The upside-down water collection system of Syntrichia caninervis

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Desert plants possess highly evolved water conservation and transport systems, from the root structures that maximize absorption of scarce ground water1–4, to the minimization of leaf surface area6 to enhance water retention. Recent attention has focused on leaf structures that are adapted to collect water and promote nucleation from humid air7–9. Syntrichia caninervis Mitt. (Pottiaceae) is one of the most abundant desert mosses in the world and thrives in an extreme environment with multiple but limited water resources (such as dew, fog, snow and rain), yet the mechanisms for water collection and transport have never been completely revealed. S. caninervis has a unique adaptation: it uses a tiny hair (awn) on the end of each leaf to collect water, in addition to that collected by the leaves themselves. Here we show that the unique multiscale structures of the hair are equipped to collect and transport water in four modes: nucleation of water (awn) on the end of each leaf to collect water, in addition to that collected by the leaves themselves. Fluid nucleation is accomplished in the unique multiscale structures of the hair are equipped to collect and transport water in four modes: nucleation of water droplets and films on the leaf hair from humid atmospheres; collection of fog droplets on leaf hairs; collection of splash water from raindrops; and transportation of the acquired water to the leaf itself. Fluid nucleation is accomplished in nanostructures, whereas fog droplets are gathered in areas where a high density of small barbs are present and then quickly transported to the leaf at the base of the hair. Our observations reveal nature’s optimization of water collection by coupling relevant multiscale physical plant structures with multiscale sources of water.

One of the most common desert mosses in the world, Syntrichia caninervis is widely distributed across the drylands of the Northern Hemisphere from the Mojave Desert in the United States through parts of Europe, to the Gurbantunggut Desert in China10,11. Many moss shoots cluster as patches and cover the desert soil to make biological soil crusts which protect the delicate soil beneath (Fig. 1a,b). When the weather is dry, the mosses are dehydrated and appear dark brown or black in colour (Fig. 1c); however, precipitation events including dew, fog, mist or rain can rehydrate and turn the moss-patch covered surface green within seconds (Fig. 1d). A key feature of each moss leaf is a fibre or ‘leaf hair point’ (awn) growing out from its distal terminus. Our high-speed imaging and environmental scanning electron microscope (ESEM) reveals that the awns are adapted to collect water quickly (Figs 2 and 3b and Supplementary Videos 1–3). Recent studies imply that the moss awn may be important in terms of water collection and transportation. Tao and Zhang20 report that patches of moss with awns accumulate more dew than patches with awns experimentally removed. Their study shows that the presence of moss hairs correlates with a significant increase in absolute water content when wet and inversely correlates with water loss during the dehydration process; however, the mechanisms of water collection and retention were not elucidated.

Climatic variation has driven the evolution of unique plant structures that provide competitive advantages for survival in hostile environments1–3,13,14. For example, common survival strategies include: the minimization of the leaf surface area to reduce water loss8, hydrophobic leaf surfaces to maximize throughfall to the root system9, leaf structures designed to collect water10, energy gradients generated by the conical plant geometry and chemical characteristics of the surfaces to externally transport water droplets to advantageous places on the plant9, and extensive root systems for maximal collection of scarce ground water4,5. However, desert mosses have no true roots or ‘conventional’ water transport systems such as vascular bundles. Instead, rhizoids (root-like structures) anchor the plants to the ground and rely on their above-ground structures for water collection, transportation and storage. The moss species found in arid areas such as S. caninervis have adapted to the scarcity of water by developing other unique structures.

On average the S. caninervis moss shoots that we studied were 3–8 mm in height (including rhizoids), with about 20 leaves. A semitransparent awn grows out from the tip of the leaf (Fig. 1d) and appears white. In general, the awns are 0.5 to 2 mm long and have a slight axial twist. The base of the awn is 10–50 µm in diameter and continually tapers in circumference towards the distal end. Awns on the leaves of S. caninervis are extremely delicate, and as such do not offer protection from animals, as cactus spines do. It has been argued that the clusters of moss awns benefit the plant by blocking or reflecting harmful ultraviolet sunlight16. However, the sparse density of awns (one per leaf) suggests that ultraviolet protection is not the primary purpose of the awn (Fig. 1c,d). Whereas the awns make up a negligible area and volume when compared with the total plant, they correlate to more than 20% of the dew collection12. In a related five-year field study, we observed that the growth of the moss is diminished if the awns had been experimentally removed. Thus, one may infer that moss awns participate in water collection.

