



Research

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Hierarchical structures of cactus spines that aid in the directional movement of dew droplets

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Three species of cactus whose spines act as dew harvesters were chosen for this study: *Copiapoa cinerea* var. *haseltoniana*, *Mammillaria columbiana* subsp. *yucatanensis* and *Parodia mammulosa* and compared with *Ferocactus wislizenii* whose spines do not perform as dew harvesters. Time-lapse snapshots of *C. cinerea* showed movement of dew droplets from spine tips to their base, even against gravity. Spines emanating from one of the areoles of *C. cinerea* were submerged in water laced with fluorescent nanoparticles and this particular areole with its spines and a small area of stem was removed and imaged. These images clearly showed that fluorescent water had moved into the stem of the plant. Lines of vascular bundles radiating inwards from the surface areoles (from where the spines emanate) to the core of the stem were detected using magnetic resonance imaging, with the exception of *F. wislizenii* that does not harvest dew on its spines. Spine microstructures were examined using SEM images and surface roughness measurements (R_a and R_z) taken of the spines of *C. cinerea*. It was found that a roughness gradient created by tapered microgrooves existed that could potentially direct surface water from a spine tip to its base.

This article is part of the themed issue 'Bioinspired hierarchically structured surfaces for green science'.

1. Introduction

Even though the surface of the Earth is made up of about 70% water, only 2.5% of this is fresh water that is fit for human use. The majority of this fresh water is tied up in glaciers or is deep underground [1]. Water shortage is currently an ongoing global concern, which is reflected in the fact that water scarcity is one of the United Nations' Millennium Development Goals [2]. It is imperative that this water need is addressed and, with a growing global population, novel ideas must be explored. Dew, fog and rainwater collection has taken place for hundreds of years, but to date only minimum information based on nature has been used to inform the design of such harvesting devices. Unlike fog and rain water, dew is a source of water that has the potential to be exploited all year round, with moisture always being present in the air to a greater or lesser degree depending on the humidity [3]. With this in mind, a review of airborne moisture harvesting species of plants and animals dwelling in arid regions was carried out by Malik *et al.* [4]. That review stimulated this particular study on cacti that are able to survive in arid regions of the globe.

The Atacama Desert is the driest place on the Earth [5] and is host to the cactus *Copiapoa cinerea* var. *haseltoniana*. This particular species of cactus was observed to condense dew on its spines [6, p. 67] and so became a focus of this study, together with two other known species of cactus from different regions that were also observed to condense dew on their spines, namely *Mammillaria columbiana* subsp. *yucatanensis* and *Parodia mammulosa*. *Ferocactus wislizenii* was also considered because according to Shreve, 1916 (cited in [6]) dew does not condense on its spines. Previously, the dew-harvesting efficiency of these four species of cactus was examined and the hydrophilic/hydrophobic nature and microstructure of their spines were considered [7]. It was found that *C. cinerea* was the most efficient dew harvester of the four species and that only the spines of *F. wislizenii* did not condense dew droplets, due to their hydrophobic nature, most probably due to the pronounced microstructures found on their spines.

As a consequence of this previous work, the current study was formulated with the aim of gaining deeper understanding of what happens to the dew droplets that form on the dew-harvesting spines and why *C. cinerea* is the most efficient at harvesting dew. Koch *et al.* [8] discuss the evolution of such plants that inhabit desert regions and how they have evolved structural and functional relationships that can inspire future smart surfaces, which is the aim of this particular research (i.e. to inform the design of a future biomimetic water-harvesting device).

Other studies have focused on fog water; that is, Ju *et al.* [9] observed fog droplets being directed even against gravity from the tips of *Opuntia microdasys* to their bases and Cao *et al.* [10] also noted the directional movement of fog water on the conical spines of cacti. In fact, biomimetic-inspired microstructured surfaces have been found to enhance surface transportation of water [11]. Unlike such studies that have focused on fog water harvesting on cactus spines, the spines of cacti have also been found to be an important feature in increasing the amount of dew harvested by certain cactus species [7]. Thus, the spines were the main points of interest in this study with the aim of informing a future airborne harvesting device. It has been pointed out by Ju *et al.* [9] that, at this point in time, it is unclear how cacti use fog harvesting by their spines. With this in mind, this study's focus has been to better understand how cacti use airborne moisture.

The challenge of this particular research study has been to assess how and if dew droplets move along cacti spines and whether there is any evidence to suggest that the dew from these spines is transported internally to the plant through the areoles. Assessment of these water movement mechanisms has stemmed from the fact that this study has broad interest across many disciplines and, as a consequence, has been uniquely positioned with regard to access to measurement equipment. This has included the use of magnetic resonance imaging (MRI) and other techniques to determine the transport of water on the surface of the cacti and within its stem with the focus being on whether cacti use dew droplets as a source of water, other than ground water transported by their root system. To achieve this, an initial assessment was conducted to determine whether the dew droplets on the spines move and if so, in which direction. The stem of the plants was also examined to evaluate for vascular tissue, thus further assessing the transport of water.

