



Water flow in two Cactaceae species: standardization of the method and test under different drought conditions

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Abstract

Investigating water flow in the vascular system of plants is important to identify the water path and conduction capacity of different plant species, mainly in succulent species living in dry regions. This study aimed to standardize a method to track water flow in the xylem of *Mammillaria bocasana* and *Echinocereus reichenbachii* var. *fitchii* (Cactaceae) and test it under different drought conditions. The plants were kept under greenhouse conditions to perform the split root method, water flow tracing, and different drought treatments. The plants of each species were separated into three treatments: constant irrigation, drought with water and dye, and drought with dye. Plants were cut 24 h after staining, total and lumen diameters were taken, and the relative theoretical hydraulic conductivity was calculated. The absorption method was adequate for the tracing of water flow, and it worked in all the treatments of the drought experiment. Conducting elements, including wide-band tracheids, were stained violet and were located near the vascular cambium. In *Mammillaria bocasana*, half of the vascular cylinder was stained, while in *Echinocereus reichenbachii* var. *fitchii*, the entire cylinder was stained due to the cortical bundles. *M. bocasana* had a higher lumen diameter and relative theoretical hydraulic conductivity than *E. reichenbachii* var. *fitchii*. With the absorption staining method, the flow of water was traced, and differences in conduction under water stress conditions between the two species of cacti were detected. These results suggest that cacti species living under water stress solve the water movement in different ways.

Keywords Conductive cells · Water movement · Xylem · Acid fuchsin · Split root · Cacti

1 Introduction

Water transport through vascular tissue is essential for different physiological and metabolic functions, such as photosynthesis and nutrient transport (Javaux et al. 2016; Liu et al. 2020). Conductive cells have characteristics such as the presence of perforation plates and pits that allow the diffusion of water axially and laterally (Tyree and Zimmermann 2002). The movement of water from the roots to the leaves (or modified photosynthetic stem as in cacti) is due to the difference in water potential among roots, leaves, and the atmosphere, the general plant metabolism, and the environment in which the plant develops (Martotell et al. 2014;

Chen et al. 2022). This movement caused by the water potential difference is called the driving force (Liu et al. 2020). Hydraulic conductivity is one of the variables that study and understand the mechanics of fluids within the conductive vessels of plants (Pire et al. 2007). The flow of water through the stem depends on the number of solitary or grouped vessels, the average number of vessels, and the lumen diameter of the vessels (Liu et al. 2020). The last trait is related to the amount of water moving through the vessel: the higher the value, the greater the amount of water that passes through the lumen as established by the Hagen–Poiseuille law of fluid hydraulics (Ellerby and Ennos 1998; Sperry et al. 2006; Pan et al. 2015). However, in conductive tissue, not all vessels will be functional because some may have obstructions, cavitation, and embolisms, and other cellular elements of the xylem, such as tracheids, fibers, or parenchyma, may store water (Umebayashi et al. 2007).

The methods used to tracing path of the water flow in the xylem are (1) the injection of dyes directly into the xylem (Sano et al. 2005), (2) the placement of the branches into

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a beaker containing a staining solution (Kitin et al. 2010), (3) cutting stem or branch with a chisel so that the dye penetrates without generating embolisms due to the entry of air into the conductive tissue (McElrone et al. 2021), and (4) applying the dye directly to the roots (Salguero-Gómez and Casper 2011). The tracing of water flow in the xylem with dyes has been carried out in conifers (Kozłowski and Winget 1963; de Fay et al. 2000), some monocots (Hargrave et al. 1994; Tang and Boyer 2008), and some dicots (Ellmore and Ewers 1986; Sano et al. 2011). In herbaceous species, only *Arabidopsis* has been tested by using a vacuum pump to generate water flow through the plant (Jupa et al. 2015). However, this type of water flow tracing cannot be applied to some cacti because they have succulent stems (Nobel 2006; Montesinos-Navarro et al. 2019), different growth forms as globose or depressed-globose stems (Hernández-Hernández et al. 2011; Vazquez-Sánchez et al. 2017), and diverse and complex wood anatomy (Mauseth 2006; Ogburn and Edwards 2009); which are different characteristics from the plant models that are commonly used.

Cactaceae species have a diversity of growth forms (Vázquez-Sánchez et al. 2012), hydraulic, and biomechanical strategies to live in different environmental conditions (Schwager et al. 2013; Kim et al. 2018). Most species live in arid and semi-arid regions (Gómez-Hinostrosa and Hernández 2000), where the limiting factors for plant development are a lack of water and high temperatures (Lipiec et al. 2013; Hatfield and Prueger 2015), which modify the morphology (Edwards and Donoghue 2006), physiology (Andrade et al. 2007), and anatomy of the xylem (Stone-Palmquist and Mauseth 2002; Nobel 2006). Anatomically, cacti have three different cell matrices in their conductive tissue (Mauseth 2006). Fibrous species that have columnar, arboreal, and shrub growth forms have vessel elements (VE) and fibers (F) in the wood (Arias and Terrazas 2001; Terrazas et al. 2005). Dimorphic species in juvenile stages present wide-band tracheids (WBT) and VE, and after increasing in size exclusively develop VE and F (Mauseth 1989; Garcia et al. 2012). Non-fibrous species maintain VE-WBT throughout their lives (Vázquez-Sánchez et al. 2017; Maceda et al. 2018), and very few species exclusively maintain VE–parenchyma (P) (Mauseth and Stone-Palmquist 2001).

Studies on water conduction have focused mainly on fibrous species such as *Opuntia* spp. (Pimienta-Barrios et al. 2003; Kim et al. 2018), *Selenicereus undatus* (Haworth) D.R.Hunt (Nerd and Neumann 2004), and *Carnegiea gigantea* (Engelm.) Britton & Rose (Barcikowski and Nobel 1984). However, due to the anatomical diversity, sizes, and growth forms of Cactaceae, it is important to investigate and standardize appropriate methods for the analysis and labeling of water flow under normal and water stress conditions, which will expand the understanding of the physiology and anatomy of these non-fibrous species that live in conditions

of water stress. Therefore, the objectives of this study were to determine the appropriate method to track the water flow through the secondary xylem and to identify the differences in the water flow of two different cactus species with abundant non-lignified P and the presence of VE and WBT under different wet/dry conditions. The hypothesis is that there are differences in the method of adding the dye to the conductive tissue, and we expect differences in the marking of water flow between the two species analyzed.

