

RESEARCH PAPER



# Adaptations facilitate the invasion of *Cylindropuntia rosea* (DC.) Backeb. (Cactaceae) in the highlands of southwestern Saudi Arabia

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## ABSTRACT

The colonization and expansion of any plant species into a novel environment depend on its structural and functional characteristics. Therefore, developing better control measures for any invasive plant species requires examining and understanding the mechanisms underlying its reproduction and adaptation to the environment it invades. Recently, a novel exotic species *Cylindropuntia rosea* (DC.) Backeb. has been identified in Baljurashi, Al-Baha province, in southwestern Saudi Arabia. Reports suggest that this species may become invasive with the current rate of habitat expansion in Baljurashi. Although *C. rosea* is an important invasive species, most of its morpho-anatomical and physiological characteristics have not been examined. Therefore, the aim of this study was to investigate the morpho-anatomical and related physiological adaptations of *C. rosea* in its new habitats in the southwestern highlands of Saudi Arabia. We observed that the species is well-equipped for invasion with traits to handle semi-arid conditions, including some morphological and anatomical features, CAM photosynthetic pathway, high growth rate, and highly effective defense mechanisms against herbivores and insects. These morpho-anatomical and physiological characteristics contribute to the high invasiveness of this species in Saudi Arabia.

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## 1. Introduction

Natural ecosystems are under threat from logging, pollution, climate change, and invasive species, because of increasing human populations and activities.<sup>1</sup> Recently, invasive species, defined as non-native (alien) species intentionally or unintentionally introduced outside their native range owing to human activities,<sup>2</sup> have emerged as one of the important human-related ecosystem stressors. Such species have high colonization rates, with the potential of spreading to wide habitat ranges.<sup>3</sup> Having altered ecosystems worldwide, invasive plant species spread aggressively and pose serious threats to biodiversity,<sup>4</sup> as they incur high ecological and economic costs.<sup>5</sup> In addition to affecting biodiversity and degrading native vegetation, invasive plant species affect human health and tourism.<sup>6</sup>

Semi-arid or disturbed ecosystems with low species diversity are more susceptible to invasions by plant species than complex ecosystems.<sup>4,5,7</sup> Furthermore, these vulnerable ecosystems have recently been at a higher risk of species invasions than others.<sup>8</sup>

The 1,500 species of the family Cactaceae<sup>9</sup> are among the most detrimental invasive species worldwide. The members of this family, native to the arid regions of the New World (Americas), have recently invaded several inhabited parts of all continents.<sup>10</sup> This can be partly attributed to the fact that these species can rapidly adapt to various types of arid habitats.<sup>10,11</sup>

Of the approximately 48 exotic cactus species in Saudi Arabia, three species belonging to the genus *Opuntia*, namely *O. dillenii* (Ker Gawl.) Haw. {*O. stricta* var. *dillenii* (Ker Gawl.) L. D. Benson}, *O. stricta* (Haw.) Haw. var. *stricta*, and

*O. ficus-indica* (L.) Mill., have been identified as invasive species.<sup>12,13</sup> These three species have been observed in southwestern Saudi Arabia for a long time. Recently, a novel exotic species *Cylindropuntia rosea* (DC.) Backeb. was identified in Baljurashi, Al-Baha province, in southwestern Saudi Arabia.<sup>14</sup> Reports suggest that this species may become invasive given its current rate of habitat expansion in Baljurashi.

*Cylindropuntia rosea* (common name: Hudson pear) is a branched, cylindrical cactus species, native to central Mexico, and has invaded eastern Spain, southern Africa, and parts of southern and eastern Australia.<sup>10,15,16</sup> Furthermore, this species is considered as one of the most invasive cactus species in several arid regions of the world.<sup>10,15</sup>

The colonization and expansion of any plant species into a novel environment depend on its structural and functional characteristics.<sup>4,17</sup> Therefore, developing better control measures for any invasive plant species requires examining and understanding the mechanisms underlying its reproduction and adaptation to the environment it invades. Nevertheless, there have been few studies on the adaptive characteristics of invasive plant species in stressful habitats.

Although *C. rosea* is an important invasive species, most of its morpho-anatomical and physiological characteristics have not been examined. Therefore, the aim of this study was to investigate the morpho-anatomical and related physiological adaptations of *C. rosea* in its new habitats in the southwestern highlands of Saudi Arabia. In this study, we attempt to answer several questions to figure out the relationship between the

morpho-anatomical and physiological characteristics of *C. rosea* and the adaptations of this plant to the invaded ecosystems. These questions are 1) does the plant have morpho-anatomical characteristics that help it to avoid the biotic and abiotic effects? And 2) does the plant have physiological characteristics (e.g. photosynthetic pathway and growth rate) that help it to adapt to the newly invaded habitat?

