



Anatomical Studies for Adaptational Aspects in the Stem of *Cynanchum forskaolianum* (Schult.) Meve & Liede

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DRY habitats of southwestern Saudi Arabia are home to many stem-succulents, of which *Cynanchum forskaolianum* inhabit a wide range in these harsh environments. In this study, some anatomical and ultrastructure features of stem in *C. forskaolianum* were examined by using light microscopy, scanning electron microscopy and transmission electron microscopy to investigate adaptational aspects that enable this plant to cope with its stressful habitats. The stem of the plant has multiple morpho-anatomical adaptations of which low surface/volume ratio is an indication of voluminous capacity to store water. Thin boundary layer results in reduced heat-storage capacity. Papillose shape of epidermal cells together with thick epicuticular wax with thin cuticle reduces water loss. Sunken stomata with deep encryption as well as low stomatal frequency decrease transpiration and enhance water use efficiency. The large substomatal cavities with intercellular spaces in chlorenchyma promote gas exchange and diffusion of CO₂. Ultrastructure of chlorenchymatous cells showed that chloroplasts have many plastoglobuli and low stacking of thylakoids, which corresponds to high light stress and leads to chloroplast protection against photoinhibition. Cortex cells have highly undulated walls that lend flexibility during drought. Ultrastructure of these walls revealed light packed fibrillar material, which can play a major role in such flexibility, enabling cells to easily lose and refill with water to support activity of adjacent chlorenchyma cells. Xylem characteristics increase safety of water transport with less vulnerability to cavitation. These anatomical and ultrastructure features of stem show *C. forskaolianum* as a highly adaptable species in its dry habitats.

Keywords: Adaptation, *Cynanchum forskaolianum*, Dry habitats, Stem anatomy, Ultrastructure.

Introduction

Cynanchum L. is a genus of scrambling or twining stems of Apocynaceae. This genus comprises about 315 species, widespread, occurring from the southern parts of south Africa, north and eastwards through Arabian Peninsula into the drier parts of the Indian subcontinent, as well as central deserts of Australia (Meve & Liede, 1996; Liede, 2004; Bruyns, 2005). Many species in the genus are stem-succulent. In Saudi Arabia, *Cynanchum* includes three species, which were formerly under genus *Sarcostemma* (*C. forskaolianum*, *C. viminalis* and *C. arabicum*) that grow in dry habitats of southwestern regions (Meve & Liede, 1996; Bruyns, 2005; Meve & Liede-Schumann, 2012). *C. forskaolianum* (Schult.) Meve & Liede (= *Sarcostemma forskaolianum* Schult.)

is a cylindrical stem-succulent, producing tall, pendulous many-branched stems, usually tangling covers on bushes or trees up to 3m (Masrahi, 2012). This species is restricted to dry habitats of Southwestern Saudi Arabia and North Yemen, from near sea level (some islands of the Red Sea, Jazan region) to about 800m a.s.l. (Meve & Liede, 1996; Masrahi, 2012). Stems of *C. forskaolianum* are stout, 4–7 mm in diameter, blue-green, strongly glaucous with thick, perceptibly wax cover. Physiologically, this species has CAM photosynthetic pathway as most succulent species of Apocynaceae.

Photosynthetic organ of shoot has often been considered the most morphologically and anatomically variable organ of the plant (Dickison, 2000). All cylindrical stem-succulent

forms exhibit low surface to volume ratio (S/V ratio) which greatly reduce transpiration and maximize capacity to store water (Mauseth, 2000), making them more tolerant to protracted drought (Williams et al., 2014; Griffiths & Males, 2017). Nevertheless, cylindrical-stemmed succulents are, morphologically and anatomically, highly diverse (Mauseth, 2004; Williams et al., 2014). This diversity in morpho-anatomical characters is reflected in its physiological functions, which are more related to prevailing climatic conditions (Dickison, 2000; Males, 2017). In this respect, distribution of *C. forskaolianum* in dry habitats of Southwestern Saudi Arabia and North of Yemen is an indication to having many adaptational features, of which anatomical traits represent the prominent aspects.