Previous studies and observations of nucleation and transport on spider webs, fine fibres, narrow leaves and spines8,17–19 give examples of water collections on fibre-like structures. However, most of these examples are of single water collection processes on slender bodies. Ju et al.7 reported that spines on Opuntia microdasys operate as a multifunctional integrated fog harvesting system.
However, the mechanisms of surface phenomena due to nano- and submicrometre structures were not experimentally supported. An ESEM has been used to observe the microscale water collection process occurring on *Cotula fallax*. That work revealed the special construction of fine fibres covering the leaves of *C. fallax* to be a three-dimensional hierarchical water collection and storage system. However, the mechanisms and relationship between the size of the features on the plant and the scale of the water collected and retained were not elucidated or discussed.

We hypothesize that four methods of water capture and transport are displayed by the awns of *S. caninervis*. Each type of water capture is directly related to the scale of certain geometric surface features (Fig. 4). The smallest longitudinal nanogrooves (marked by green arrowheads in Fig. 1h,j) have a characteristic size of approximately 200 µm.

Figure 1 | Morphology of *S. caninervis* and the associated awns. **a,b**, Biological soil crusts formed by *S. caninervis* in the Gurbantünggüt Desert, China (a) and the Great Basin, USA (b). **c**, Photograph of a dry moss shoot. **d**, Photograph of a rehydrated moss shoot. **e–g**, SEM photographs of the surface of a moss awn, including highly magnified views. **h**, A tilted high-magnification photograph of a surface moss awn, where micro- and nanogrooves are marked by yellow and green triangles, respectively. **i**, Local cross-section of the moss awn from a cutting plane marked by a red dashed line in **h**. **j**, Magnified view of the area enclosed by the blue box in **i**.

Figure 2 | Nucleation of dew on a moss awn surface. Time and pressure are increasing from **a** to **f**. **a–c**, The nanogrooves (purple arrowheads) are initially filled by nucleated water as pressure in the ESEM increases from 706.6 to 879.9 Pa, and the temperature stage is set to 4 °C. At this temperature, the vapour pressure of water is 813.5 Pa; a detailed discussion is presented in the Supplementary Information. **d–f**, Eventually the developing thin water film covers the nanogrooves (purple arrowheads) and fills the microgrooves (yellow arrowheads) of the awn as the vapour pressure is slowly increased. The moss awn moves within the field of view from **a** to **f** as it collects water. To help locate the positions of nano- and microgrooves, purple and yellow dashed circles mark two particles on the surface that are eventually filled with water. See Supplementary Video 1.
100 nm deep and 200 nm wide, and provide favourable nucleation sites by reducing the energy barrier for nucleation for dew collection (see Supplementary Information). Finely spaced longitudinal micro-grooves (marked by yellow arrowheads in Fig. 1h,i) are typically around 3 µm wide at the rim and 1.5 µm deep, and provide favorable fog (microscopic droplet) collection sites (see Supplementary Information). Small barbs along the length of the awn are angled slightly outwards and point towards the distal end (Fig. 1f), providing collection depots for water until droplets form and attain a size sufficient for the conical shape of the fibre to provide a path and energy for droplet transport from tip (∼5 µm) to base (∼40 µm). Colonies of S. caninervis are tightly packed and the cluster of awns on each leaf provide a splash reduction and collection method for rain droplet absorption (Supplementary Fig. 2). These modes are integrated into a water capture and transport system that appear to have evolved to maximize water collection. Similar integrated systems spanning several scales may have evolved in other plants14.

Nucleation, the smallest size of water capture, is the process by which a liquid water phase (dew droplet) is nucleated and grown from a gas phase that is saturated or supersaturated with water. In such a case there is no pre-existing liquid phase before nucleation of the dew. We hypothesize that specific surface structures of the awn are the sites of heterogeneous nucleation of dew. By analysing the free energy of heterogeneous nucleation from vapour onto the surface of the moss awn it is clear that nucleation is favourable in nanogrooves and that the half-groove angle (α < 90° defined in Supplementary Fig. 3) results in more favourable nucleation sites. We used an ESEM to observe the nucleation process (Fig. 2). In Fig. 2c, the first sign of condensed water appears on the surface of the nanogrooves (finely spaced lines marked by the violet arrowhead) as revealed by the disappearance of fine structure. The regions with dotted outlines show features that remain constant and in focus to show that the loss of fine structure on the nanogrooves is not a defocusing artefact. When exposed for longer periods of time to the same pressure and temperature, more water appears in the nanogrooves and eventually fills the microgrooves (Figs. 2d–f). This is due to continuing condensation of more water vapour on the previously nucleated water droplets and...
Figure 4 | Multifunctional hierarchical water harvest mechanisms of the moss awn. The concentric shaded areas illustrate the functional mapping A–D, between the size scales of the structures on the moss awn and the size scales of the water. The arrows show how the plant is a water collecting system consists of hierarchical mechanisms that work together efficiently capturing all available water. A: Nucleation improves the overall surface properties by providing a film of water. Overall wettability is improved, providing more favourable nucleation, fog harvesting (solid red arrow) and water transport (dashed red arrow). B: Fog collection (microgrooves) and water accumulation (barbs) prepare large droplets for transport (solid yellow arrow). C: Awn to leaf water droplet transport (conical awn) prepares the awn for the next set of droplets (dashed yellow arrow). D: Rain droplet splash is absorbed by the flexibility (cluster of moss shoots), hydrophilicity and shape (conical) of the awn (solid blue arrow). We theorize that the microstructures in a portion of the total water resources available to S. caninervis

