Advances in Research on the Formation and Absorption Mechanisms of Condensed Water by Epidermal Hairs of Desert Plants: Postprint

Authors: Alayi Khanat, Liu Yanxia, Lan Haiyan

Date: 2024-03-01T00:00:00+00:00

Abstract

Desert plants have evolved highly sophisticated structural features to adapt to long-term water-deficient conditions, enabling them to absorb water from the air, retain it on their surfaces, and transport it internally. Leaf surface appendages such as epidermal hairs (trichomes) hold significant biological importance in the collection, storage, and transport of condensed water. Based on current research progress, this paper briefly reviews the biological and ecological effects of condensed water on desert plants, and elaborates on the theory relating leaf surface wettability to water-harvesting capacity. Building upon this foundation, we focus on elucidating the crucial role of specialized leaf surface structures (epidermal hairs) in the processes of condensed water formation, transport, and absorption, and summarize relevant research methodologies for the retention and absorption of condensed water on plant surfaces. This provides a theoretical basis for deepening our understanding of the strategies employed by desert plants to harvest condensed water driven by epidermal hair structural characteristics, as well as the stress-resistance mechanisms of arid desert plants.

Full Text

Abstract

Desert plants have evolved highly specialized structural adaptations to collect, retain, and transport atmospheric water under chronic water scarcity conditions. Leaf surface appendages such as trichomes play a crucial biological role in the collection, storage, and transport of condensed water. This review synthesizes current research progress on the biological and ecological effects of condensed water on desert plants, elucidates theoretical frameworks linking leaf surface wettability to water harvesting capacity, and emphasizes the critical functions of specialized leaf surface structures (trichomes) in the formation, transport, and absorption of condensed water. We also summarize methodological approaches for studying water retention and absorption on plant surfaces, providing a theoretical foundation for understanding trichome-driven water collection strategies in desert plants and their drought resistance mechanisms.

Keywords: desert plant; condensed water; leaf surface wettability; trichome; ecological effect

Introduction

Water resource inputs for plants in desert regions are extremely limited, primarily comprising atmospheric precipitation and condensed water [?]. Due to significant diurnal temperature variations, water vapor from soil evaporation and plant transpiration condenses when encountering sufficiently cool ground or plant surfaces, particularly during spring and autumn seasons with large temperature fluctuations [?]. As a clean water source, condensed water holds important ecological significance for desert plants facing extreme water scarcity [?]. The primary pathways for water absorption on leaf surfaces include stomata [?], cuticles [?], hydathodes [?], and trichomes [?], among which trichomes have been demonstrated to perform multiple functions [?]. The presence of trichomes increases leaf surface wettability and water retention time [?], allowing condensed water to be retained as droplets within the trichome layer [?] and ensuring maximum water acquisition [?]. Foreign scholars have developed fog collection materials by mimicking the water harvesting behavior of trichomes on desert plants such as *Salsola crassa* [?]. While international research on this topic has spanned nearly a century, domestic studies have only emerged in the past two decades. This review synthesizes global research on the formation and absorption mechanisms of condensed water by trichomes, aiming to provide insights for future investigations into the interactions between desert plant specialized structures and plant function.

1 Ecological Effects of Condensed Water on Desert Plants

Water vapor in the air condenses into droplets on cool plant surfaces and is subsequently absorbed by the plant. This phenomenon is common in xerophytes and halophytes [?], whose specialized or accessory structures facilitate atmospheric water absorption, making condensed water an important water source for desert plants.

1.1 Quantity and Duration of Dew Formation on Plant Surfaces

In desert regions, warm moist air near the ground (particularly fog) readily forms condensed water when encountering cool plant surfaces [?]. The frequency of foggy days in desert areas depends primarily on geographic location and other factors [?]. Fog deposition events in arid and semi-arid regions mainly occur from May to September. Although summer precipitation decreases, large diurnal temperature variations increase fog deposition, particularly during June-August when strong fog collection occurs. In contrast, autumn precipitation increases while fog deposition decreases [?]. The average fog water amount is typically about 0.21 $\mathrm{L \cdot m^{-2}}$, with peak values reaching approximately 0.16 $\mathrm{L \cdot m^{-2}}$ in the early morning [?]. Studies of riparian forest plants on the eastern edge of the Taklamakan Desert show that canopy dew formation days and amounts during the growing season are substantial [?]. Analysis of nearly 30 years of meteorological data reveals that dew amounts exceed rainfall amounts for about one-fifth of the time, demonstrating that condensed water represents a crucial water resource in the Taklamakan Desert region [?].