## 2. Materials and methods

### 2.1. Site description and sample collection

*Cylindropuntia rosea* samples were collected from the primary invasion site in the rocky habitats near Heznah, Baljurashi (19° 51' N, 41° 33' E; **Figure 1**), at an altitude of 2,000–2,020 m asl, in September 2020. The study area exhibited temperatures ranging between 22–27°C in summer and 10–15°C in winter, reaching a maximum of 34°C and a minimum of 6°C in summer and winter, respectively, and a precipitation rate of 300–500 mm yr<sup>-1</sup>.<sup>18,19</sup>

### 2.2. Determination of morphometrical characteristics

Fresh fully turgid and drought-stressed stems were sectioned using a sharp razor. In contrast, root sections were prepared

from samples stored in 70% ethanol. Subsequently, all sections were stained with neutral red<sup>20</sup> and observed under a light microscope.

The diameter of turgid stems were measured using a caliper, and fresh stem cross-sections were used to measure morphometrical characteristics, namely the Surface area to Volume (S/V) ratio and the average thickness of the boundary layer ( $\delta^{bl}$ ). The S/V ratio was calculated using the following formula for cylindrical stem:<sup>21</sup>

$$S/V \text{ ratio} = 2/r, \quad (1)$$

where  $r$  is the stem radius (mm).

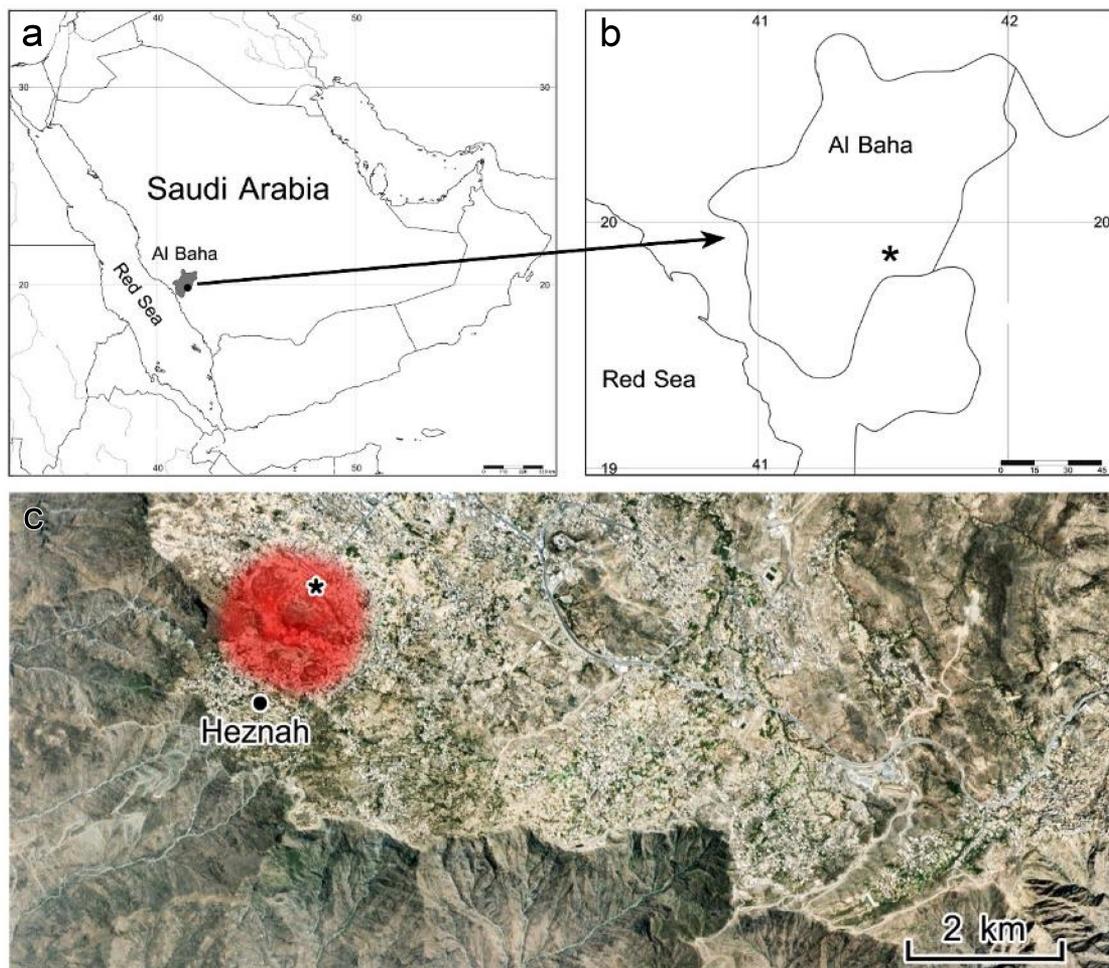
$\delta^{bl}$  (mm) was calculated using the formula for cylinder as follows:<sup>22</sup>

$$\delta^{bl} = 5.8 \sqrt{d/v}, \quad (2)$$

where  $d$  is the cylinder diameter (m) and  $v$  is the ambient wind speed (m s<sup>-1</sup>). 1 m s<sup>-1</sup> was the average daily wind speed under normal circumstances.<sup>23</sup>