The objective of the present study was to investigate some anatomical and ultrastructural features of stem-succulent in *C. forskaolianum* and its ecological adaptation in prevailing harsh conditions of SW Saudi Arabia.

Materials and Methods

Site description and samples collection

Stem samples of *C. forskaolianum* were collected during mid-June to early July, 2019 from its natural habitats in dry rocky areas east of Tihama, Jazan Province, southwestern Saudi Arabia (17° 00' N, 42° 57' E, Fig. 1). Plant was identified by a field guide of regional flora (Masrahi, 2012). The climate is characterized by high annual mean temperature of 31.2°C and low summer precipitation rate of 290mm yr⁻¹ (Masrahi,

2012).

Anatomical studies by light microscopy (LM)

To study fresh stem cortex (water storage parenchyma), hand sections of stem were made with a sharp razor. The sections were then stained with neutral red (Foster, 1965). Other stem samples were cut into small pieces about 1-2mm, fixed in 2% glutaraldehyde in 0.1M Na-Cacodylate buffer, pH 7.2 and subjected to a vacuum for 1-4min every 15min for 2hrs on ice. Samples were dehydrated in a series of ethanol (60min each concentration), infiltrated with resin mixtures (propylene: resin 2:1, 1hr; 1:1, 1hr; 1:2, 1hr (v:v)) and in pure resin overnight at room temperature. Samples were finally embedded in blocks which were incubated at 60°C until complete polymerization.

Semi thin sections were prepared on glass slides through cutting at 1µm using ultramicrotome (Leica EM-UC6). Sections were stained with Toluidine blue (2%) and examined by light microscope (LEICA ICC50 HD).

Measurements of some morphometrical characters (S/V ratio, average thickness of boundary layer δ^{bl}) were made from fresh cross-sections of stem, in which stem diameter was measured by caliper. S/V ratio was calculated from formula for cylindrical stem (Mauseth, 2000):

$$S/V \text{ ratio for cylindrical stem} = 2/r$$

where r is stem radius (mm). Average thickness of boundary layer (δ^{bl}) was calculated from formula for cylinder (Nobel, 2005):

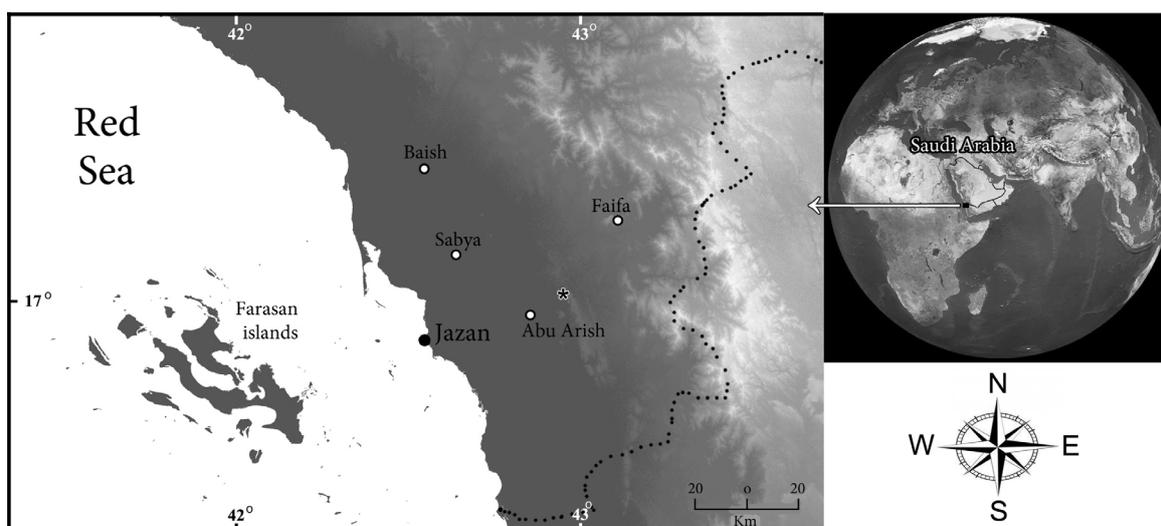


Fig. 1. Location of *Cynanchum forskaolianum* in the east of Tihama, Jazan province (indicated by an asterisk).

$$\delta^{bl}(\text{mm}) = 5.8 \sqrt{d/v}$$

where d is the cylinder diameter in m, v is the ambient wind speed in m s^{-1} ($= 1 \text{ m s}^{-1}$ as average daily wind speed in exposed places of the habitat).