2 Materials and methods

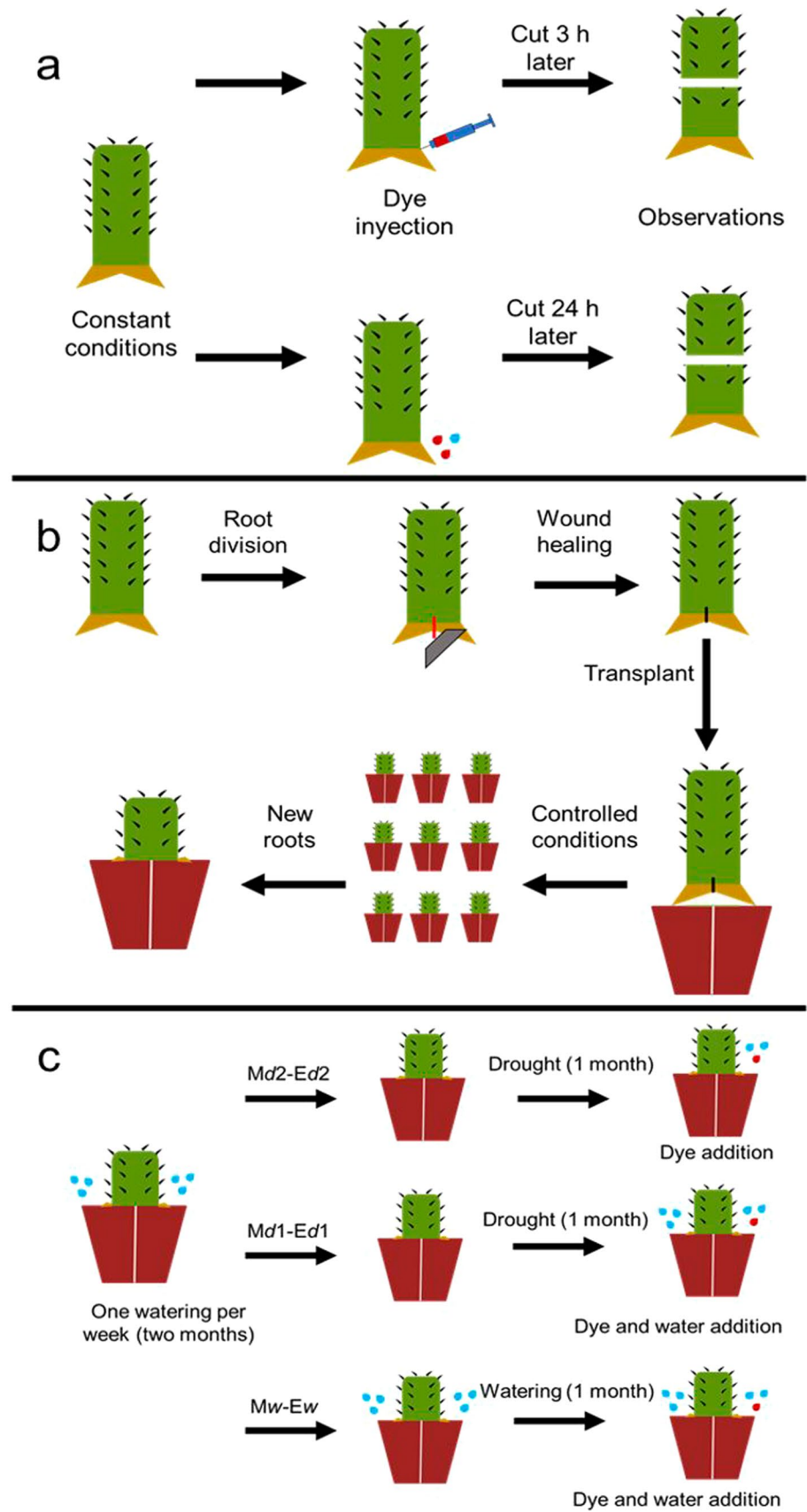
2.1 Plant material and dye application

One-year-old plants of *Mammillaria bocasana* Poselg. and *Echinocereus reichenbachii* (Terscheck ex Walp.) J.N.Haage var. *fitchii* (Britton & Rose) L.D.Benson (Cactaceae) were obtained from the Botanical Garden at the National Autonomous University of Mexico. The dye used to trace water movement was an aqueous solution of acid fuchsin. Acid fuchsin stain has been used in various histological studies for tracing water flow through vascular tissue (Kraus et al. 1998) and diffusion between conductive elements with radial and axial parenchyma cells (Fritz and Ehwald 2013; Jupa et al. 2015). Acid fuchsin is easily distributed in conjunction with water compared to basic stains such as safranin or basic fuchsin (Sano et al. 2005). Furthermore, acid fuchsin travels a greater distance during the ascent of water through vascular tissue (Umebayashi et al. 2007). The recommended acid fuchsin aqueous solution is 0.1–5% for water flow experiments (Iida et al. 1992), since at concentrations higher than 5%, the ascent is slow, and at concentrations lower than 0.1%, the staining quality is low (Umebayashi et al. 2007). To trace the water flow in the two Cactaceae species, a 0.2% aqueous solution of acid fuchsin was prepared and filtered through a 0.45- μ m nylon membrane following Kitin et al. (2010).

Two different methods of adding the dye to the vascular tissue were tested. The first method was based on the injection of the dye into the vascular tissue (Fig. 1a) (Sano et al. 2005). In this method, 0.1 ml of dye was injected into the upper part of the main root, and observations were made 3 h later. The second method was based on Salguero-Gómez and Casper (2011) with some modifications. In this method, the roots on the one side were carefully uncovered from the substrate to slowly add 5 ml of the dye; the roots were again covered with the substrate, and 20 ml of distilled water was added to the substrate. Observations were made 24 h later to allow plants to take up water derived from plant evapotranspiration.