### 2.3. Scanning electron microscopic analysis

Stem surface and root anatomical characteristics were investigated in detail using a scanning electron microscope (JEOL



**Figure 1.** Study range (in red) with samples collection site indicated by an asterisk.

SEM; JSM-IT500HR, ASIA PTE. Ltd., Singapore). Stem surface characteristics included spines, glochids (Figure 3, c & d), and the epidermis. The epidermis was examined in two sets of slides: one set was directly examined to determine the presence of epicuticular wax on the surface, whereas the other set was treated with chloroform for approximately 30 min to examine the stem surface after the removal of the epicuticular wax. We used transverse sections of roots to study the xylem.

All samples were mounted on the electron microscope stub using a double-sided carbon tap, sputter-coated with gold, and examined under a high vacuum at an accelerating voltage of 5 kV. Elemental analysis of druses (Figure 5e) was performed using energy dispersive X-ray spectroscopy (EDS) attached to a thermal field emission electron microscope (JSM-7100 F; JEOL Ltd.).

#### 2.4. Physiological characteristics

For investigating species invasion and adaptations to local conditions, two physiological parameters were examined, namely the type of photosynthetic pathway and growth rate. Although most Cactaceae members primarily use the CAM pathway, some members exhibit the C3 pathway.<sup>24</sup> We used the titratable acidity method to verify the occurrence of CAM photosynthetic pathway in *C. rosea*.<sup>25</sup> In this method, chlorenchyma cell sap was first extracted by grinding a known mass of the tissue in distilled water (1 gm/10 ml distilled water), and it was then filtered through layers of muslin to determine its titratable acidity using 0.01 M NaOH and phenolphthalein (indicator).

The growth rate was determined for two sets of plants to determine the effects of temperature on the growth of plants in the study area compared to those at low altitudes. One set was grown at a mean temperature of 25°C under partial shady conditions (similar to on-site conditions), whereas the other set was grown at 32°C under exposed conditions (Figure 2). Both sets of plants were irrigated once a month and their

growth rates were determined by measuring the length of freshly sprouted branches (mm/d).

### 3. Results

#### 3.1. Morpho-anatomical characteristics

*Cylindropuntia rosea* was widely distributed at the study site and preferred shaded and rocky microhabitats (Figure 2a–c). The shoot system comprised branched cylindrical stems, reaching up to 1 m in length, with detachable stem segments covered with dense spines. Spines were clustered in groups of 4–7, protruding from the areoles and bearing small bristles called glochids. The root system was shallow and spread a few centimeters below the soil surface (Figure 2d).

The spines were long (up to 5 cm in length), with fragile papery sheaths and surfaces covered with retrorse barbs (Figure 3a–b). By contrast, glochids were not longer than 1,000  $\mu\text{m}$ , but covered with retrorse barbs (Figure 3c–d) and dense mat of trichomes at the base. Stem segments were 10–15 cm long and 1.6–2.5 cm in diameter, with distinct tubercles bearing areoles on the top (Figure 4a).

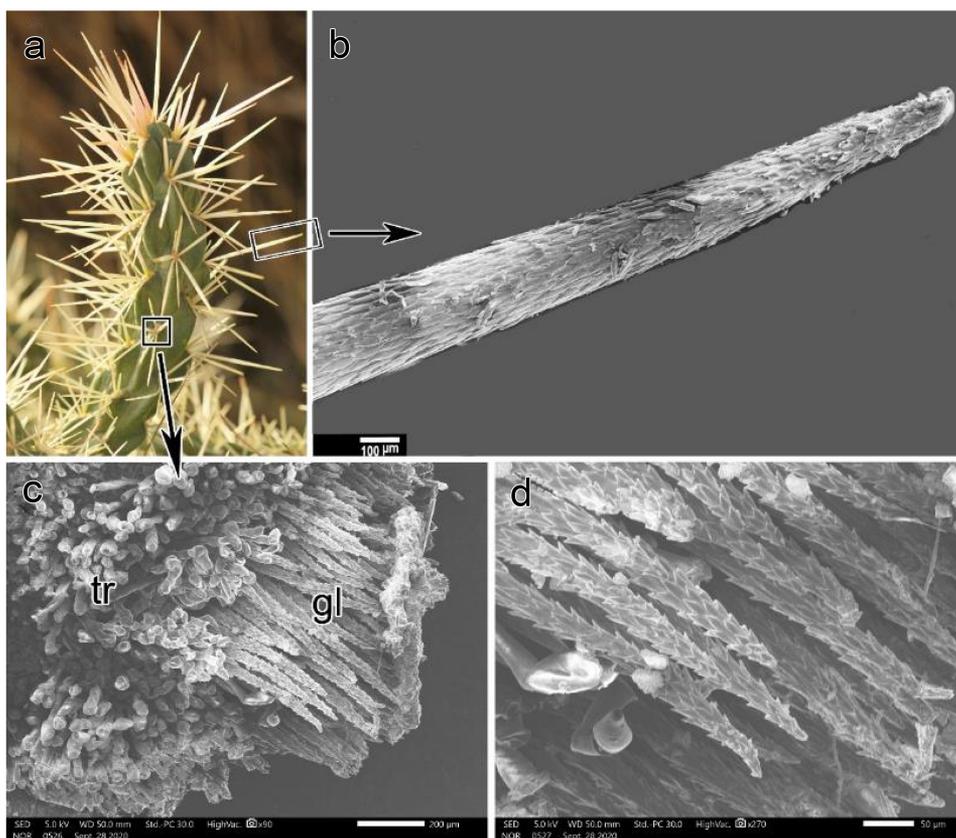
At an average wind speed, the surface to volume (S/V) ratio and thickness of the boundary layer ( $\delta^{\text{bl}}$ ) of stem segments were 0.16  $\text{mm}^{-1}$  and 0.93 mm, respectively (Table 1). Furthermore, stems were covered with crust-type epicuticular wax [according to the classification proposed by<sup>26</sup>], and the epidermis below the wax exhibited a rough surface, with epidermal cells exhibiting convex projections (Figure 4c, 5b). The average cuticle thickness was 5.5  $\mu\text{m}$  (Table 1).