2. Material and methods

The work in this study has been to explore the movement of dew droplets on the spines of the cactus under investigation to assess what happens to these surface droplets. As *C. cinerea* was found to be the most efficient at harvesting dew [7], it was chosen for time-lapse imaging of dew droplets that had nucleated on its spines, at the end of a dewy night. This was followed up with further exploration of the cactus stems and spines to yield further information, to piece together to gain a deeper understanding of how the cactus manages and uses this harvested water.

(a) Dew droplet movement on *Copiapoa cinerea*

Copiapoa cinerea was placed outside on a dewy night for dew droplets to form on its surface. Before sunrise, the plant was then moved to a position that was shielded from wind and direct sunlight (from the rising sun) to minimize any potential evaporation. A Dino-lite camera was then used to take time-lapse images of the plant. The lens of the camera was adjusted until the individual dew droplets on the spines were resolved. Initially, images were taken every 15 s over a 5 min period, but this did not prove long enough and so a longer time frame was chosen based on initial observations on the plants following a dewy night.

To assess dew droplet movement, the time-lapse images of *C. cinerea*, covering a period of 30 min, with a frame rate of 1 every 2 min (i.e. 15 frames in total), were analysed. Six clearly visible and easy-to-measure spines with an unobscured view of dew droplets were selected. Dew droplet movement was analysed by measuring an approximate droplet distance travelled over the time taken. As an average spine length was known for this species of plant (i.e. 8.6 mm), a series of frames was input into a bespoke image analysis software package. A spine was chosen and from this, the distance of a dew droplet from the spine base (at the areole) to their location further up the spine was measured. Movement was then determined by repeating this for a series of images for the same spine.

Three spines were analysed over a 10 min interval (using images 1 and 5) and the other three spines over a 22 min period (using images 1 and 11). Even though this experiment was not repeated, dew droplet movement had been observed previously and hence was followed up with movement analysis. Each spine was considered a unique data point that when analysing several could be considered repetition of this investigation under the same conditions.

(b) Fluorescent nanoparticle experimentation

In order to explore whether or not water is transported along the cactus spine into the body of the plant, the spines were immersed in distilled water containing the fluorescing agent FluoSpheres® Carboxylate-Modified Microspheres (0.02 µm, yellow-green fluorescent (505/515), 2% solids, from Life-technologies™). The aim was to assess movement of water on the surface of the spines of *C. cinerea* and into the stem of the cactus. This was explored using a Nikon A1SI laser scanning confocal microscope. For this case, a 488 nm laser line was used for fluorescence excitation and a 500–560 nm wavelength emission window was set for each image. As the fluorescent microspheres were 20 nm in diameter, they were not too large to block any microchannels on the surface of the spines for which a tip average channel width is approximately 3.6 µm and a base average channel width of approximately 5.1 µm applies. Thus in the event that transport occurred, the fluorescing particles were considered small enough to pass through the areoles into the stem. This was considered to be a pilot study, simply to gauge the potential to test for the movement of water along spines into the stems.

Within this experiment, the spines of the plant were dipped in the fluorescent liquid for 1 h. The spines were still attached to the plant and emanated from one of the areoles on the stem. Care was taken to ensure no other part of the plant, including the areole, touched the fluorescent liquid (figure 1a). After 1 h, the section comprising the spines and areole was removed using a blade while ensuring it did not touch the area of the plant which had been in contact with the

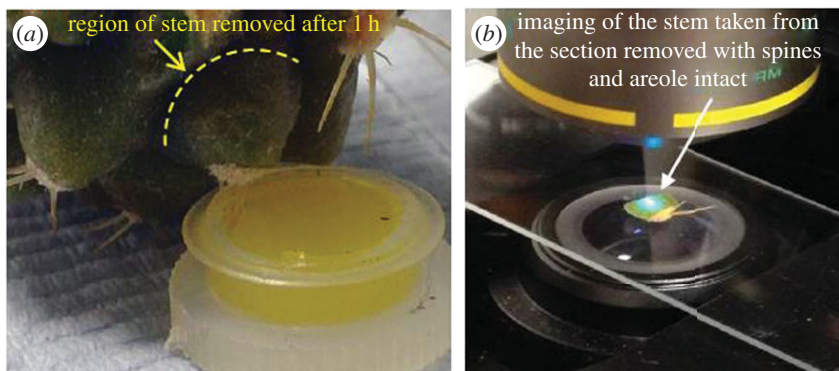


Figure 1. Fluorescent testing on *C. cinerea*. (a) Spines attached to whole plant dipped in fluorescent water for 1 h with the position of the cut indicating the area of the stem that was removed (after 1 h) and (b) imaging of the stem of *C. cinerea* after 1 h of spines being dipped. (Online version in colour.)

fluorescent water (i.e. the spines). The position of the cut is marked in figure 1a and the slice being imaged is shown in figure 1b. As the confocal microscope was not able to penetrate deeply into the stem, a portion of the removed stem had to be sliced in half to establish if there was any fluorescence present within. It was cut towards the areole to make certain that no fluorescence was dragged through the stem from the spine region.

Before these images were obtained, a drop of the fluorescent water was placed onto a slide and imaged in order to isolate the fluorescent particle wavelength. This enabled the fluorescent wavelength spectrum profile to be used in order to detect the particles in the experiments. For this case, a wavelength window was set between 500 and 560 nm for each image.