Stomatal frequency (N/mm^2) was estimated microscopically. Measurements of some anatomical characters (wood characters, cortex thickness and pith radius) were made from fresh sections stained with neutral red (Table.1). Vessel frequency (VF) estimated from stem's cross-sectional area as N/mm^2 , (Masrahi, 2014). The vessels with a diameter less than $25\mu\text{m}$ were ignored because of their limited contribution to water conductivity (Ewers et al., 1997; Gutiérrez et al., 2009). Vulnerability to cavitation (vulnerability index, VI) was calculated according to Carlquist (1977).

$$\text{VI} = \text{VD}/\text{VF}$$

where VD is the vessel diameter (μm), VF is vessel frequency (N/mm^2).

TABLE 1. Some of anatomical stem characters and their values of *C. forskaolianum*.

Anatomical characters	Values
S/V (mm^2/mm^3)	0.72 ± 0.1
$\delta^{bl}(\text{mm})$	0.46 ± 0.03
SF (N/mm^2)	26 ± 3
CoT (mm)	2.99 ± 0.6
Pith radius (mm)	1.48 ± 0.3
Cortex/pith	2
WT(μm)	13.5 ± 1.7
CuT (μm)	2.7 ± 0.4
VD(μm)	39.9 ± 9.9
VF	32.8 ± 11.7
VI	1.2
TWT	Circular, AIP

(S/V= Surface: Volume ratio, δ^{bl} = Boundary layer thickness, SF= Stomatal Frequency, WT= Wax thickness, CoT= Cortex thickness, CuT= Cuticle thickness, VD= Xylem vessel diameter, VF= Xylem vessel frequency, VI= Vulnerability index, TWT= Type of wall thickening (of wood vessels), AIP= Alternate Inter-vessel pits).

All measurements were routinely repeated ($n= 3-25$) \pm standard deviation.

Anatomical studies by scanning electron microscopy (SEM)

Samples for SEM were divided into two

sets, one set of stem samples were examined directly (to reveal epicuticular wax on the stem surface), the other set of stem samples were placed in chloroform for 30min. to remove epicuticular wax. Samples were placed on the double side carbon tape on an Aluminum stub. The specimens were examined without coating by a Field Emission Scanning Electron Microscope (QUANTA FEG 450, Netherland). Measurements of some anatomical characters (thickening of epicuticular wax, stomatal frequency, type of wood vessel wall thickening) were made from SEM photomicrographs.

Anatomical studies by transmission electron microscopy (TEM)

Ultrathin sections (90nm thick) of samples were resin-embedded as mentioned above and cut using ultramicrotome (Leica model EM-UC6, USA) mounted on copper grids (400 mesh). Sections were stained with double stain (Uranyl acetate 2% for 10min, followed by Lead citrate for 5min), examined by transmission electron microscope (JEOL JEM-1400, Japan).

Results

Surface/Volume ratio of stem was 0.72, while thickness of boundary layer δ^{bl} (at average daily wind speed) was 0.46mm (Table 1). Growth habit of *C. forskaolianum* stems with surface micromorphology are shown in Fig. 2. According to the classification proposed by Barthlott et al. (1998), stem is covered with epicuticular wax of crusts manner in which crusts were continuous coverings of considerable thickness of $13.5\mu\text{m}$ as a mean (Table 1, Fig. 2B). Epidermal cells beneath epicuticular wax revealed striation manners with relatively deep sunken stomata (Fig. 2C). With thick epicuticular wax, stomata have deep encryption with external aperture in wax layer. Stomatal frequency was $26/\text{mm}^2$ as an average (Table 1).

