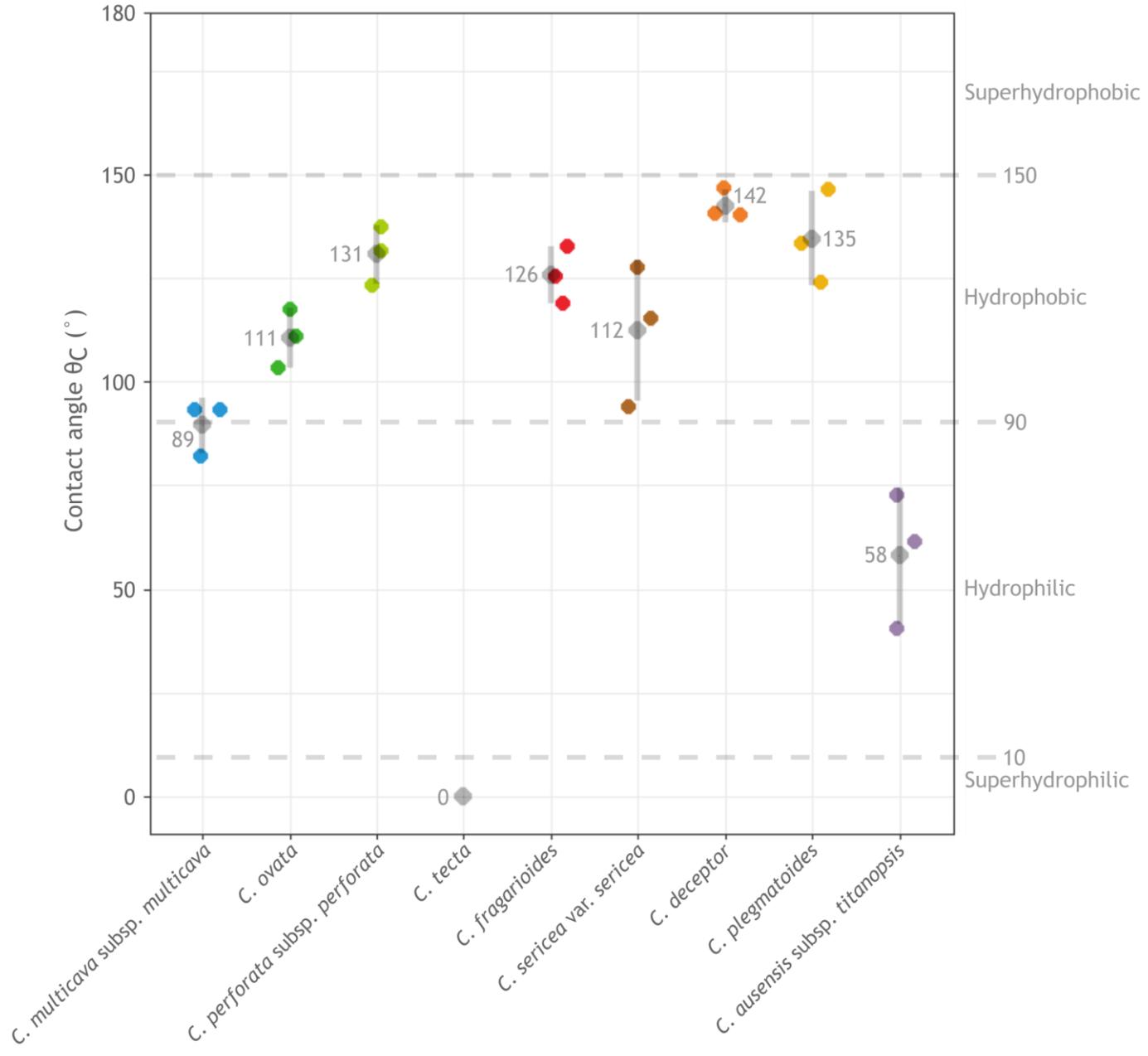


Figure 8