Water film. In all observations it appeared that the initial nucleation and growth of the dew droplet occurred on nanogrooves within a microgroove or a shallow cavity. This is consistent with the theory of nucleation in a two-dimensional groove, a three-dimensional cavity or an interior corner, in which the change in free energy of nucleation ($\Delta G_{\text{nuc}}$) is more negative (more favourable) than the $\Delta G_{\text{s}}$ on a ridge, barb or pillar (see the Supplementary Information). Moving up in scale, fog consists of tiny water droplets with diameters of 0.2–100 µm (typically 1–15 µm) and contributes to a portion of the total water resources available to S. caninervis depending on the region. We theorize that the microstructures in the form of both grooves and small barbs on the awns play key roles in fog droplet collection. By applying a similar analysis technique to the one employed for the nanogrooves we can show that when $\delta < 0^\circ$ (wetting parameter defined in the Supplementary Information and shown in Supplementary Figs 3 and 4) fog collection proceeds spontaneously. In addition, wetting the surface by nucleation improves the likelihood of $\delta < 0^\circ$, emphasizing the importance of the nanogrooves (see the Supplementary Information). Photographic observations document that when the moss awn is exposed to fog, the droplets are captured along the microgrooves and coalesce into droplets larger than fog at specific locations (see Supplementary Video 2). When droplets in these locations become large enough, they are transported along the awn towards the leaf, and a new droplet grows at the same site; this process is repeated continuously throughout the course of the exposure to the fog droplets (Supplementary Videos 3 and 4). Further, the ESEM observations reveal that water tends to collect on areas of high barb concentrations (Supplementary Fig. 1g–i). These curious behaviours imply that the structurally heterogeneous high-density regions of barbs projecting from the surface accumulate water. To test this idea, the distribution of barbs on the moss awn was correlated with the positions of the water drop collection depots when exposed to fog. Awns were imaged from three angles in a scanning electron microscope (SEM) and the resulting images were stitched together (Fig. 3c–f) to determine the location and distribution of the barbs (Fig. 3a). The same awns were then placed in a fog field and high-speed videography of the drop growth and movement was correlated to the SEM images of barb distribution (Fig. 3a,b). Our observations show a tendency of the water droplets to be pinned to an area with a cluster of barbs (locations where peaks appear in the histogram, Fig. 3a). Typically, a newly formed smaller droplet is pinned to a barb cluster. The correlation of droplet position and barb cluster (histogram peak) is marked by the colour patches with solid outlines. With a continuous fog supply, droplets accumulate and cover more local barb clusters (e.g. two to three clusters in Fig. 3b). Owing to the irregularity of the shapes and surface features of the awns, there are some exceptions, such as a droplet pinned at the bent region (large local curvature). When a droplet is large enough, it moves to the base of the awn, sometimes at relatively high velocity. The size of the droplets on the awn are far below the capillary length for water, and thus the droplet movement is not gravitational; instead it is driven by the Laplacian pressure difference introduced by the conical shape of the moss awn. A similar mechanism has been reported, and an analytical model proposed wherein a drop on a conical wire is driven from tip to base by Laplacian pressure. Experimental evidence of fast-moving low-viscosity fluid along conical fibres (10 to 100 µm in radius from tip to base) has been observed.