Transverse sections (TSs) of stem segments revealed that epidermal cells possessed druse crystals (Figure 5b), and a thick hypodermal layer was present below the epidermis.

*C. rosea* stem anatomy was similar to that of cylindrical succulent stems, wherein a thick cortex surrounds the pith, with a ring of vascular tissue between them (Figure 5). The cortex was composed of two distinguished zones, a greenish outer cortex and a whitish inner cortex (Figure 5a). The

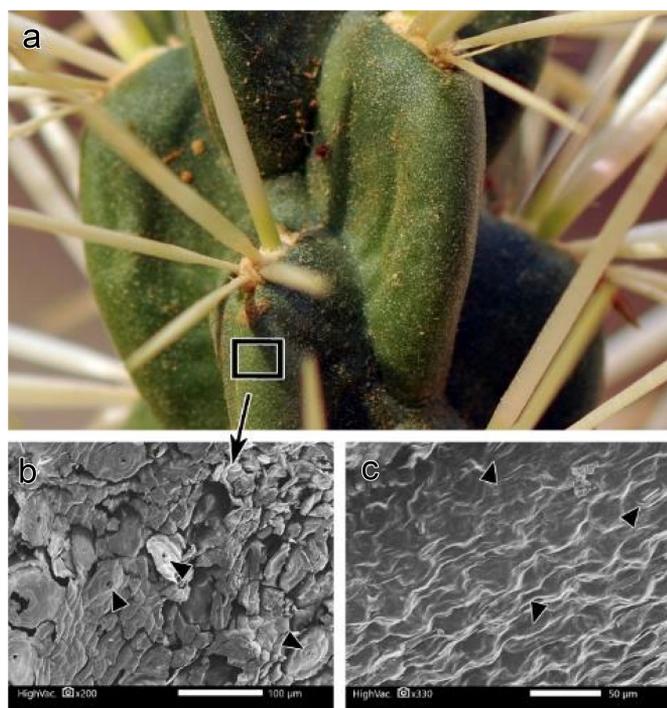


**Figure 2.** (a–c) *C. rosea* in microhabitats of the study area. (d) *C. rosea* with the root system.



**Figure 3.** Spine (a, b) and glochid (c, d) micromorphology of *C. rosea*. Note the barbs that cover the surface of both spines and glochids in SEM images (b-d). tr: trichomes, gl: glochids.

outer cortex lay below the hypodermis and was characterized by multiple layers of palisade cells (chlorenchyma), whereas



**Figure 4.** (a, b) surface of the stem with epicuticular waxes covering the epidermis (SEM image in B) and after removal by chloroform (SEM image in C).

the inner cortex was composed of water-storing parenchyma. The ring of vascular tissue predominantly consisted of wide-band tracheids (WBTs) (Figure 5c-d), representing short conduits whose secondary walls occurred as wide annular bands that projected deeply into the conduit lumen. Pith was composed of parenchymatous cells with druse crystals (Figure 5e), which were also observed in the inner and outer cortical cells. Furthermore, turgid stems exhibited completely expanded cortical cells, whereas they appeared shrunken under drought conditions (Figure 6). Moreover, cortical cells, especially inner cortical cells, exhibited highly undulated walls during drought conditions (Figure 7).