To test both methods, five plants of each species were used, and the procedures for applying the dye were

Fig. 1 Methods applied to cacti plants. **a** Comparison of two methods of plant dye addition and water flow tracing. **b** Schematic representation of the process of root division, healing, adaptation, and formation of new roots. **c** Schematic of the three treatments, two with drought and one with constant irrigation. In the last month, the dye was added to only one side of the root



compared. Then, the plants were cut transversally every 0.5 cm, and observations of the distribution of the dye were made. Based on the results obtained, a drought experiment was carried out using the most appropriate method to mark the flow of water.

2.2 Drought experiment

2.2.1 Split root

Once the appropriate method to trace the water flow was selected, the drought experiment was carried out to determine the differences in the water flow under different irrigation conditions. To trace the flow of water through the vascular tissue of the plants, the split root method based on Kassaw and Frugoli (2012) with some modifications was applied. This method allows the roots to be separated with a physical barrier that prevents the dye from spreading into the substrate when added by irrigation, so the water flow can be properly marked. The procedure consisted of randomly selecting 15 plants of *E. reichenbachii* var. *fitchii* and *M. bocasana*. At the root collar of each plant, a cut was made with a sterilized knife. To avoid fungal infection, a sulfur-based fungicide was applied, and the wound was allowed to heal for 2 weeks without irrigation (Fig. 1b and Fig. S1a).

The plants were transferred to plastic pots divided into two sections with a plastic barrier. The previously divided plant root system was transplanted such that half of the root system was placed in each section of the pot. This physical separation of the root system allowed different water conditions to be maintained in each half of the container (Fig. 1b and Fig. S1b-c). The substrate used was pumice stone with three different particle sizes (0.45, 1, and 1.4 mm) in equal proportions (1:1:1). The plants were kept for 3 months in a controlled environmental chamber at 25 °C with a photoperiod of 12-h light/12-h dark and watering every 3 weeks (Fig. 1b). After 3 months, the presence of new roots was observed, and a wet/dry experiment was carried out (Fig. 1c).

2.2.2 Wet/dry experiment

The plants of each species were divided into three treatments (with five replicates each): the first with constant irrigation and subsequent dye application denominated as *M_w* and *E_w* where *M* comes from *Mammillaria* and *E* from *Echinocereus* and *w* is constant irrigation. The second with drought and subsequently water and dye application denominated as *M_{d1}* and *E_{d1}* where *d1* is drought and water with dye. The third with drought and subsequently dye application denominated *M_{d2}* and *E_{d2}* where *d2* is drought and dye addition. The three treatments were initially irrigated once per week for 2 months to maintain the same conditions

among treatments. In the 3rd month, the first treatment (*M_w* and *E_w*) was irrigated in both sections of the pot once a week for a month. In the second (*M_{d1}* and *E_{d1}*) and third (*M_{d2}* and *E_{d2}*) treatments, water was withheld for 30 days (the 3rd month) to cause water stress (Fig. 1c), as proposed by Huang and Nobel (1993) and Nerd and Neumann (2004).

Seven days after the last irrigation, the first treatment (called constant irrigation or *M_w* and *E_w*) was irrigated with distilled water on the one side of the root, and the dye was added on the other. For the second treatment (called drought with dye or *M_{d1}* and *E_{d1}*), at 31 days of water stress, distilled water was added to one side of the root, and on the other side, the root was exposed and 5 ml of dye was added, the root was immediately covered, and 20 ml of distilled water was added. The root was exposed to ensure that the dye came into direct contact with the roots, the exposure was superficial to prevent them from breaking. For the third treatment (called drought with water and dye or *M_{d2}* and *E_{d2}*), at 31 days of water stress, one side of the root was kept dry, and dye was added to the other side in the same way as the second treatment (Fig. 1c). At 24 h after application of the dye, each plant was carefully removed from the substrate, and the epidermis and cortical parenchyma were removed, leaving only the vascular tissue. *E. reichenbachii* var. *fitchii* and *M. bocasana* had a cylindrical and globose shape, respectively, without a marked variation in the stem diameter at the apex and base; thus, the samples were taken at the middle of the stem. Longitudinal and transverse sections were made by hand using a disposable microtome knife without any type of preparation to avoid washing out the dye. Transverse sections were thicker than 1 mm, but lumina and walls were focused sharply. Photos were taken with a bright-field microscope (Olympus BX-51) to carry out anatomical observations. With the ImageJ program, measurements of 20 vessel elements (VE) and 20 wide-band tracheids (WBT) randomly selected were made for each treatment, thus 60 for each type of cell per species. The total and lumen diameter of each VE and WBT were taken to calculate the relative theoretical hydraulic conductivity based on the following formula (Gibson et al. 1984; Pimienta-Barrios et al. 2003):

$$K_h = \frac{\pi \sum d_i^4}{128\eta}$$

where η is the dynamic viscosity of the fluid (1.002×10^{-3} Pa·s) (Nobel et al. 1991), and d_i is the internal diameter of the vessel in meters. For the internal diameter of the vessels and relative theoretical hydraulic conductivity, the mean and standard deviation were calculated. The total diameter, lumen diameter, and relative theoretical hydraulic conductivity (K_h) data were subjected to the Kolmogorov–Smirnov and Shapiro–Wilk normality tests. However, even when they were base-10-logarithm-transformed, they

did not present normality. Therefore, the Mann–Whitney U-test was performed to identify differences in VE and WBT between species. To determine whether there were differences between the stained and unstained VE and WBT from each treatment of the two species, a nonparametric Mann–Whitney U-test was performed.