(c) MRI imaging

Stem images were taken using a Siemens Magnetom Skyra 3T MRI system. A T2-weighted imaging protocol was used (with echo time (TE) of 95 and repetition time (TR) of 3330) to acquire transverse and longitudinal cross-sectional planar images having a resolution 512×512 matrix at a bandwidth of 220 MHz and a slice/gap of 2.0/0.6 mm. The T2 fast spine echo with a field of view of 180/150 mm was chosen, due to its sensitivity in detecting regions of water within the cacti and, as a result, its ability to highlight localities within the cactus stems which are made up of vascular bundles. Each cactus was placed within the MRI scanner and imaged using the 32 channel phase array head coil. Cross-sectional images were acquired in the three planar regions, with each cactus having been localized in the three directions.

(d) Spine microstructures

The use of SEM images to better understand cacti spines and their surface structures [12] along with any ecological significance is a well-known method and one that this study has used [13]. A Hitachi S-4800 field emission scanning electron microscope (SEM) was used to capture images of the microstructure of spines for all four species of cacti. No coating was used in the acquisition process, giving images that were not contaminated by a deposited layer. This did result in some negative charge build-up on the spine surfaces if they were focused on at length. A low accelerating voltage (1 kV) was used throughout as the spines were deemed susceptible to charge and a mixture of upper and lower detectors was selected. For each spine, within 30 min of its removal from the plant, images were captured using the SEM. SEM images were taken at a magnification of $150\times$ at the tip, mid-section and base of each spine type (i.e. radial and central) for the four cactus species.

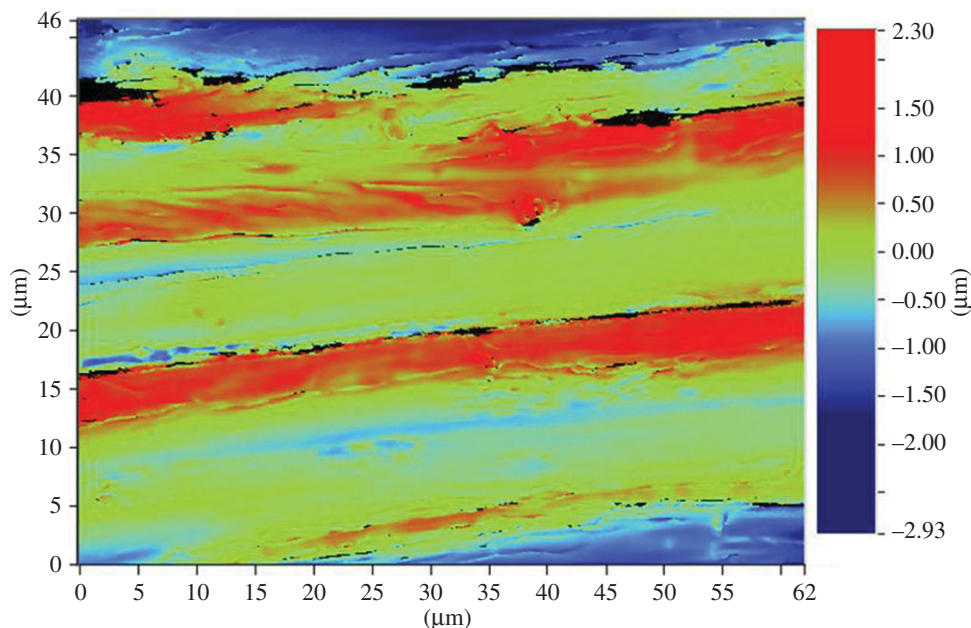


Figure 2. WLI surface roughness profile image taken at the base of a *C. cinerea* spine.

Alongside these SEM images, a white light interferometer (WLI) was used to capture three-dimensional surface profile images and data of the spines of *C. cinerea*. A Veeco WYKO® optical profiler was used to gather surface topography information using a combination of constructive and destructive light wave interference that is a non-contact method. The vertical scanning interferometry mode was used with a $1\times$ scan speed to ensure that as many data points as possible were captured (at higher speeds it was found to be less accurate as the profiler missed data points).

A back-scan of approximately $10\text{ }\mu\text{m}$ was set for each scan, which is the height above the top focal point. The length of each scan was approximately $50\text{ }\mu\text{m}$. A modulation threshold of 2% was set. During the processing phase of the surface profiles, a cylinder and tilt option was used to address the cone-like spines' geometrical curve, effectively flattening the macro profile while not altering the surface profile.

Surface roughness profiles were obtained of the surfaces of the spines at the tips and base of *C. cinerea* (figure 2) from which the grooves of the spines can be seen. These roughness profiles were used to extract R_a and R_z data at their tip and base. R_a is a measurement of the average roughness over a designated area and is the typical surface roughness measurement used [14] whereas R_z is a measure of the roughness depth. These measurements were used to further assess whether there was a surface roughness gradient from the tip to the base of these spines.