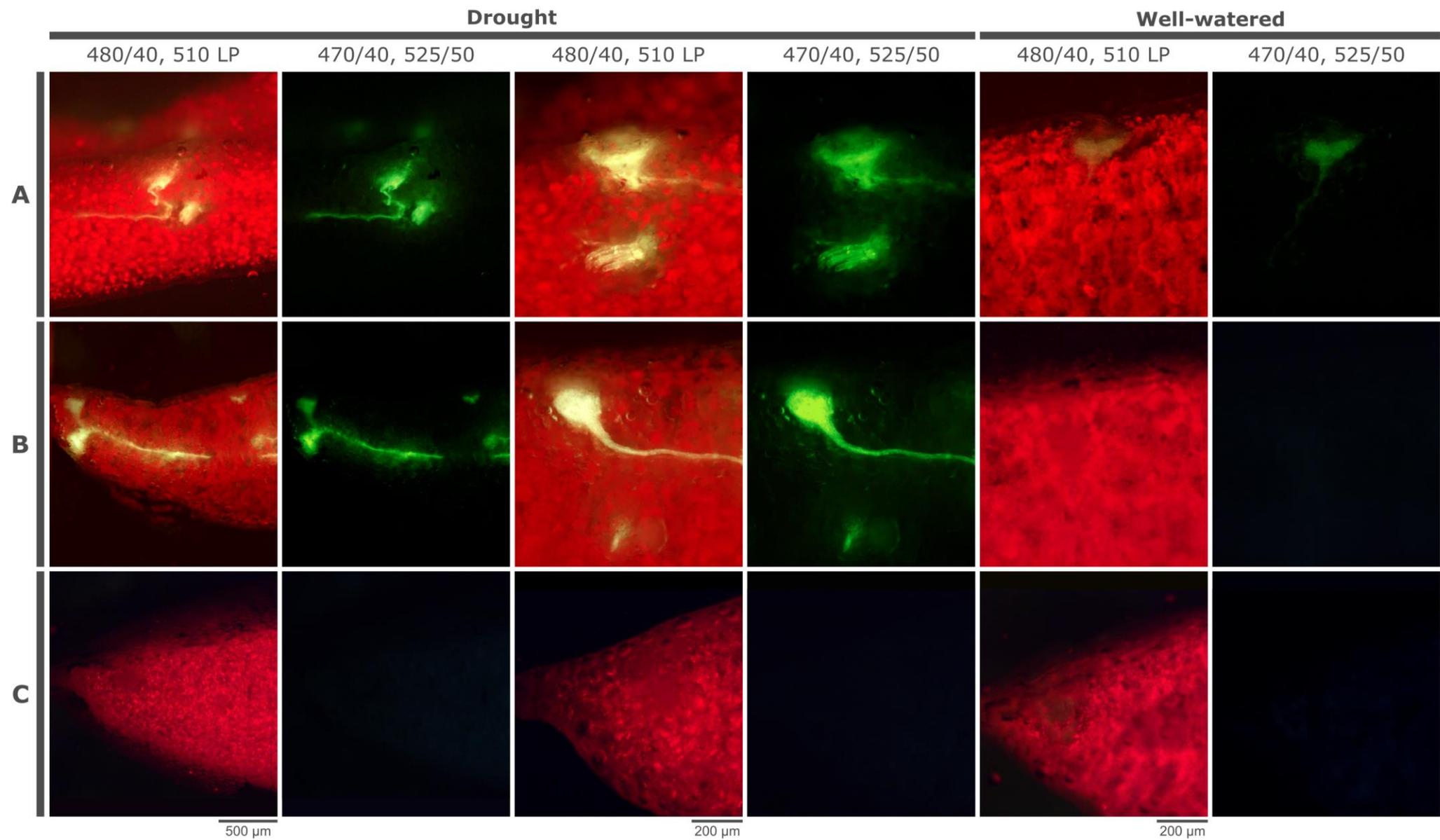


Figure 8 (cont.)