3 Results

3.1 Water flow tracing

The comparison between the tracing methods with 0.2% acid fuchsin showed that the tracing of the water flow by injection was inefficient in cacti plants. The injection pressure caused the dye to disperse through the pith and cortical parenchyma and saturate the entire vascular cylinder (Fig. 2a). The dye ascended in this way along the stem to the apex of the plant, so the dye was observed throughout the vascular cylinder, the pith, and cortical parenchyma due axial and lateral diffusion caused by the injection pressure.

The absorption of the dye through the roots showed that the staining was specific to the root where the dye

was applied because the conducting vessel elements (VE) and wide-band tracheids (WBT) were stained (Fig. 2b). Throughout the stem of the plant (Fig. 2b), it was observed that the vascular tissue remained stained up to the apical region, but the staining was specific to the conductive elements close to the vascular cambium, while the other VE and WBT were not stained. Therefore, it can be assumed that the dye tracing adequately reflected the flow of water through the vascular tissue due to evapotranspiration. In the cortical and medullary parenchyma, the presence of acid fuchsin was not detected along the stem of the plant, as occurred with the injection of the dye; therefore, this method allowed us to detect the flow of water in the two species of cacti.

3.2 Drought experiment

Both species absorbed the 0.2% acid fuchsin stain through the roots, and the water flow was traced through the vascular cylinder in different ways. In *E. reichenbachii* var. *fitchii*, water ascended through the first two or three rows of conductive cells near the vascular cambium in the three treatments (Ew, Ed1, and Ed2; Fig. 3) because the walls of the secondary thickenings were stained purple when acid

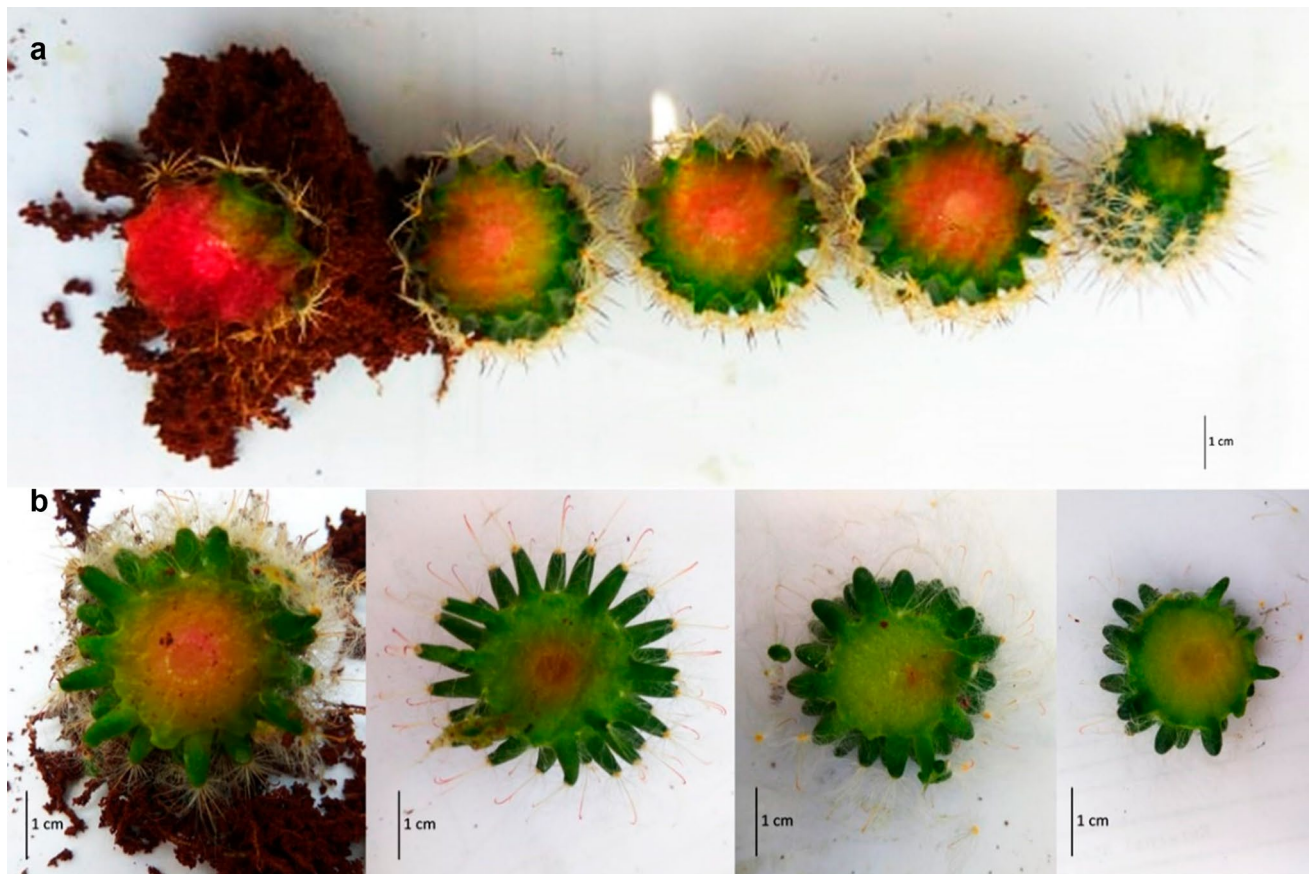


Fig. 2 Comparison of methods for tracing water flow. **a** Injection method. **b** Root absorption method