3. Results and discussion

(a) Dew droplet analysis on *Copiapoa cinerea*

Analysing the time-lapse images of dew droplets, the drops show clear movement along the spines of *C. cinerea*, towards their bases, even against gravity. It can be seen that the speed of dew droplets along these six spines was unaffected by spine orientation (figure 3). Speeds of 8.4 mm h^{-1} , 13.2 mm h^{-1} and 16.2 mm h^{-1} were measured over 10 min with droplets having moved a distance of 1.4 mm, 2.2 mm and 2.7 mm, respectively. Over 22 min, speeds of 7.1 mm h^{-1} , 7.36 mm h^{-1} and 5.18 mm h^{-1} were measured with droplets having moved 2.6 mm, 2.7 mm and 1.9 mm, respectively (figure 3). Several factors that must be considered as the driving force for this movement are surface roughness gradients, spine microstructures, the conical shape of a whole



Figure 3. The measured speed of dew droplet movement on six different spines of *C. cinerea*. Image of *C. cinerea* which shows which spines were analysed and the respective dew droplet distance travelled in millimetres per hour for varying spine orientations (each arrow points to the droplet of dew that was assessed for movement). (Online version in colour.)

spine, droplet coalescence and any thermal gradients. The dew drops that move along the spines can be seen to disappear through the areoles presumably into the stem of the plant.

When analysing the shape of these dew droplets, many could be seen to have an advancing contact angle (θ_A) that was greater than the receding angle (θ_R), whereby θ_A was closer to the spine base than θ_R . That the spines are conical in nature creates a Laplace pressure gradient that effectively drives the droplets from the regions of smaller radius (spine tip) to that of the larger radius (spine base), where contact angle hysteresis caused the droplets of water that nucleated on the spine surface to move, even against gravity, towards their bases. This Laplace surface gradient has also been reported for other species in nature [4], such as a wetted spider silk that was found to have cone-like structures [15], the spines of a fog-collecting cactus [9] and a Namib Desert grass [16]. While some species of cacti have flattened spines, such as *Sclerocactus papyracanthus* [17], in general, cactus spines can be considered to be conical in nature [18] but do vary considerably in size and dimensions and, if not straight, can be hooked, twisted or curved with an array of colours and texture [19]. The dew droplets are further driven from the tip to the base of the cactus spines by the surface roughness gradient that was found to be higher at the tip ($R_a = 0.71 \pm 0.064 \mu\text{m}$ and $R_z = 10.23 \pm 0.41 \mu\text{m}$) which had narrower microgrooves compared with the spine's bases that had wider microgrooves (and surface roughness parameters, $R_a = 0.56 \pm 0.14 \mu\text{m}$ and $R_z = 7.65 \pm 2.45 \mu\text{m}$). This gradient of roughness creates a wettability gradient which gives rise to the surface free energy gradient that acts on the droplets.

Lorenceanu & Qu  r   [20] studied the movement of water droplets against gravity on a conical wire and identified the Laplace pressure gradient as the decisive force. However, the wettability of a surface may also play a role in the harvesting of dew on cactus spines and is something that future research could explore. In fact, Luo [18] discussed the movement of fog droplets along conical cactus spines and they developed a model to interpret the movement of barrel-shaped droplets driven by liquid pressure differences within the drop. Even if the spine shapes are not conical, all are tapered from their base to their tip, which could also drive surface droplets that have formed on the spines from dew or fog to move from the area that has a lower cross-section radius to the region of higher radius [21].

The results gained above justified further analysis of the movement of water on the spines (using fluorescent labelled water) and within the stem of the plants (using MRI scans).

(b) Fluorescent nanoparticle imaging

Having captured time-lapse images of dew droplets on the surface of *C. cinerea*, which showed the drops moving from the spine tips to the bases, this was further tested using fluorescent labelled

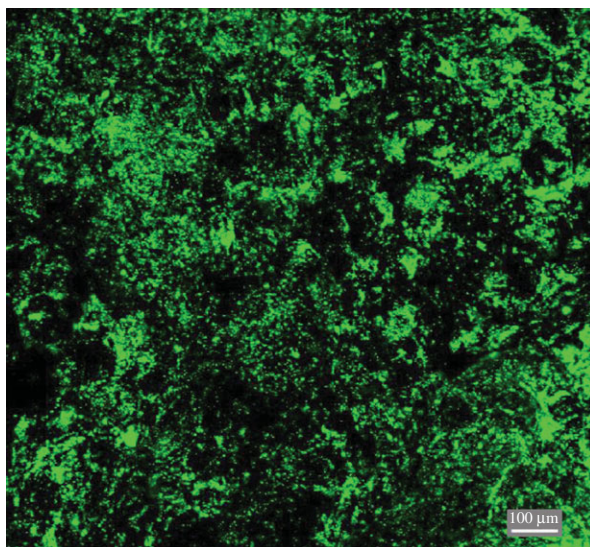


Figure 4. Distribution of fluorescent nanoparticles in the stem of *C. cinerea*.

water to assess for water transport from the surface of the spines into the stem of the plant using a Nikon A1SI laser scanning confocal microscope as described above.

As described earlier, an image of a sliced section of stem was taken and is shown in figure 4. The focus of the microscope was positioned at the furthest point from the spines, on the cortex of the stem (figure 1*b*) to determine whether water (labelled with fluorescence) had travelled along the spines, through the areole and into the stem of the plant. Figure 4 shows clearly that fluorescing particles can be seen throughout the imaged region of the spine.