Transverse section (TS) of stem revealed that the epidermal cells were papillose (Fig. 3). The papillae consisted of cuticle (of $\sim 3\mu\text{m}$ thick) overlying thick walls. The area below the stomata showed distinct substomatal cavities (Fig. 3C). Cells just below the epidermis represent the hypodermis which consists of two layers of small-rectangular cells.

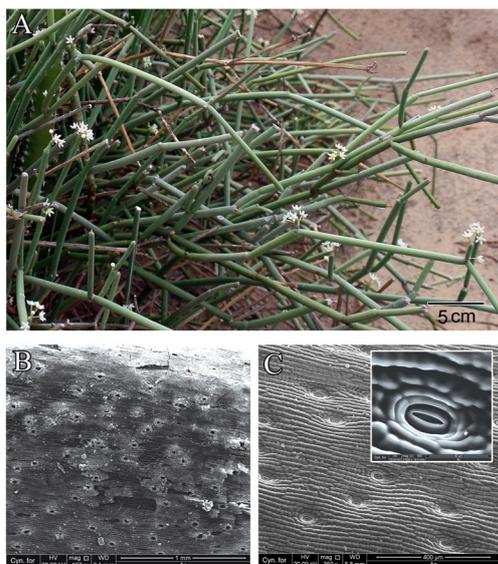


Fig. 2. (A) General Morphology of the stems, (B) Epicuticular wax of the stem surface by SEM, (C) The stem surface after removing epicuticular wax with enlarged stoma (in the frame) by SEM.

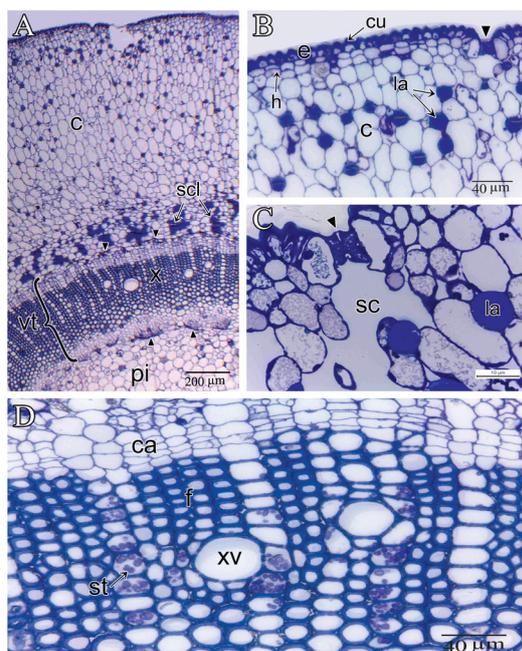


Fig. 3. (A) Cross-section of the stem to show the crushed phloem (arrowheads) by LM; c: Cortex, pi: Pith, scl: Sclereids, vt: Vascular tissue, x: Xylem, (B) Structure of the epidermis, outer cortex and stoma (arrowhead) by LM; c: Cortex, cu: Cuticle, e: Epidermis, h: Hypodermis, la: Laticifers, (C) Closed up on the epidermis, outer cortex and stoma (arrowhead) by LM; sc: Substomatal cavity, la: Laticifers, (D) Vascular tissue by LM; ca: Cambium, xv: Xylem vessel, f: Fibers, st: Starch granules.

Cortex which constitutes the larger part of the body, is composed of large parenchymatous cells with large intercellular spaces, especially in the outer part (Fig. 3B). The outer part of the cortex (outer cortex) represent the photosynthetic cells (Chlorenchyma), containing many chloroplasts. The cells containing chloroplasts gradually disappear towards the inner cortex. Ultrastructure of chlorenchymatous cells showed chloroplasts with low stacking degree of thylakoids and containing many plastoglobuli (Fig. 4) as well as prominent starch grains. Laticifers are widely distributed between parenchyma cells of cortex (Fig. 3b). The inner cortex had cells with undulate walls. In dry season, these walls were highly undulated (Fig. 5). High magnification by TEM showed that undulated cell wall was lightly stained fibrillar material (Fig. 6). The final layers of cortex (of inner cortex) had separate bundles of sclereids.