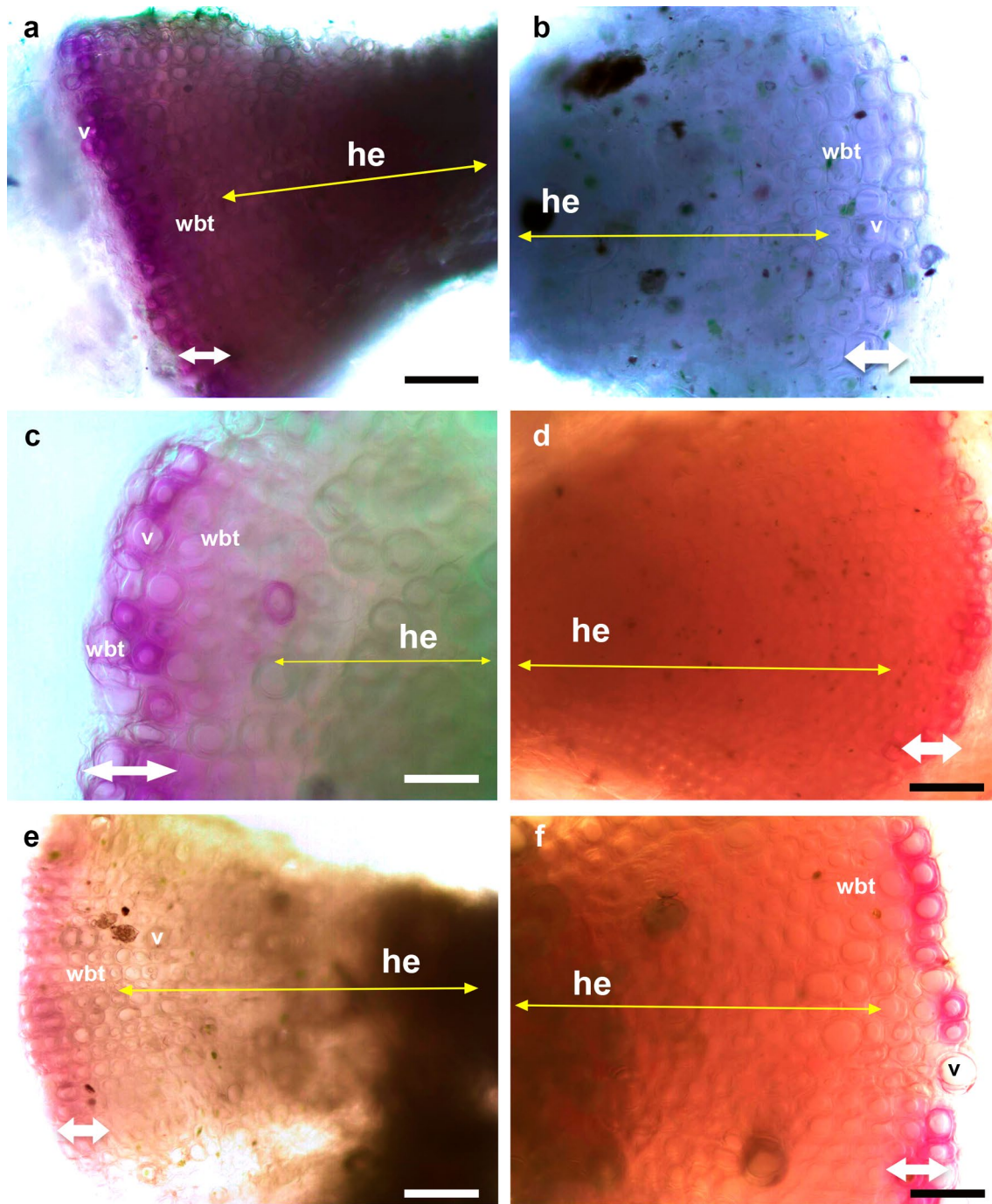


Fig. 3 *Echinocereus reichenbachii*. var. *fitchii*. **a, b** Test Ew. **c, d** Test Ed1. **e, f** Test Ed2. VE vessel elements. WBT wide-band tracheids. P parenchyma. SA White double-headed arrow sapwood. He heartwood. Scale a, d, e: 100 μ m; b, c, f: 50 μ m

fuchsin ascended through the lumen of the conductive elements. The subsequent VE and WBT close to the pith did not present staining in the walls except for one or two vessels that showed staining in the secondary wall (Fig. 3c). The Ew treatment showed some fascicles without staining because even though the root was divided, in both sections, there were constant application and absorption of water (Fig. 3a

and b). In the Ed1 and Ed2 treatments, the first rows of all the bundles of the vascular cylinder were stained with the dye, even the bundles whose roots were not dyed (Fig. 3c–f).

In the three treatments of *M. bocasana* (Fig. 4), the fascicles of the vascular cylinder that corresponded to the root where the dye was applied showed staining in the thickenings of the secondary walls of the VE and WBT. Similar to