(c) MRI imaging

Ju *et al.* [9] discussed how the areoles consist of trichomes which are conical features that create a strong capillary force which rapidly absorbs water that comes into contact with them. This process has been explored in this study, initially observing dew forming on the spines of all but *F. wislizenii* and finding that time-lapse images showed droplets moving along the spines and disappearing into the areoles and finding fluorescent water in the stems, the four plants were placed in an MRI scanner and images were taken (figure 5).

It was clear to see from these images that there was not only a change in density from the known core cylindrical vascular bundles, but also similar dense regions forming lines from the central region to the spines (and thus areoles from which the spines emanate; figure 5*a–d*). The exception to this was *F. wislizenii* (figure 5*e,f*).

This can be more clearly seen by superimposing an MRI image over a Dino-lite image of the same plant to illustrate the spines that emanate from the stem exterior (figure 6). It is clear that these spines align with the change in density of these darker areas, the apparent vascular threads, thus the spines are like an external root system that directs water into the stems.

It can be concluded that the species of cactus, in this study, that are known to use their spines to harvest dew, possess an internal pathway for water to be transported from the spines to the stem central cylindrical vascular tissue. These outwardly radiating vascular threads, mentioned by Powell & Weedon [22], act as a mechanism that transports water to the cactus stem cortex (which stores the water). However, no link could be found in the literature between these vascular threads and that of transporting dew or fog water from the spines of a cactus.

There have been some previous studies that have looked at MRI scans of cacti. Zotev *et al.* [23] studied three-dimensional MRI images of the cactus species *Gymnocalycium mihanovichii* Hibotan,

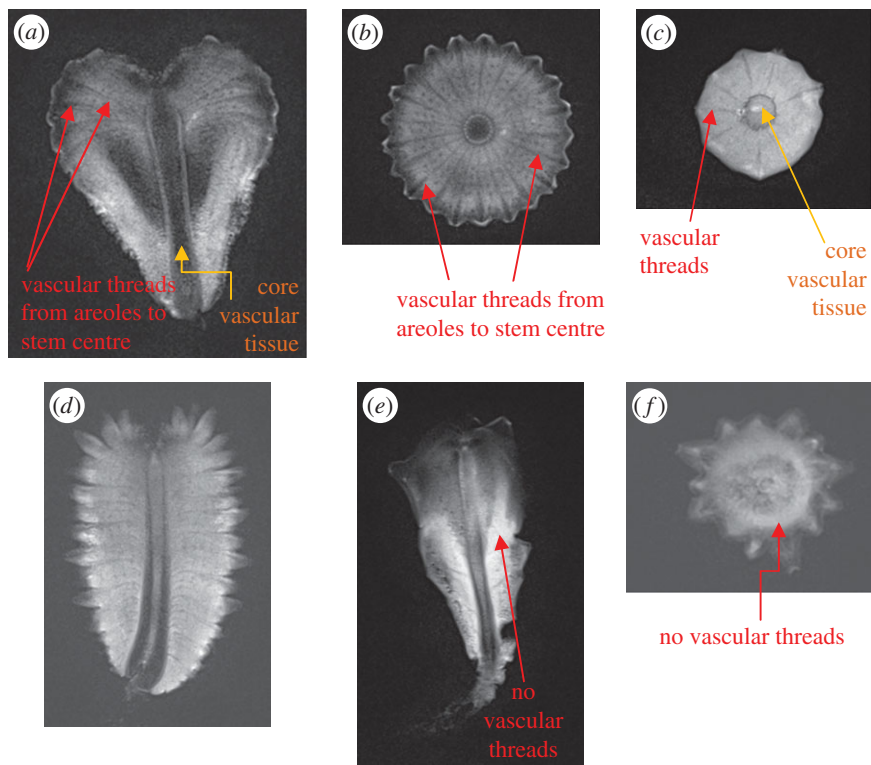


Figure 5. MRI images of four species of cacti. MRI images of (a) longitudinal cross section of *P. mammulosa* showing changes in density from the areoles to the cylindrical core vascular tissue and central pith, (b) top-down transverse plane image of *P. mammulosa*, showing changes in density from the areoles to the cylindrical core vascular tissue and central pith, (c) top-down transverse plane image of *C. cinerea*, showing changes in density from the areoles to the cylindrical core vascular tissue and central pith, (d) longitudinal cross section of *M. columbiana* showing changes in density from the areoles to the cylindrical core vascular tissue and central pith, (e) longitudinal cross section of *F. wislizenii* showing no changes in density from the areoles to the cylindrical core vascular tissue and central pith and (f) top-down transverse plane image of *F. wislizenii* showing no changes in density from the areoles to the cylindrical core vascular tissue and central pith. (Online version in colour.)