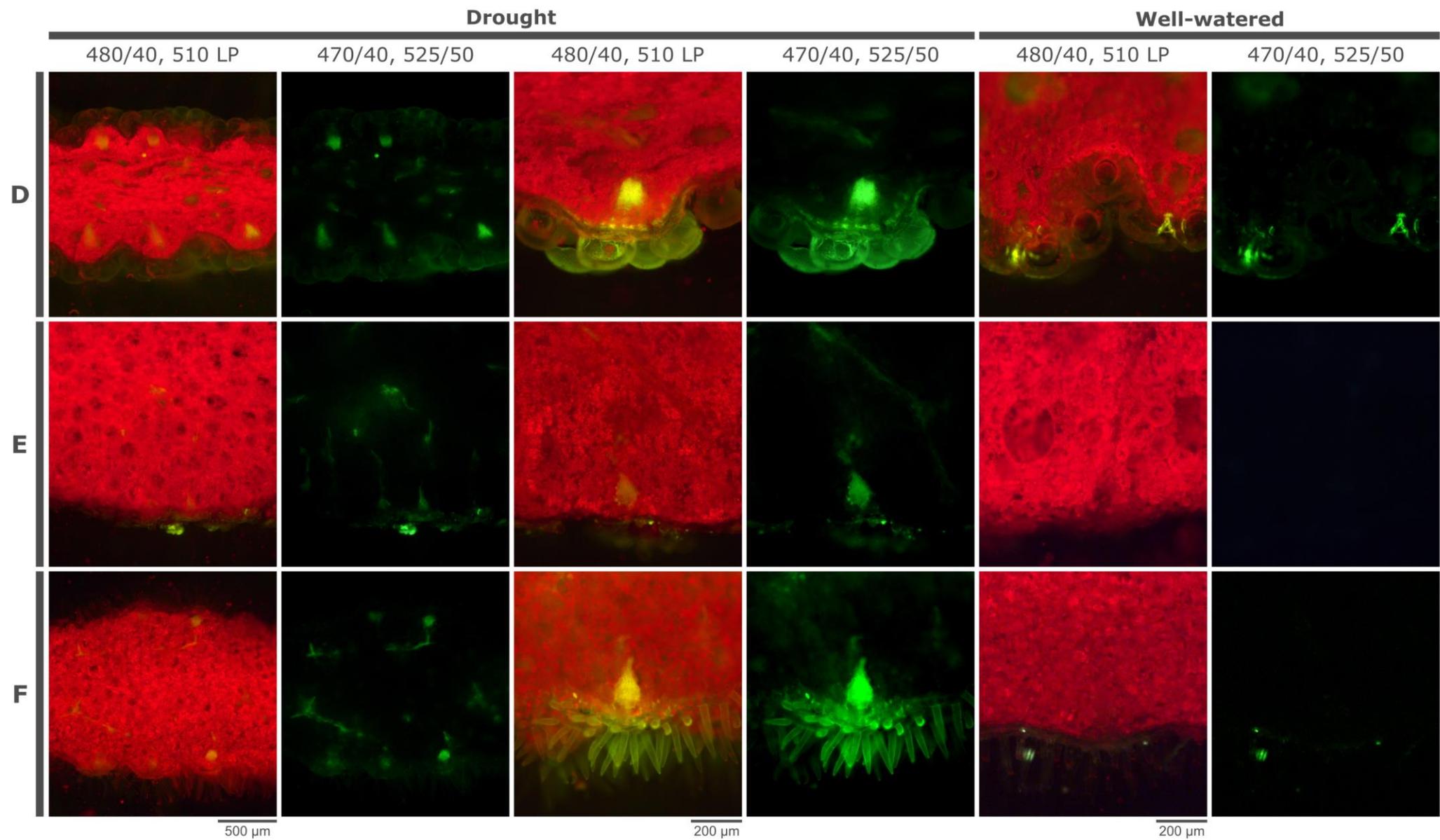


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