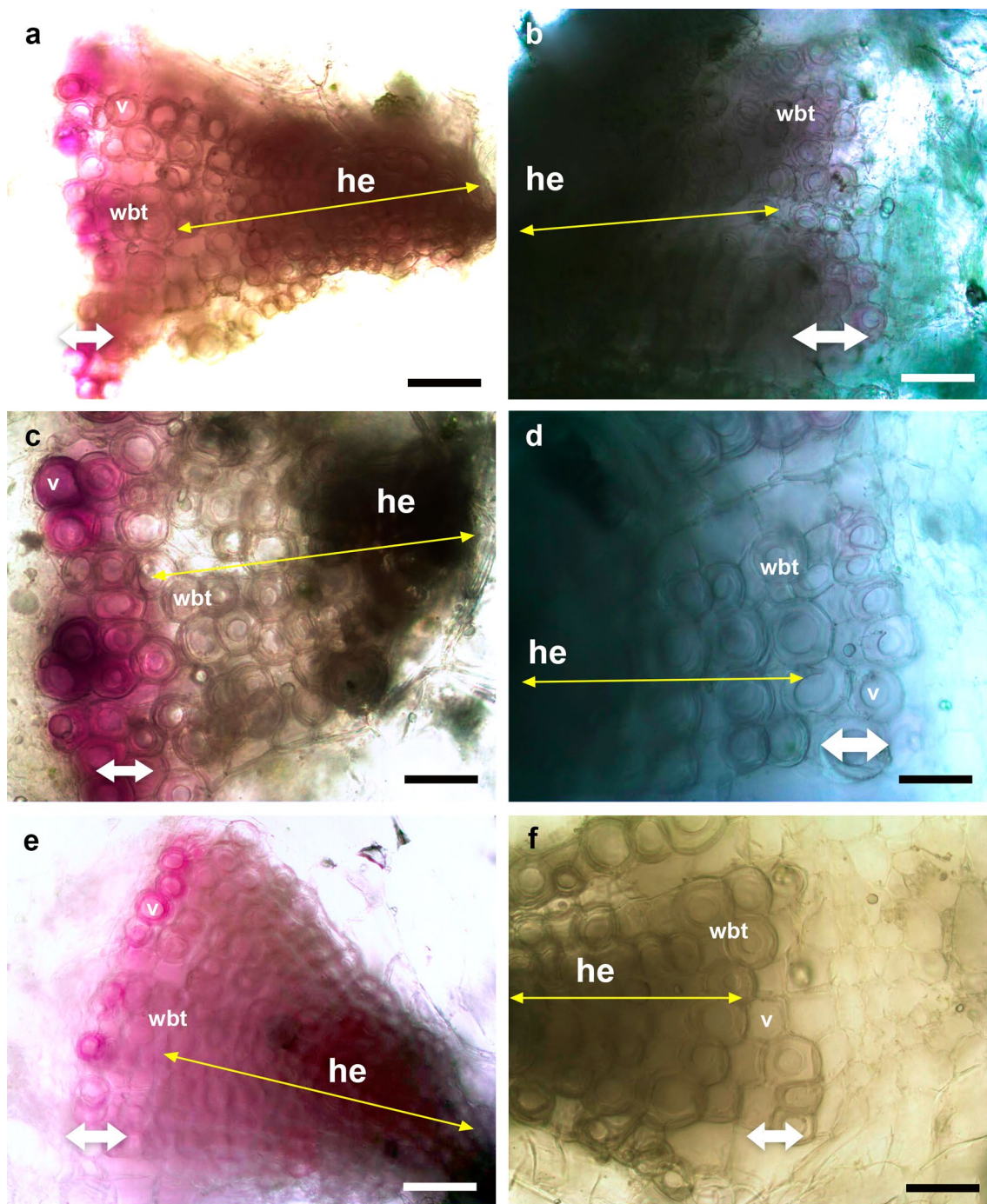


Fig. 4 *Mammillaria bocasana*. **a, b** Test Mw. **c, d** Test Md1. **e, f** Test Md2. *VE* vessel elements. *WBT* wide-band tracheids. *P* parenchyma. *D* White double-headed arrow. *He* heartwood. Scale a, b, e: 100 μ m; c, d, f: 50 μ m

Echinocereus, only the first three rows of VE and WBT that were close to the vascular cambium were stained, and no stained walls were observed in the conductive cells close to the pith (Fig. 4). In the fascicles that corresponded to the region of the roots where only water was applied in Mw and Md1 and the regions without water in Md2, staining of the conductive elements was not observed because there was

no flow of water through these fascicles (Fig. 4d and f). In both species, the dye did not saturate the walls of the VE and WBT adjacent to those that were stained, which indicates that the staining was specific at the time the water ascended due to plant evapotranspiration.

In both species, the secondary wall thickenings were helical in VE and annular and helical in WBT (Fig. S2). When

comparing the means of total diameter, lumen diameter, and relative theoretical hydraulic conductivity in VE and WBT between both species, there were significant differences ($p < 0.05$) in all variables (Table 1). The VE of *M. bocasana* had lumen diameters (27.6 μm) and K_h values ($2.2 \times 10^{-15} \text{ m}^4 \text{ MPa}^{-1} \text{ s}^{-1}$) greater than those of *E. reichenbachii* var. *fitchii*. In the WBT, the differences between the two species were significant, and *M. bocasana* had the highest total diameter, lumen diameter, and hydraulic conductivity values (Table 1).

The comparison of the hydraulic conductivity of dyed and undyed conductive elements showed no significant ($p > 0.05$, Mann–Whitney U) differences between the dyed and undyed WBT–VE in the three treatments (Table 2).

4 Discussion

The results showed that the absorption of the dye by the root is the best method for the two studied species. This method allowed us to support the proposed hypotheses that there were differences in the path of water flow under different wet/dry conditions between the two cacti species. Tracheary elements (VE/WBT) lumen diameters and theoretical hydraulic conductivity (K_h) were also different; however, there were no differences in K_h between stained and unstained conductive cells.

4.1 Water flow tracing

In this study, the dye injection method and measurement of flow water 1 m after the injection (Umebayashi et al. 2007; Sano et al. 2011) were tested in cacti. However, due to the pressure exerted on the un lignified parenchyma tissue and mainly primary walls in the conductive elements, the dye diffused into the parenchyma of both cortex and pith; therefore, this method was not adequate for tracing the water flow (Fig. 2). This agrees with Geitmann (2006) and Kim et al. (2014), who show that injection methods present complications: The results cannot be extrapolated due to the variation in the size of the plants, the type of

Table 2 Comparison of the theoretical hydraulic conductivity between dyed and undyed conductive elements for each treatment where n is 20 cells of the *Echinocereus reichenbachii* var. *fitchii* and *Mammillaria bocasana*

Species	Conductive element	Test	K_h ($\text{m}^4 \text{ MPa}^{-1} \text{ s}^{-1}$)	
			Dyed	Not dyed
<i>E. reichenbachii</i> var. <i>fitchii</i>	VE	Ew	0.897×10^{-18}	1.098×10^{-18} ns
		Ed1	1.514×10^{-18}	0.785×10^{-18} ns
		Ed2	1.005×10^{-18}	1.125×10^{-18} ns
	WBT	Ew	1.057×10^{-18}	0.626×10^{-18} ns
		Ed1	1.535×10^{-18}	1.147×10^{-18} ns
		Ed2	1.362×10^{-18}	1.070×10^{-18} ns
<i>M. bocasana</i>	VE	Mw	1.916×10^{-17}	1.158×10^{-17} ns
		Md1	1.712×10^{-17}	2.020×10^{-17} ns
		Md2	1.857×10^{-17}	1.216×10^{-17} ns
	WBT	Mw	5.446×10^{-18}	5.622×10^{-18} ns
		Md1	5.537×10^{-18}	2.513×10^{-18} ns
		Md2	4.018×10^{-18}	1.399×10^{-18} ns

ns. There were no significant differences with Mann–Whitney U-test ($p > 0.05$)

organ (root, stem, or branch), and the appropriate location on the stem of the plant for the injection of the dye. This method is also difficult to compare when using a complete plant or only a part of it (a branch, for example), and even if the dye is standardized, it is difficult to trace the natural flow of water through the plant, which causes misinterpretations about the conductive routes of water flow (Kim et al. 2014).