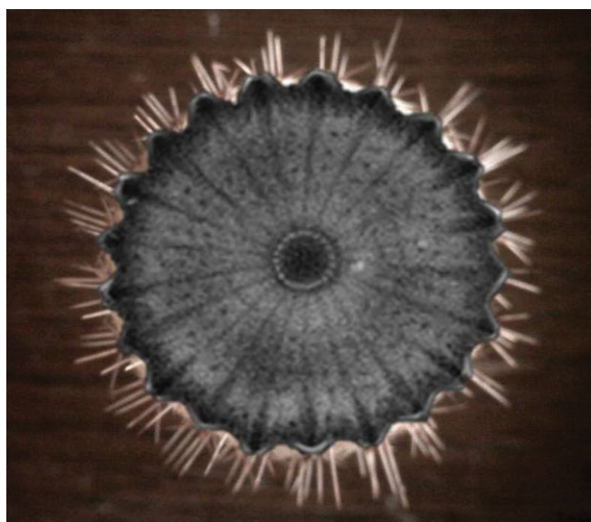


Figure 6. MRI image of *P. mammulosa* placed over a Dino-lite image of the same plant. (Online version in colour.)

but the image resolution was not clear and vascular threads were absent. Burdková & Kriz [24] and Pokludová & Gescheidtová [25] took MRI scans of a Euphorbia cactus to study their stems, but again vascular threads could not be seen, in the same way that was found for *F. wislizenii* in this study.

(d) Surface spine microstructures

SEM images at three points along a spine are presented in figure 7, all taken at a magnification of 150 \times . It can be seen from the images at the tip, mid-section and base of each spine that there is a variation in microstructures (figure 7). *Copiapoa cinerea*, the most efficient dew-harvesting species, surprisingly has microfins on the mid-section of its spines (as does *M. columbiana*). These are not as dense or as big as the micro fins seen covering the spines of *F. wislizenii*. Dew has been observed to form on these finned regions of *C. cinerea* and is clearly not a deterrent in the formation of dew, if they are not compactly arranged as is the case with the fins of *F. wislizenii*. As was discussed in Malik *et al.* [7], these microfins, which have also been observed on the *Turninicarpus* cactus by Mosco [26], render the surface hydrophobic and could explain their unsuccessful ability to harvest dew on their surfaces. Furthermore, Malik *et al.* [7] found that the microgrooved nature of *C. cinerea* (along with the other dew-harvesting spines of *P. mammulosa* and *M. columbiana*), which were narrower at the tips of the spines compared with the wider grooves at their bases, creates a roughness gradient that drives water from the tip to the base of the spines; something that was also discussed by Roth-Nebelsick *et al.* [16] for the microgrooves of the *Stipagrostis sabulicola* Namib grass. These microgrooves have been found as convergent structures that aid in the directional movement of harvested airborne water [4].

It should be noted that all tips were fairly free from large microstructures, including *F. wislizenii* but no dew was observed on any part of *F. wislizenii* spines (other than in one solitary occasion). The mid-sections of all the spines with the exception of the small radial spines of *M. columbiana* have microstructures that protrude from their surfaces. These microprotrusions are not as densely compacted as those on *F. wislizenii* with *P. mammulosa* being the only one of these having tile-like microstructures with the tile ends protruding. These small, scattered microstructures could aid in the formation of dew on the spine surfaces by acting as condensation focal points.

The findings of the water uptake shown by the fluorescing particles found in the stem of *C. cinerea* must be taken into account here. This shows strong evidence of a transport system from the spines of some cacti and into the body of those cacti species in which the surface water flows on leaving the spines. With regard to wettability, the contact angles obtained by Malik *et al.* [7] show the spines of three of the cacti species to be hydrophilic, with approximate contact angles of 60°, 35° and 40° for *C. cinerea*, *M. columbiana* and *P. mammulosa*, respectively. The spine of *F. wislizenii* on the other hand was found to be hydrophobic with an approximate contact angle of 120° (this could be explained by these microstructures trapping air and creating a surface that is hydrophobic). Thus as contact angle is inversely proportional to the degree of wetting, it can be stated that, with the exception of *F. wislizenii*, the spines of the other three species have a high degree of wetting, and *F. wislizenii* spines possess a low degree of wettability. Furthermore, as is discussed in detail by Quéré [27], the hydrophobic or hydrophilic substrate has wetting characteristics that are enhanced by surface roughness. That is, surface roughness increases the degree of non-wetting on a hydrophobic surface as a droplet will rest on the surface protrusions in a Cassie–Baxter state [28]. However, if roughness increases on the surface of a hydrophilic material, the surface will become more hydrophilic due to surface wetting characteristics being modified that lower the contact angle of the surface [29]. It is clear from the SEM images that the central curved spines of *F. wislizenii* have the greatest number of surface microfeatures, closely followed by the straight radial spines of *F. wislizenii*; these would effectively cause these spines to have high surface roughness parameters, which would increase their hydrophobicity.

The fact that *C. cinerea* survives in the driest place on the Earth, with no rainfall at times for years, would indicate that it uses other forms of moisture to survive. Both dew droplets and fog are present in the Atacama Desert and as such would act as a constant source of water for these