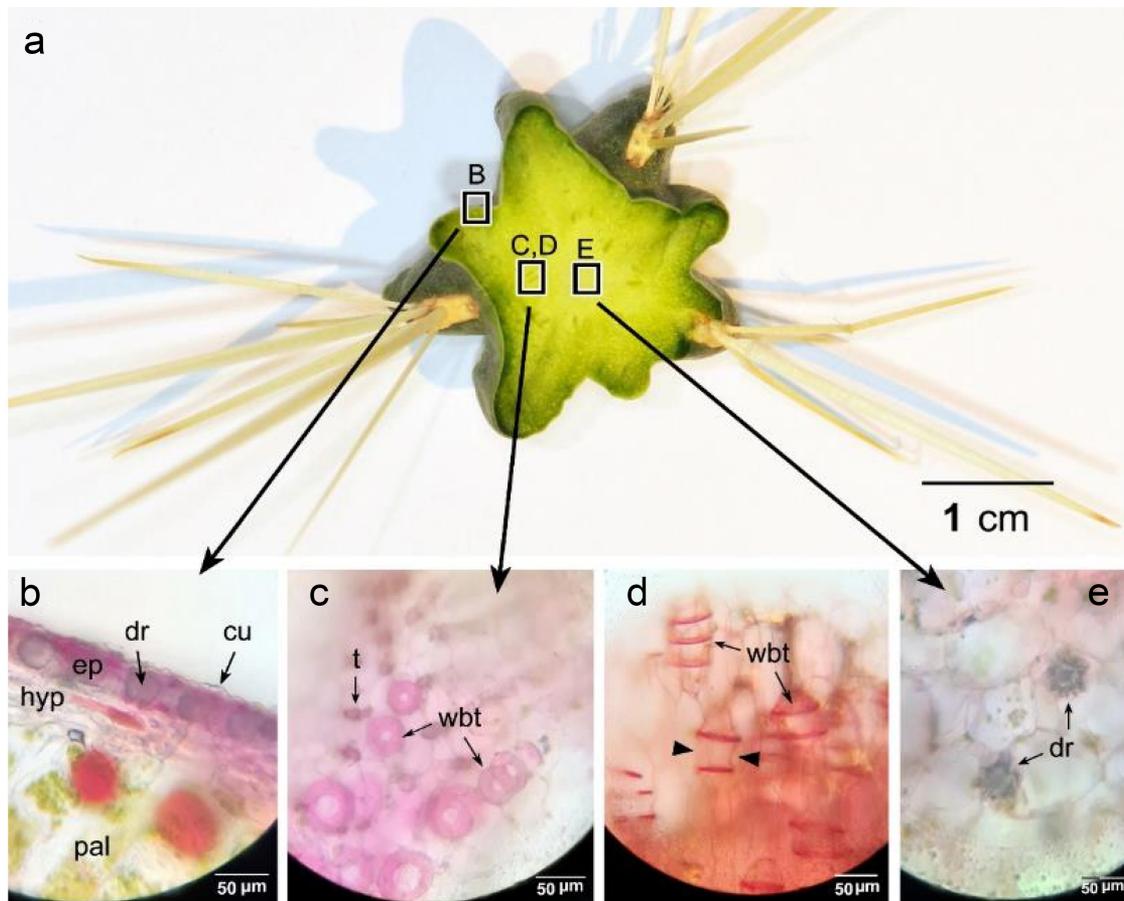
TS of adult roots revealed a well-developed periderm and a narrow cortex (Figure 8a-b) composed of parenchymatous cells. Fibrous wood (secondary xylem) with large unligified ray cells occupied most of the root (Figure 8a-b). We also observed vessels, solitary and in groups of 2-4, with wall thickenings and scalariform or circular bordered pits (Figure 8c-d). Additionally, elemental analysis of druse crystals scattered in both cortical and ray cells (Figure 8a, c) revealed that they were composed of approximately 35% calcium, 33% carbon, and 31.5% oxygen (Figure 9).

### 3.2. Physiological characteristics

Titrate acidity in the early morning (6.30 a.m.) and at the end of the day (6.30 p.m.) were 155 and 38 micro equivalent

**Table 1.** Some morpho-anatomical and physiological parameters of *C. rosea*.

Parameter	value	
Stem diameter (mm)	25.2 ± 3.1	
Surface to Volume (S/V) ratio (mm <sup>2</sup> /mm <sup>3</sup> )	0.16 ± 0.02	
The thickness of boundary layer ( $\delta^{bl}$ ; mm)	0.93 ± 0.05	
Cuticle thickness ( $\mu$ m)	5.54 ± 1.5	
Titratable acidity ( $\mu$ eq. g <sup>-1</sup> f.w.)	at 6.30 a.m.	155.3 ± 14.5
	at 6.30 p.m.	38.3 ± 1.7
Growth rate (mm/day)	at 25°C	2.6 ± 0.4
	at 32°C	0