Pith represented the central part of stem, consisting of parenchymatous cells and surrounded by ring of vascular tissue of amphiphloematic xylem (Fig. 3A). Pith had a smaller radius than did cortex (Table 1) in which cortex/pith ratio was 2.

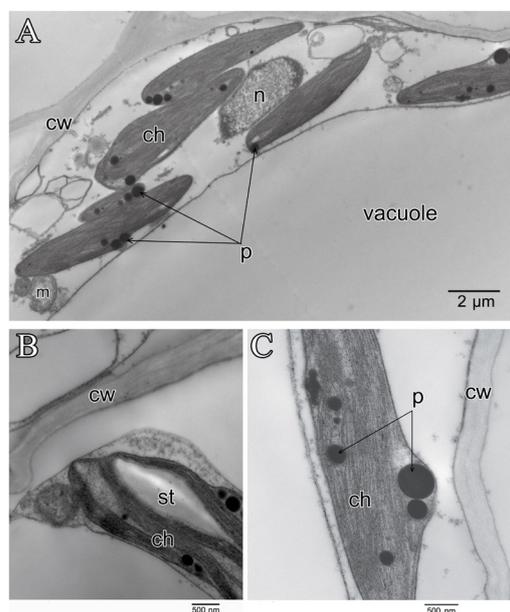


Fig. 4. (A) Chlorenchyma cell by TEM; ch: Chloroplasts, cw: Cell wall, n: Nucleus, p: Plastoglobuli, m: Mitochondrion, (B, C) Closed up on the chloroplasts to show low stacking degree of thylakoids by TEM; st: Starch granule.

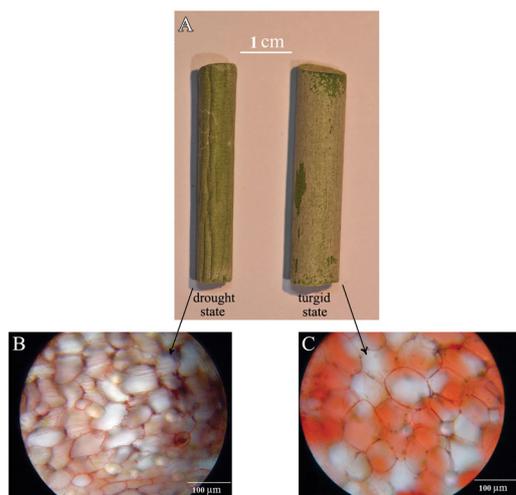


Fig. 5. (A) Stem during drought and turgid state, (B) Cortex cells in drought state [Note undulated cell walls in case of drought], (C) Cortex cells in turgid state, in which cell wall is in full extension.

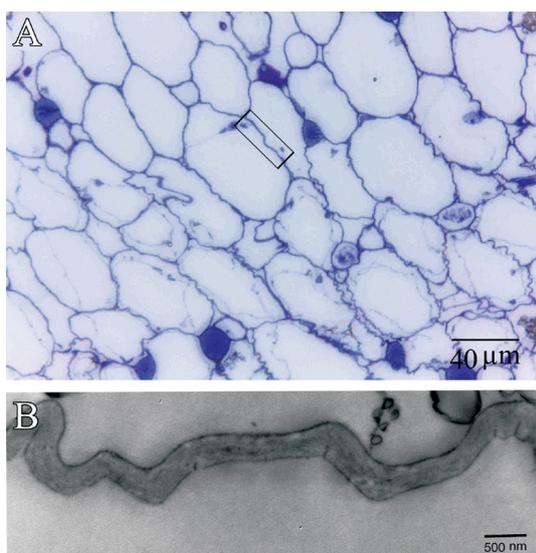


Fig. 6. (A) Cortex with undulated cell walls by LM, (B) Close up of an undulated cell wall to show lightly stained fibrillar material by TEM.