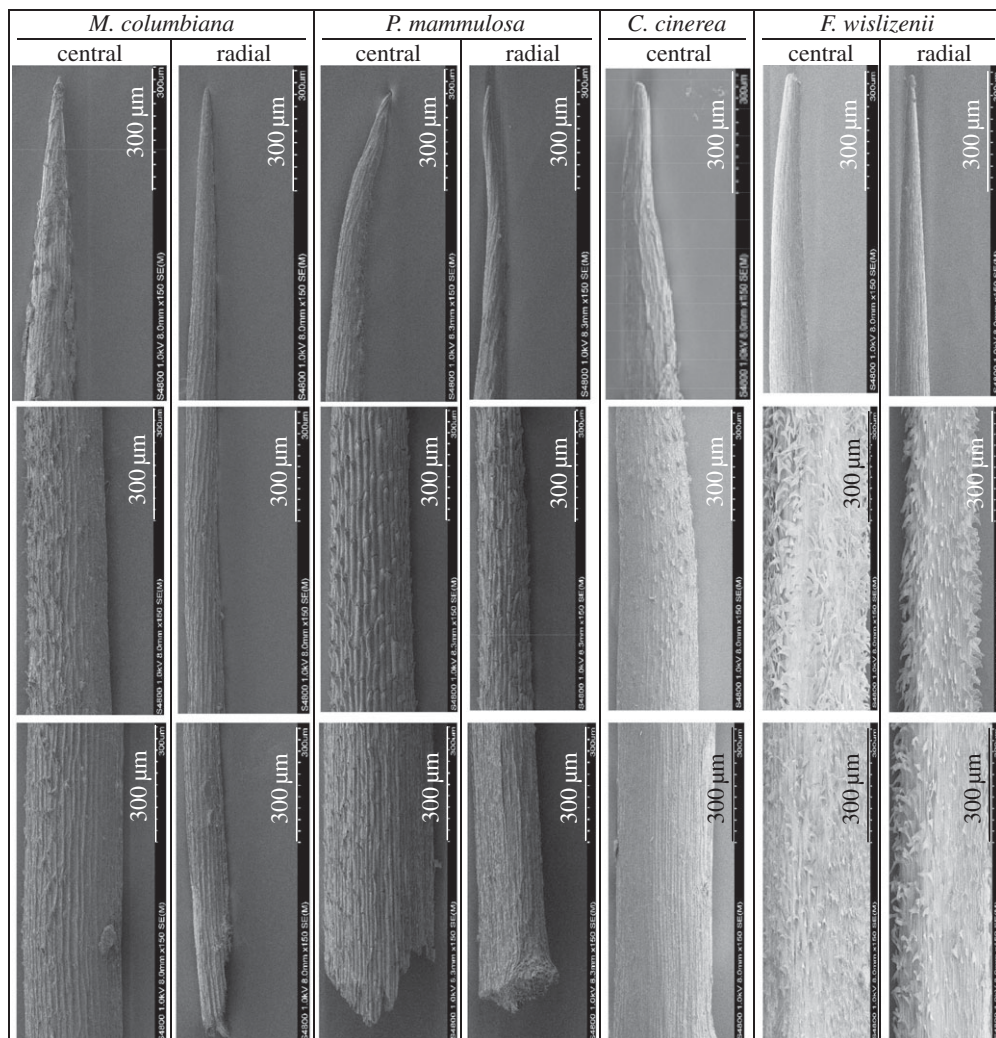


Figure 7. SEM images showing the spine microstructures of the four cacti under investigation. SEM images taken with a magnification of $150\times$ at the tip, mid-section and base regions of the spines.

plants. When it comes to both fog and dew water, the droplets that condense on the cactus spines, would have to have a mechanism such that water is transported along the spine to its base where it can enter the plant through the areoles.

Even though one cannot necessarily generalize with regard to the different cactus species spines (as seen from the SEM images, their make-up is quite different), the MRI images showing the presence of vascular tissue stretching in a line from the areoles at the stem surface to the main cylindrical vascular bundles at the stem core validate and back the line of thinking that dew or fog droplets are transported along the spines and used by the plants.

Having found that dew droplets move from the tip to the base of the spines of *C. cinerea*, the surface roughness parameters of these spines were measured at the tip and the base to further assess the surface roughness. Using the WLI, R_a and R_z were measured (figure 8) and it was found that there was a roughness gradient on these spines which would encourage water to be driven from the rougher area to the less rough regions by the effective gradient of surface free energy (i.e. from the tip of the spines to the base).

The tips of *C. cinerea* spines possess narrower microgrooves compared with their wider base microgrooved regions. Considering both the roughness parameters (R_a and R_z), this gradient