**Figure 5.** A. Transverse sections (T.Ss.) in the stem revealed the inner structure, with light microscopy images (b-e). B. epidermis with hypodermis and chlorenchyma cells. C. Wide-band tracheids in transverse section (T.S.) and longitudinal section (L.S.) (d). Arrowheads show the primary wall bowing inward between annular rings of the secondary wall. E. pith with druse crystal in some cells. cu: cuticle, dr: druse crystal, ep: epidermis, hyp: hypodermis, pal: palisade cells, t: tracheid, wbt: wide-band tracheids.

per gram (fresh weight), respectively, indicating that crassulacean acid metabolism (CAM) photosynthetic pathway is functional in *C. rosea* (Table 1). Moreover, the growth rate of stem segments was approximately 2.5 mm/d at 25°C. However, at a higher temperature (32°C), there was no noticeable growth in the stems (Figure 10).

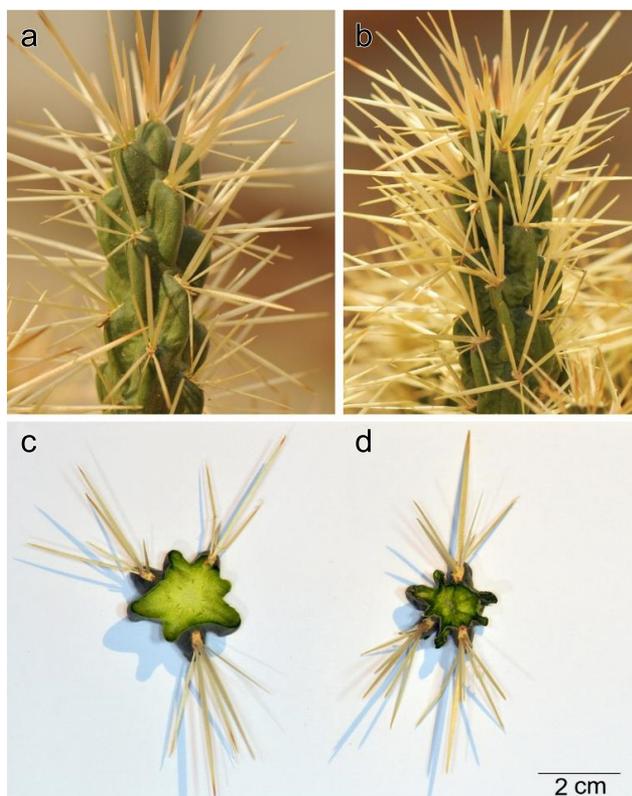
#### 4. Discussion

The degree of invasiveness and colonization rate of an alien species in a new geographical region largely depends on its structural and functional characteristics.<sup>3,4</sup> Among all the invasive plant species worldwide, cacti represent one of the most widespread and harmful species.<sup>10</sup> Their succulent nature,

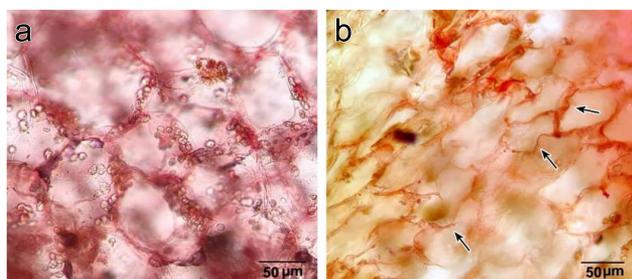
a wide range of growth forms, and several other structural and functional traits make them extremely adaptable to different arid and semi-arid habitats.<sup>10,11,27</sup>

Baljurashi is a semi-arid habitat<sup>28</sup> with several microhabitats, such as those between rocks, under the canopy of trees and shrubs, and along the roadside. The concomitance of climatic characteristics of habitat, with structural and functional traits of *C. rosea*, seemed to have facilitated its invasion into the region.

*C. rosea* stems are densely covered with spine clusters, which make them more defensive and help deter herbivores. This technique of defense is very common in plant species, see.<sup>29-31</sup> Moreover, dense glochids, at the base of each spine cluster, can easily dislodge and attach to any passing herbivore.



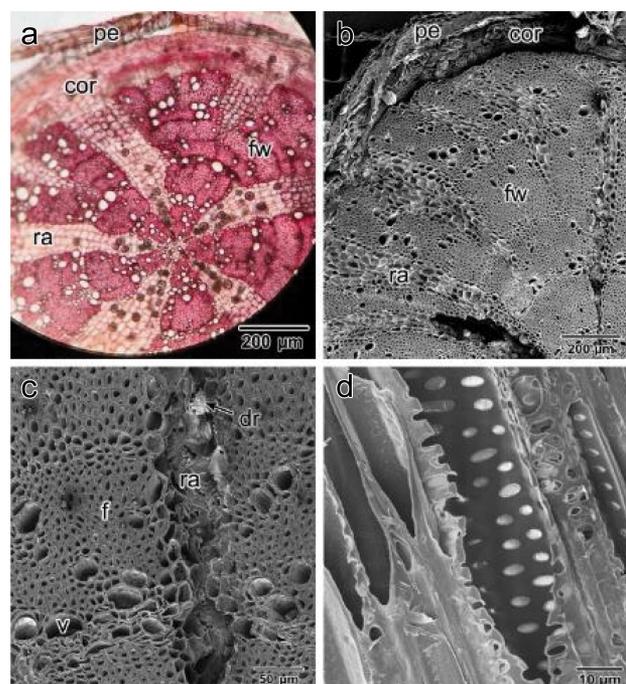
**Figure 6.** A., C. stem at turgid state. B., D. stem at dry state. Note: high shrinkage of the stem in the dry state.