The method of absorption through the root proposed by Salguero-Gómez and Casper (2011) had good results in the cactus species studied here. Since no injury was caused to the periderm or cortical parenchyma, the dye was directly absorbed and traced the flow of water through the xylem. No staining was observed in parenchyma cells of the cortex or pith. Since the stain is specific to the conductive xylem elements, misleading interpretations about the water flow routes are avoided (Kim et al. 2014), and it is useful for water stress experiments and water flow tracing.

Table 1 Comparison of total diameter, lumen diameter, and relative theoretical hydraulic conductivity between VE and WBT, where n is 60 for each cellular type in *Echinocereus reichenbachii* var. *fitchii* and *Mammillaria bocasana*

Species	Conductive element	Total diameter (μm)	D_i (μm)	K_h
<i>E. reichenbachii</i> var. <i>fitchii</i>	VE	$17.3 \pm 2.6^*$	$13.8 \pm 2.9^*$	$1.071 \times 10^{-18} \pm 0.845 \times 10^{-18}^*$
<i>M. bocasana</i>	VE	$33.0 \pm 4.1^*$	$27.6 \pm 4.3^*$	$1.647 \times 10^{-17} \pm 1.069 \times 10^{-17}^*$
<i>E. reichenbachii</i> var. <i>fitchii</i>	WBT	$21.4 \pm 1.6^*$	$14.4 \pm 1.7^*$	$1.133 \times 10^{-18} \pm 0.479 \times 10^{-18}^*$
<i>M. bocasana</i>	WBT	$28.0 \pm 3.9^*$	$19.1 \pm 3.8^*$	$4.089 \times 10^{-18} \pm 3.078 \times 10^{-18}^*$

*Significant differences in VE and WBT between species with Mann–Whitney U-test ($p < 0.05$). D_i : lumen diameter. K_h : relative theoretical hydraulic conductivity

4.2 Drought experiment

The three treatments proposed for both studied species reflected three possible wet/dry physiological conditions: with constant irrigation and subsequent dye application; with drought and subsequent water and dye application; and with drought and subsequent dye application. The drought in the second and third treatments lasted 30 days because cacti can withstand up to 81% water loss (Barcikowski and Nobel 1984), and some species, such as *Ferocactus acanthodes*, can withstand stressful drought conditions for up to 40 days (Nobel et al. 1991). In this study, stress was not produced for more than 30 days because some roots may die after 35 days (Huang and Nobel 1993) and interfere with dye uptake.

In both species, water absorption was detected in all three treatments. The staining of the first two rows of VE and WBT close to the vascular cambium represents the sapwood region, whose main function is to transport water and nutrients (Longui et al. 2012; Diaz-Maroto et al. 2017). Heartwood corresponds to the region without staining or with few stained VE because it is characterized by nonconductive vessels (Kitin and Funada 2016) and the accumulation of starch, soluble sugars, amino acids, and organic compounds such as tannins, gum, resins, and mineral elements (Taylor et al. 2002; Latorraca et al. 2011).

In cacti, the delimitation of sapwood and heartwood has not been proposed; in the studied species, the sapwood region is thin and covers one to three rows (Figs. 3 and 4). In both species, no treatment showed significant differences in the relative theoretical hydraulic conductivity between dyed and undyed conductive elements (VE and WBT), which allows us to infer that despite having the same characteristics for water conduction, the tracheary elements, considered heartwood, stop transporting water and probably only store it because no organic compounds in their lumen were detected. The VE and WBT close to the vascular cambium actively transport water during evapotranspiration. However, to confirm the storage of water in the heartwood of cacti, further analyses are necessary, such as freezing the stems, which allows for determining the presence of stored water (Pratt and Jacobsen 2018).

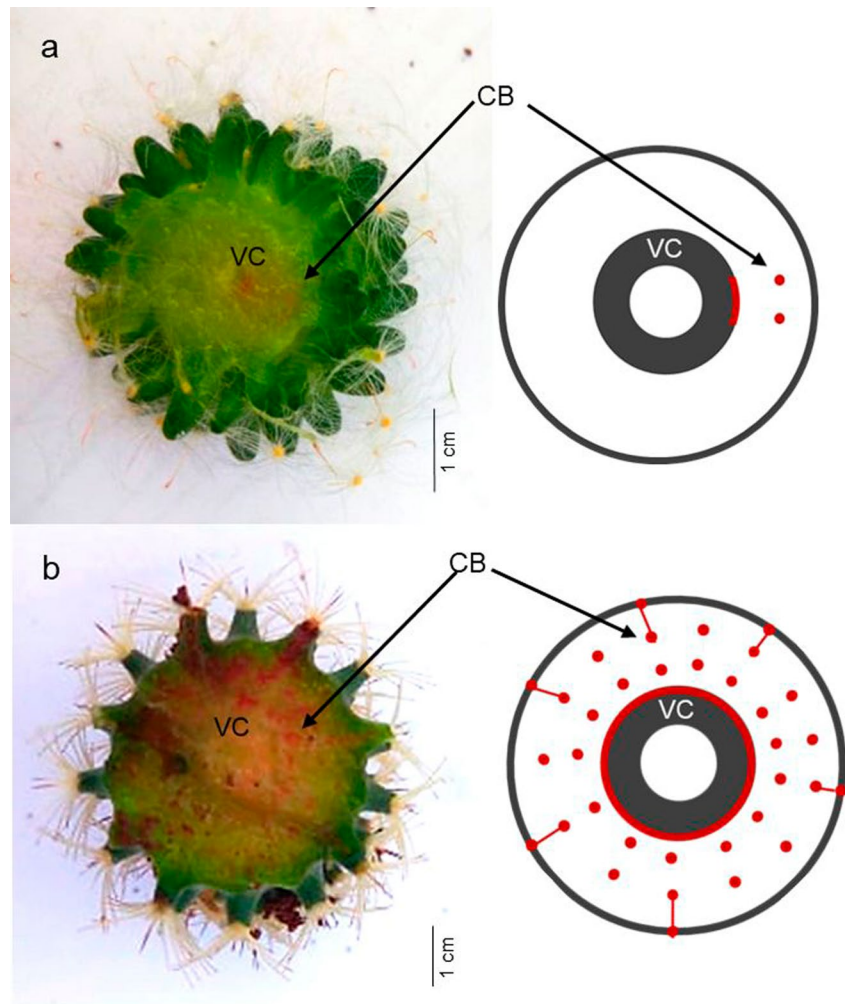
The relative theoretical hydraulic conductivity (K_h) used in this study allows us to identify the relative efficiency of water flow through the conductive elements of the xylem. The K_h formula provides an approximation of the efficiency of water flow in species of Cactaceae with different growth forms (Gibson et al. 1984; Pimienta-Barrios et al. 2003). In the studied plants of *M. bocasana*, the VE had higher diameter and K_h (Table 1) values than *E. reichenbachii* var. *fitchii*, since *M. bocasana* had wider diameters, it may be interpreted that these species are more susceptible to cavitation (Jacobsen and Pratt 2018). However, recent studies have shown that plants have a wide variation in hydraulic