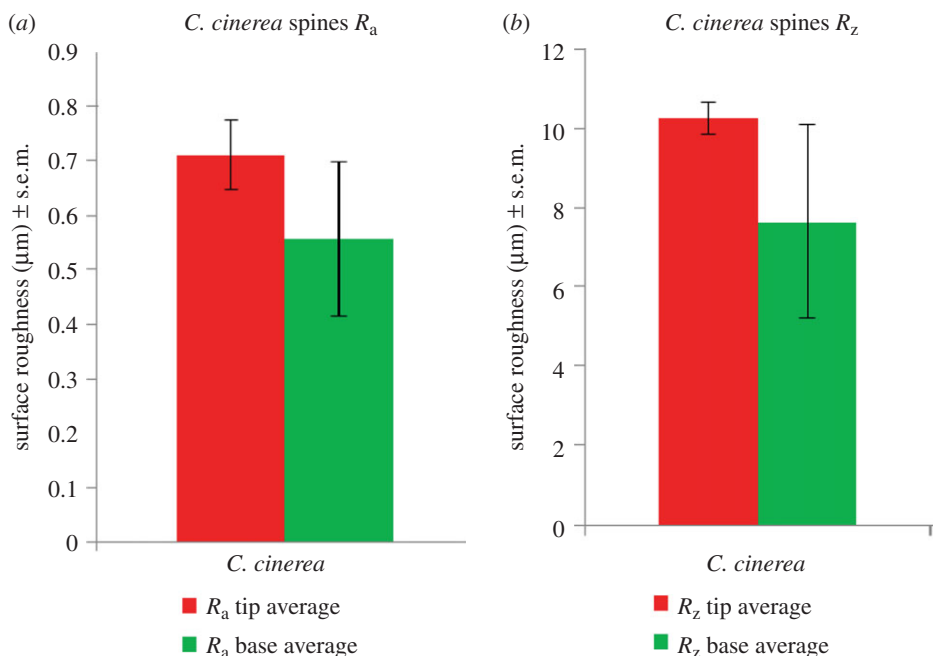


Figure 8. Arithmetical mean surface roughness parameters at the tip and base of *C. cinerea* spines for (a) parameter R_a and (b) parameter R_z . (Online version in colour.)

was found for both these parameters. This could help to explain the observed (during the time-lapse images of dew droplets on their surfaces) directional movement of water from their tips to their bases.

4. Discussion

As laboratory conditions could not be used due to condensation in a climate chamber being totally different to dew formation on the plants that have cooled by radiative cooling and dew forming on their surface, plants had to be observed on dewy nights. Because dew droplets do not collide with the surface as is the case with fog, but instead form on a surface that is at or below dew point temperature, the cacti surfaces had to cool radiatively.

Hence, this being a novel area, the aim has been to uncover new processes which would then require further detailed testing. For dew droplet movement to be assessed, weather conditions had to be favourable for dew to form (i.e. high relative humidity, little or no wind and no solar heating and clear skies) on the cacti spines (and stems) to be analysed. It should be noted that even though there would be some evaporation, this study's observations and measurements showed the droplets moving from the tip to the base of the spines (which was also observed on other occasions in the field) and captured the same using time frame images. The plant was removed from the rising sun (and subsequent solar heating) and from windy conditions to reduce the effect of evaporation and to ensure no further dew droplets formed on the spines (as there was still a high relative humidity). Thus, only movement of water was assessed, excluding all of these other influences that would interfere with these observations.

Dew droplets that formed on the spines of *C. cinerea* following a dewy night were observed to move even against gravity towards the base of the spines. Only the most efficient dew harvester (of the four species examined in this study), *C. cinerea*, was focused on. This movement was further explored with the use of fluorescent water. The spines emanating from one of the areoles of *C. cinerea* was submerged for an hour in water labelled with fluorescent particles. The spines

along with the areole and region of the stem they were attached to was removed and the stem was imaged. Fluorescence was transported from the spines to inside of the plant.

MRI images highlighted a clear difference within the stems of the three species whose spines harvest dew, compared with *F. wislizenii* whose spines do not act as dew harvesters. That is, the stems of all but *F. wislizenii* contained inner channels (known as vascular tissue threads) from the areoles that emanate from spines on the plant's surface to the stem's core cylindrical vascular tissue and pith. The function of these channels is probably part of a mechanism to use airborne moisture for the plant's survival in arid climates.

The MRI images support the finding that dew condenses on the spines of the cactus species in this study, because the water transporting channels from the areoles to the stem's centre occur in three of the species examined (whose spines are known to harvest dew) yet are absent in *F. wislizenii* (whose spines are known not to harvest dew). Even though this study was restricted in looking at a young *C. cinerea*, which is known to live in dewy/foggy climatic conditions, future studies could look at whether these features (that of the microstructures on the spines, movement of dew droplets and vascular threads from the areoles to the core of the stem) are present in adult plants of the same species.

We thus conclude that the spines' conical nature (or tapered geometry) gives rise to a Laplace gradient and along with the microstructures (which create a surface roughness gradient) effectively directs surface water into the stems, with the exception of *F. wislizenii*. It should be kept in mind that cactus spines are multifunctional [30], shading the stem of the plants from the sun [30,31], acting as a defence mechanism against predators, along with being a feature of moisture collecting [4,9]. Certain spines, such as those of *F. wislizenii*, may not have the function of facilitating dew water to aid their survival, which is what appears to be the case for *C. cinerea*.

5. Conclusion

This study demonstrates the ability of the spines of *C. cinerea* to direct dew from their tips to their bases and for this water to enter the stems through the areoles and to act as another source of moisture for the plants along with their root system. This may explain why *C. cinerea* is the most efficient dew harvester of the four species studied and could become key elements in any man-made dew-harvesting device. Future fabrication of the relevant macro- and microstructures of these cacti surfaces could enhance the amount of airborne moisture that could be harvested on a potential device, along with maximizing the amount of this condensed water that is driven into a collector. The challenge of designing such a device will be to balance macro- and microfabrication in an economically viable way such that the biomimetic inspiration it is based upon remains, as far as is feasible, as close to the inspired surfaces that were found to increase harvesting efficiency. This is a new area of research which provides the basis for understanding water transport on the spines of certain species of cacti and goes some way in understanding water uptake by these plants and their subsequent functional adaptation to their environment.

Competing interests. We declare we have no competing interests.

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