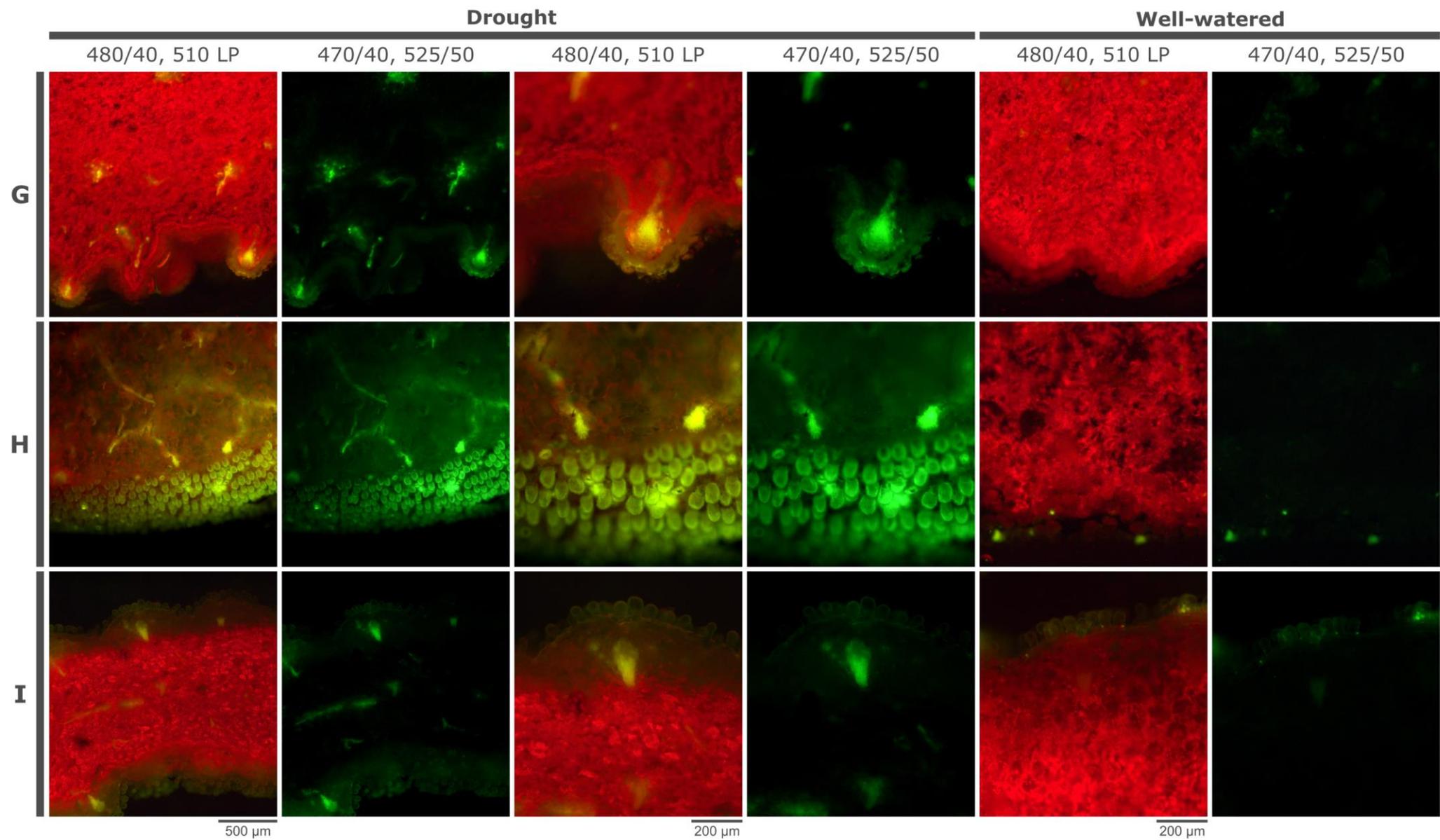


Figure 9