At larger scales, rainfall (raindrops vary from 0.67 to 5 mm in diameter) is another significant, though inconsistent, water source for desert mosses. We propose that the high-density clusters of flexible leaves and awns provide a method for maximum retention of falling droplets by absorbing a majority of the impacting droplet and reducing losses from splashing. We postulate that when a droplet impacts a cluster, a majority of the droplet energy is absorbed by the flexible features and the fluid is quickly absorbed by the micro-structures of the leaf and awn. Smaller secondary satellite droplets moving outwards and are intercepted by awn(s) from base to tip (see Supplementary Video 5 and the blue arrow of Fig. 4). The capillary force introduced by the conical shape of the moss awn reduces the speed of the splash droplets in contact with the awn compared with airborne motion alone such that the entire droplet may eventually be captured by the moss. High-speed video captures the impact of simulated raindrops on a patch of dry moss (Supplementary Fig. 2a–d and Supplementary Video 5) with water impact on a dry soil surface from the same height (9 m, Supplementary Fig. 1e–g). Comparatively, there is only a rare tiny splash droplet travelling outwards from the moss patch along the moss awn after raindrop impact (Supplementary Fig. 2c); and these splash drops only travelled upwards to a relatively low height (shown in Supplementary Fig. 2d and Supplementary Video 5). This implies that a cluster of moss shoots reduces splash effectively and the rain drop is captured by the moss. The anti-splash rain drop absorption mechanism is especially important for the moss at the boundaries of the moss patches from which water is lost most easily but which have the greatest growth potential.

These observations of water collection and transport along the moss awn show that it is an integrated water collection system based on multiscale structures. Structures of different sizes interact with water of different scales, as shown by the hierarchical diagram of Fig. 4. Nucleation involves the smallest structures and is presented as the first level of hierarchy. When fog or rain is not available, nanogrooves harvest water when the atmosphere attains the dew point. In this case, water molecule clusters (of size less than 1 nm) in the gas phase cluster and condense on the nanogrooves of the moss awn to form a thin water film that eventually fills the nanogrooves and sometimes the microgrooves (Fig. 4, hierarchy A).
When fog droplets are available (of typical size larger than 1 μm), the microstructures (microgrooves and barbs) help collect and gather the impinging water into much larger droplets as shown in Fig. 4, hierarchy B. The non-uniform distribution of barbs creates clusters that collect water on the moss awn and prepares larger droplets for water transport (yellow arrow). Rapid water transport occurs when the droplets become large enough to move from barb clusters to the base of the awn as illustrated in Fig. 4, hierarchy C (further data shown in Supplementary Videos 3 and 4). The droplet can travel from the awn to the leaf as fast as 10–20 mm s⁻¹ when the water droplet size exceeds a critical value (transported tip to leaf in 50–200 ms). Once the detached volume of the droplet is moved to the leaves, the now-wetted moss awn is again ready to gather more water for the transport of another droplet to the leaf (dashed yellow arrow, Fig. 4).

Our results demonstrate that S. caninervis utilizes coupled multi-scaled structures to collect water from many available sources. S. caninervis is an example of how bryophytes adapt to scarce water environments by efficiently using their small structures, providing physics-based evidence of previously speculative function. We anticipate that comprehensive water collection and transport mechanisms unveiled by the moss awn will lead to the design and development of more efficient water harvesting and transport devices that can be employed in regions with scarce water resources. Further, we propose that it is likely that other plants utilize similar structural hierarchies for optimization of various biological processes from water collection to reproduction.

Methods

Materials. The moss samples (S. caninervis) were collected in Rush Valley, Utah, USA.

Morphology. Optical images of the moss were photographed with a digital camera (Canon SD11). The microstructures of the awns were recorded by a SEM, FEI XL30 FEG. Each awn sample was initially coated with Au/Pd 60/40% using a Quorum Q 150 T ES sputter, and a 1 μm Pt protective layer. The awns were then cut into cross-sections and imaged by a FEI Helios Nanolab 600.

Nucleation experiments. An ESEM, FEI XL30 FEG, was used to observe the nucleation process on awns. Each sample was attached to the stage with conductive tape and the temperature was set to 4 °C. Pressure in the ESEM chamber was controlled to adjust the relative humidity.

Fog harvest. Several moss awns were horizontally fixed and exposed to fog generated by a therapeutic humidifier. A high-speed colour camera (Phantom v1610) was used to film the fog collection process at 8,000 frames s⁻¹ (fps). The normalized barb distributions on each awn were reconstructed from stitched SEM pictures (FEI XL30 FEG) of each moss awn.

Rain drop impact. A high-speed colour camera (Phantom v1610) was employed to record the water impact on the moss clusters (dry and wet) at 16,000 fps. Droplets were released from 9 m and were between 2 and 5 mm in diameter.

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References


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Author contributions

N.W. and Y.Z. originated the research on S. caninervis and provided anatomical studies, both macro and microscopic. Z.P., T.T.T. and W.G.P. designed the experiments, and Z.P. and T.T.T. performed the experiments and analysed the data. Z.P. and W.G.P. proposed the mechanisms of nucleation on the moss awn. W.G.P., Z.P. and T.T.T. wrote the text.

Additional information

Supplementary information is available online. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to T.T.T.

Competing interests

The authors declare that they have no competing financial interests.