**Figure 7.** A. inner cortex cells in a turgid state. B. inner cortex cells in a dry state. Note highly undulated cell walls in the dry state (Arrows).

Both spines and glochids are covered with retrorse barbs, making them extremely noxious; they can readily penetrate animal skin and are difficult to remove. Additionally, stem segments are detachable and attach to cattle and other animals that forage on *C. rosea*, contributing to its dispersal.<sup>16,32</sup>

The cylindrical shape of *C. rosea* remarkably reduces its surface area, which increases its volume (low S/V ratio), indicating high water-storage capacity and low transpiration rate.<sup>21,23</sup> Another feature related to shape that alters the adaptability of an invasive species is  $\delta^{bl}$ , which is a thin layer of still air closely fitted to the surface.  $\delta^{bl}$  considerably affects transpiration and heat storage capacity.<sup>23,33</sup>  $\delta^{bl}$  in *C. rosea* stems was relatively high (0.93 mm) because of their large diameter, which reduced transpiration, and therefore, latent heat loss, leading to high heat-storage capacity.<sup>23,34</sup> The heat storage capacity further increases because of CAM photosynthetic pathway, wherein stomata are closed during the day. By



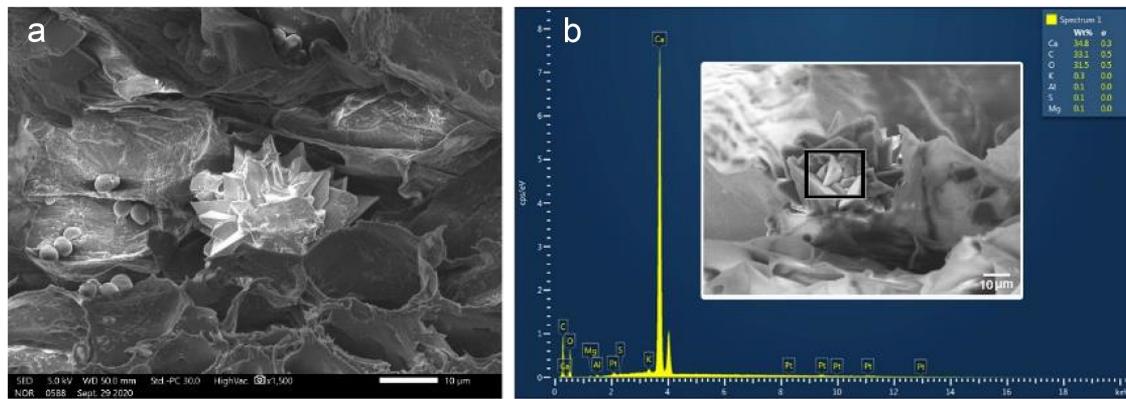
**Figure 8.** Mature root anatomy. (a) light microscopy image, (b) SEM image. Note: fibrous wood with many vessel elements and large unligified rays (ray parenchyma) between them containing many druse crystals. (c) SEM image of fibrous wood with vessel elements. (d) SEM image of longitudinal section (L.S.) in a vessel element showing circular bordered pits in wall thickening. pe: periderm, cor: cortex, fw: fibrous wood, ra: ray, dr: druse crystal.

contrast, tubercles on stems enhance the ability of plants to acclimatize to altered water content<sup>11</sup> and contribute to an increase in the surface area, to some extent,<sup>27</sup> thereby increasing the growth rate and decreasing the heat storage capacity. Epicuticular wax, a thick cuticle, and a thick hypodermis also contribute to reducing water loss.<sup>35</sup> These characteristics help promote growth and invasion in semi-arid environments with moderately (not high) temperatures, similar to those at the study site.