Xylem was composed of fibers with scattered vessels and ray parenchyma containing starch grains (Fig. 3D). Mean of vessel diameters was $\sim 40\mu\text{m}$, whereas vessel frequency was $32.8/\text{mm}^2$ (Table 1). Calculated vulnerability index of xylem vessels was 1.2. Type of vessel wall thickening revealed circular pattern with alternate inter-vessel pits. Outer and inner phloem revealed crushed cells.

Discussion

High temperature and low precipitation rates in lowlands of Southwestern Saudi Arabia make them highly stressful habitats (Le Hou rou, 2003; Masrahi, 2012). These harsh conditions lead to formation of xeromorphic vegetation with diverse life forms, of which stem-succulents being most prominent aspect (Masrahi, 2012). It is known that stem-succulents are conspicuously dominant in stressful hot dry habitats (Williams et al., 2014). These stem-succulents have morpho-anatomical features that reflect physiological function with highly relevant to resilience to environmental conditions (Males, 2017; Grace, 2019). Most of morpho-anatomical features in stem-succulents concentrated on store and reserve massive amount of water to use it efficiently for photosynthesis (Nobel, 1988; Williams et al., 2014).

Cylindrical stem-succulents have high volume to surface with low S/V ratio (Mauseth, 2000). This characteristic means that there is high capacity to store water, with low surface area that reduces water loss by transpiration. In the same time, low surface area will reduce area availability for photosynthesis (Gibson & Nobel, 1986; Mauseth, 2000). So, it is clear that S/V ratio in succulents reflects a correlation between water status in plant tissues and environmental factors, especially water availability (Nobel, 1988). In habitats with protracted drought, like study area, having of low S/V ratio and large capacity for water storage is an advantageous trait for *C. forskaolianum* stem. Another feature related to shape and S/V ratio is the thin boundary layer of 0.46mm in *C. forskaolianum* stem. Such thin stem boundary layer has little heat-storage capacity and can maintain an optimum temperature for metabolic activities without transpirational cooling (Gibson, 1996). Furthermore, cylindrical stem is less than a normal leaf shape for intercepting direct solar irradiance as only half of the stem can be fully exposed at any specific moment (Gibson, 1998). The papillose shape of epidermal cells may contribute to restricting or impeding air flow (Maricle et al., 2009), which helps to conserve water with such thin boundary layer.

Epicuticular wax of *C. forskaolianum* stem was relatively thick ($13.5\mu\text{m}$), while cuticle was thin ($\sim 3\mu\text{m}$) comparing to many other succulents (Loza-Cornejo & Terrazas, 2003; Mauseth, 2004). Concomitance of both epicuticular wax and cuticle

plays an important role in reduction of water loss via cuticular transpiration (Evert, 2006; Dinter & Haas, 2008). On the other hand, construction costs of cuticle lipid materials are more than double that of polysaccharides (Poorter & Villar, 1997) which means that plants may spend considerable costs to construct thick wax and cuticle. Construction of thick epicuticular wax and thin cuticle is, metabolically, low to medium-cost helping to get efficient layer against water loss.

Sunken stomata have been linked with dry habitats of high irradiance (Gibson, 1983; Jordan et al., 2008). Thick epicuticular wax in *C. forskaolium* stem lead to deep encryption of stomata with external aperture in waxy layer. Sunken stomata have been considered to decrease stomatal conductance and consequently reduce transpiration (Roth-Nebelsick, 2007). In addition, such encrypted stomata create humid microclimatic conditions directly above the stomatal pore, allowing stomata to remain open longer than those without encryption (Gibson, 1983). These features of sunken stomata greatly enhance water use efficiency and carbon assimilation, especially with CAM photosynthetic pathway of the plant. Furthermore, stomatal frequency was 26/mm². This value of stomatal frequency is at the lowest range of plants, in which non-succulents have generally more than 100/mm² whereas succulents have 15-70/mm² (Gibson & Nobel, 1986; Evert, 2006). While such stomatal frequency would tend to reduce rate of CO₂ but, at the same time, greatly reduce water loss (Sundberg, 1986). These characters of stomata in association with low S/V ratio of the stem lead to high stem water potential and therefore extend nocturnal CO₂ uptake even in dry season (Gibson & Nobel, 1986).