safety when the diameters are less than 40 μm of lumen diameter (Jacosen and Pratt 2023; Isasa et al. 2023) as is the case of both species studied. In addition, *M. bocasana* reaches a maximum height of 10 cm (Nuzhyna and Baglay 2016), while *E. reichenbachii* var. *fitchii* reaches a maximum height of 40 cm (Taylor 1988), so the water could rise due to the phenomenon of capillarity, which is typical of small or herbaceous plants (Vilagrosa et al. 2012). In addition, both species have cortical and pith parenchyma where they accumulate water to withstand water stress (Secorun and De Souza 2011; Scalisi et al. 2016), which minimizes the possible cavitation of the vessels. In addition, the K_h in the VE of *E. reichenbachii* var. *fitchii* is narrower (Table 1), and the cortical bundles fulfill the function of distributing water into the cortical tissue and the regions of the vascular cylinder without water availability (Hearn 2009; Ogburn and Edwards 2010), so cortical bundles would be participating in water conduction to avoid water stress damages. In *M. bocasana*, staining of some cortical bundles was also observed, but it was scarce (Fig. 5). Liu et al. (2020) note that for *Populus tremuloides* Michx., the non-staining of the leaves and lateral branches may be because there is no direct connection between the xylem of the stem and the xylem of the branches, situation that could be similar to what we observed in *M. bocasana*. Cortical bundles occur in most members of the Cactoideae subfamily (Mauseth 1995), and their development facilitates the storage of water along the cortical parenchyma of the stem (Mauseth 2018), as found for other Caryophyllales (Cunha Neto et al. 2023).

The presence of WBT in *E. reichenbachii* var. *fitchii* and *M. bocasana* (Figs. 3 and 4) could prevent VE from cavitating by avoiding embolism dispersion and efficiently transferring water across the primary wall by lateral diffusion as suggested by Mauseth (2004, 2018). In both species, the WBT in the first layers of the fascicle near the vascular cambium were also stained with 0.2% acid fuchsin. This finding supports the hypothesis proposed by Mauseth et al. (1995) that WBT not only function in water storage but also participate in its flow to transfer water to the VE.

In Cactaceae, except *Pereskioideae* (Mauseth 2006), WBT are present in almost all species (Mauseth 2004) and their function is similar (Perrotta and Arambarri 2018). They occur in juvenile stages in fibrous species (Godofredo and Melo-de-Pinna 2008; Arruda and Melo-de-Pinna 2010) and in adult species (Maceda et al. 2018). They have two sizes mainly related to the initial and radial spindle cells (Melo-de-Pinna et al. 2006). The development of WBT with annular and helical secondary walls allows plants to dehydrate without damaging the vascular tissue (North and Nobel 1998; Loza-Cornejo and Terrazas 2011) and is the result of living in conditions of intense light and high temperatures (Landrum 2008). Therefore, both in Cactaceae and in other related families (Portulacaceae and Aizoaceae), WBT

Fig. 5 Images and staining scheme of the xylem and cortical bundles of *E. reichenbachii* var. *fitchii* (a) and *M. bocasana* (b). VC vascular cylinder. CB cortical bundles



have evolved several times independently (Mauseth 2004; Speck et al. 2018; Hesse et al. 2020). The difference in water conduction between *E. reichenbachii* var. *fitchii* and *M. bocasana* can be part of the anatomical, structural, and physiological strategies that plants have to withstand stressful conditions of drought and high temperatures.

Flow and drought tracing methods can be applied to species whose morphological and anatomical characteristics (such as members of Aizoaceae, Crassulaceae, and Portulacaceae) do not allow the use of conventional injection methods. Therefore, in the future, it is important to test the effectiveness of this method in other species with characteristics similar to those of the cacti that were analyzed in this study.

The standardization of the dye absorption method through the root served to observe differences in the water flow between the two species of cacti. The flow through the secondary xylem in *E. reichenbachii* var. *fitchii* was different from that observed in *M. bocasana*. In the first

species, the xylem and cortical bundles were stained, while in the second species, only half of the xylem was stained. The first layers of conductive elements were stained in both species and WBT participated in the flow of water. Future research on the water flow of a greater number of cacti, both columnar and shrubby, will serve to identify how they withstand water stress conditions.

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Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability <https://doi.org/10.6084/m9.figshare.24018993>

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