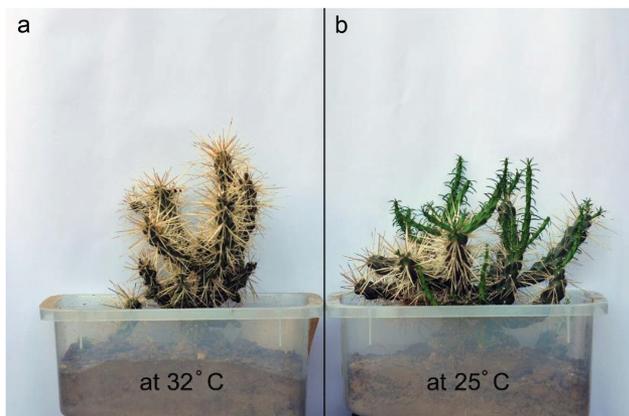
The anatomy of *C. rosea* stem revealed patterns of fundamental tissues in similar cylindrical cacti and other succulents. Although both the cortical and pith cells are large and store water, the inner cortex represented the main tissue for the storage of available water, which can be used during drought conditions.<sup>36,37</sup> Recurrent changes in stem turgidity under drought and flood conditions indicate high flexibility of the cell walls of the inner cortex, which appear highly undulated (collapsible) under drought conditions. By contrast, water in these collapsible cells replaces the water lost from photosynthetic chlorenchymatous cells of the outer cortex, thereby maintaining the physiological functions of photosynthetic tissues even under drought conditions.<sup>23,36</sup>

Wide-band tracheids (WBTs) occur in many genera of the family Cactaceae and few genera of other families that inhabit xeric habitats.<sup>38,39</sup> They improve safe water transport (protecting against embolism), water storage, and rehydration.<sup>39,40</sup> The tracheids represented the dominant xylem conduits in *C. rosea* stems.

The root system in *C. rosea* is shallow, similar to other succulents, which enables high water uptake following light



**Figure 9.** A. druse crystal in ray parenchyma of the root. Note: starch grains on the left. B. EDX spectrum of druse crystal showing a high percentage of Calcium.



**Figure 10.** A. *C. rosea* grown at a mean temperature of 32° in a fully exposed condition (unshaded), and B. grown at a mean temperature of 25° in a partially shady condition. Note new stem segments growth at 25°.

rains.<sup>41</sup> Extensive fibrous, woody roots with numerous vessels provide support to these vessels, which promote effective water conduction.<sup>42</sup> Moreover, wall thickenings in these conduits (scalariform to circular bordered pits) provide strength, thereby reducing the risk of collapse and embolism under severe drought conditions.<sup>42,43</sup> Furthermore, the large parenchymatous ray cells between the fibrous wood are unligified, with thin walls, and may serve as water storage tissues in roots, thereby helping the plants to withstand dehydration and prevent root shrinkage under drought conditions.<sup>44</sup>

Druse crystals are widely distributed in nearly all the tissues of *C. rosea* examined, from the stem epidermis to its cortex and pith, as well as the cortex and ray cells in the roots. These crystals are multifaceted stellate and roughly spherical in shape. The energy-dispersive X-ray spectroscopic (EDS)-spectrum of druse crystals revealed the presence of high amounts of calcium, followed by those of carbon and oxygen, with all three elements representing more than 99% of the total crystal content. This indicated the occurrence of calcium oxalates (CaOx) in *C. rosea*. CaOx crystals are formed from endogenous oxalic acid and calcium from the environment.<sup>45</sup> The functions of CaOx crystals, including Ca ion regulation, mechanical support, and protection against grazing depend upon their amount, morphology, and distribution in tissues.<sup>45–47</sup> Similar to the dense spines and glochids protecting *C. rosea* against

cattle grazing, CaOx crystals in the epidermis and cortex also help prevent herbivory.<sup>45,46</sup>

CAM photosynthetic pathway in *C. rosea*, similar to most cacti and other succulents, represents a physiological adaptation to arid and semi-arid habitats,<sup>23,48</sup> as this pathway exhibits high water-use efficiency, (high carbon gains per unit of water lost).<sup>27,48</sup> Although most plants with a CAM photosynthetic pathway grow slowly, the growth rates of *C. rosea* stem segments are relatively high under a favorable temperature range (from approximately 25°C to < 30°C) and as exhibited at Hiznah (the study site). These characteristics improve the ability of plants to vegetatively reproduce and help ensure the rapid expansion of the species. This temperature range may represent the maximum favorable temperature for CO<sub>2</sub> uptake, as most cacti have an optimum temperature for CO<sub>2</sub> uptake of < 24°C.<sup>49</sup> Additionally, most highly productive cacti inhabit areas with annual rainfall exceeding 300 mm yr<sup>-1</sup>,<sup>49</sup> similar to that of the study site.

## 5. Conclusions

The high invasiveness of *C. rosea* at Baljurashi probably reflects the high adaptability of the species to new habitats, particularly rocky niches and other microhabitats. Furthermore, the morpho-anatomical characteristics of *C. rosea* ensure a high water-storage ability and reduce water loss. Moreover, the CAM photosynthetic pathway, high growth rate, and highly effective defense mechanisms against herbivores and insects contribute to a successful invasion by this species. Therefore, it is important to design risk assessment plans for the proactive control and management of this species to prevent its expansion and invasion into other areas. With integrated planning, containing *C. rosea* on-site will be an attainable goal.

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