The prominent substomatal cavities and large intercellular spaces in chlorenchyma greatly enhance gas exchange between atmosphere and photosynthetic tissue by having large internal surfaces, leading to efficient diffusion of CO₂ (Nobel, 2005), and may compensate for both low ratio of S/V and low stomatal frequency through which CO₂ must diffuse.

Ultrastructure of chlorenchymatous cells showed chloroplasts with many plastoglobuli and low thylakoid stacking. Plastoglobuli serve as extrathylakoidal reservoir of lipids, continuously accumulate as photosynthetic products in chloroplasts at high light conditions (Austin et al.,

2006; Lichtenthaler, 2013; van Wijk & Kessler, 2017). Large and numerous plastoglobuli are observed also in stem succulent *Echinocactus acanthodes* (Thomson & Platt, 1973). These and other findings demonstrate the role of plastoglobuli in response to environmental stresses, especially high light, protecting thylakoids from photo-inhibition and photo-oxidation (Lichtenthaler, 2013; van Wijk & Kessler, 2017). The chloroplasts with low stacking degree of thylakoids were observed in plants growing in high light conditions, which also seems to serve as adaptations against photodamage (Lichtenthaler, 2013). On the other hand, starch grains observed in chloroplasts are indication to an active photosynthesis in which large grains were found as feature in high light chloroplasts (Lichtenthaler & Meier, 1984; Evert, 2006).

Laticifers are widely distributed between cortex parenchyma cells, which are characteristic for Apocynaceae. While a general aspect of laticifers that they serve as system to sequester toxic secondary metabolites in plants, protecting them against herbivores (Evert, 2006), distribution manner of laticifers and nature of latex in these ducts is found to assist in keeping metabolic activity as well as conserving water during dry seasons (Masrahi, 2009).

Nearly in all stem-succulents, inner cortex represents the main water-storage part (Nobel, 1988; Mauseth, 2004). Parenchyma cells of this part easily lose greater fraction of water without plasmolyzing (Mauseth, 2004). Plants with CAM photosynthetic pathway have cyclic manner of water moving between chlorenchyma and water-storage parenchyma (Sayed et al., 1994). Nocturnal malate accumulation in chlorenchyma during the night increases osmotic pressure in these cells leading to water uptake from low osmotic pressure cells of adjacent water-storage parenchyma. At the dusk, water moves more readily towards the water-storage parenchyma (Nobel, 1988; Borland et al., 2018). The preferential loss of water from water-storage parenchyma tissue allows the photosynthetic chlorenchyma cells to remain active, maintaining a positive net CO₂ uptake rate for a longer period even during drought (Nobel, 1988, 2006). The keystone for maintaining this cyclic manner of water movement between two adjacent tissues is high flexibility of cell wall in water-storage parenchyma. Water-storage parenchyma of *C.*

forskaolianum stem revealed highly undulated cell walls, especially during drought, maintaining turgor state of chlorenchyma. Ultrastructure of undulated cell wall showed lightly stained fibrillar material, indicated to lightly packed fibrillar material (Ben-Arie et al., 1979; Gritsch & Murphy, 2005). Although most parenchyma cells have very thin walls, water- storage parenchyma seems to be special in this feature (Mauseth, 1995, 2004; Gritsch & Murphy, 2005) in which the pattern formed by cellulose microfibrils in these walls play a major role of such high flexibility (Emons & Mulder, 2000).

Furthermore, the observed Cortex to pith ratio (C/P) of 2 indicated that cortex constituted a larger storage volume than pith did in stem of *C. forskaolianum*.

Xylem vessel characteristics also reflected medium to relatively high resistance to cavitation VI value (Carlquist, 1977). Cavitation in xylem conduits resulting in breakage of water columns by air bubbles under great tension of dry condition (Masrahi, 2014), which may lead to dysfunction of xylem conduits, reducing capacity to transport water and increasing drought stress in plants. On the other hand, circular thickening of xylem vessel walls gives them strength against collapse under drought stress (Masrahi, 2014). Such features of xylem vessels in *C. forskaolianum* stem, as well as characters of water-storage parenchyma cells that near to xylem elements, increase safety of water transport with less vulnerability to cavitation even in the dry seasons.

Conclusion

Stem of *C. forskaolianum* shows multiple anatomical and ultrastructure features to cope with its dry habitat in southwestern Saudi Arabia. Low S/V ratio reflected high water storage capacity. Thin boundary layer reduces heat-storage capacity. Pappilose thin walled epidermal cells with thick epicuticular wax, sunken stomata, and low stomatal frequency greatly reduce transpirational water loss. Large substomatal cavities with intercellular spaces in chlorenchyma enhance gas exchange and CO₂ diffusion. Chloroplasts in chlorenchyma cells have many plastoglobuli and low thylakoid stacking which is an adaptation to high light stress and protects chloroplasts from photoinhibition. Cortex represents large water-storage part in

the stem, with cells having high flexible walls. Ultrastructure of these walls revealed light packed fibrillar material which facilitate transfer of water to adjacent chlorenchyma cells. Xylem characteristics increase safety of water transport with less vulnerability to cavitation. All these features in the stem represent effective adaptational strategies against high stressful habitats.

Ethical approval: Not applicable.

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دراسات تشريحية للمظاهر التكيفية في ساق نبات *Cynanchum forskolianum*

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تعتبر البينات الجافة جنوب غرب المملكة العربية السعودية موطناً للعديد من عصاريات الساق، ومن ضمنها النوع *Cynanchum forskolianum* الذي ينتشر في مدى واسع ضمن هذه البينات الصعبة. في هذه الدراسة تم إظهار بعض الخصائص التشريحية وسمات التركيب الدقيق للساق في النوع *C. forskolianum* بواسطة المجهر الضوئي، والمجهر الإلكتروني الماسح والمجهر الإلكتروني النافذ؛ وذلك لكشف السمات التكيفية التي تمكن هذا النوع من مقاومة إجهادات بيئته. تضم ساق النبات عدة تكيفات مظهرية وتشريحية، من ضمنها قلة نسبة مساحة سطح الساق إلى حجمه والتي تشير إلى سعة داخلية كبيرة لتخزين الماء. الطبقة الحدية للساق تقلل من سعة الاحتفاظ بالحرارة. خلايا البشرية ذات الشكل الحلمي مع سماكة طبقة الشمع فوق الأدمة وقلة سماكة الأدمة كل ذلك يقلل من فقد الماء من الساق. الثغور الغائرة بتجويفها العميق إضافة إلى قلة التردد الثغري يؤدي إلى التقليل من معدل النتج ويعزز من كفاءة استخدام الماء. الفراغات تحت الثغرية الكبيرة مع المسافات البينية للنسيج الكلورنشيبي يعزز من التبادل الغازي وانتشار ثاني أكسيد الكربون. التركيب الدقيق للخلايا الكلورنشيبية أظهر احتواء البلاستيدات الخضراء على العديد من الحبيبات البلاستيكية الدهنية *plastoglobuli* ونمط تراص ضئيل لأغشية الثيلاكويد، مما يشير إلى تعرض النبات إلى إجهاد ضوئي عالٍ وتؤدي هذه التغيرات في التركيب الدقيق إلى حماية البلاستيدات الخضراء من التثبيط الضوئي. خلايا القشرة ذات جدران عالية المرونة تساعدها في التأقلم خلال الجفاف. التركيب الدقيق لهذه الجدران أظهر تكدساً ضئيلاً للمكونات اللبيفية؛ مما قد يلعب دوراً كبيراً في مرونة هذه الجدران ويسهل للخلايا فقد وإعادة الملء بالماء دعماً لنشاط الخلايا الكلورنشيبية المجاورة. خصائص نسيج الخشب في الساق تزيد من نقل الماء بأمان وفعالية مع قابلية أقل للانسداد بفقاعات الهواء أثناء الجفاف. هذه الخصائص في التشريح والتركيب الدقيق للساق تظهر أن نبات *C. forskolianum* يمثل نوعاً ذو تكيفية عالية في بيئته الجافة.