1.2 Biological Effects of Plant Condensed Water

Foliar water uptake (FWU) is a common phenomenon in desert regions due to diurnal temperature effects that cause water vapor near the surface to condense [?]. Research demonstrates that leaf surface structures can significantly alter leaf wettability and water retention characteristics, including epicuticular wax [?], stomata [?], and trichomes [?]. The absorption of water by leaf surfaces creates chemical energy gradients within leaves, typically described by "water potential" ( ). Since leaf interiors are usually water-saturated (high water potential) while the atmosphere is unsaturated (low water potential), water flows outward (transpiration) [?]. For leaves to absorb water, leaf water potential must be lower than that of the surrounding microenvironment [?]. When condensed water forms on localized leaf surfaces, it creates a low water potential microenvironment that enables direct foliar absorption, significantly altering leaf water status [?].

1.3 Ecological Effects of Plant Condensed Water

Although foliar dew absorption has been demonstrated in many plants [?], its ecological significance remains debated. Monteith [?] hypothesized that if leaf surface condensed water evaporates too quickly, it would not significantly affect internal water content; conversely, if plants absorb sufficient water through roots, small amounts of foliar-absorbed condensed water would not contribute substantially to plant adaptation. However, opposing views suggest that in arid environments where condensation frequently occurs, water obtained through leaf absorption can have significant ecological effects even without long-distance transport. Liu et al. [?] studied the desert ephemeral plant *Lappula semiglabra* and found that removing leaf trichomes significantly affected water absorption, causing notable changes in leaf thickness, weight, leaf water potential, net photosynthetic rate, stomatal conductance, and aboveground biomass (dry weight). This demonstrates that trichomes are important water absorption structures.

2 Formation and Retention of Condensed Water on Desert Plant Leaf Surfaces

Many desert plant leaves are pubescent [?], creating rough interfaces with the leaf epidermis that form "air pocket" structures favorable for capturing atmospheric water droplets. This creates a superhydrophobic surface between the liquid and solid phases [?]. When encountering small droplets comparable to surface roughness scales, such as fog-formed droplets measuring 1-40 m [?], these can infiltrate the "air pockets" and overcome the superhydrophobic state, leading to water retention and spreading on leaf surfaces [?]. This model is known as the "Cassie-Baxter" model, while superhydrophobic surfaces may cause larger droplets to detach from leaf surfaces [?].

2.1 Leaf Surface Wettability Characteristics

Wetting represents the ability of a liquid to maintain contact with a solid surface, resulting from intermolecular interactions and typically characterized by the measurable contact angle of water droplets at the gas-solid-liquid interface [?]. The contact angle inversely measures adhesion between liquid and solid; smaller contact angles indicate greater spreading area, while larger contact angles indicate less contact and greater sphericity [?]. Differences in leaf surface wettability determine droplet contact angle size, influenced by factors including trichome quantity and morphology [?], epidermal cell microstructure [?], wax layer microstructure and composition [?], and stomatal number and distribution [?]. These relationships can be expressed by the wetting equation:

$$\gamma_{LV} \cos\theta = \gamma_{SV} - \gamma_{SL}$$

where γ_{SV} is solid-vapor interfacial tension, γ_{LV} is liquid-vapor interfacial tension, γ_{SL} is solid-liquid interfacial tension, and θ is the contact angle [?].

2.2 Factors Influencing Leaf Surface Wettability

Many desert plant leaves are covered with trichomes. Research shows that trichome density and structure significantly affect leaf wettability [?]. Different trichome densities result in different water interaction patterns: sparse trichome surfaces, moderately hairy surfaces, and dense trichome surfaces interact differently with water droplets [?]. Contact angle correlates positively with trichome density [?]; when trichome density exceeds 4000 per cm^2, a trichome canopy structure forms, creating stronger hydrophobicity [?]. Studies show that desert plant leaves covered with dense conical trichomes can achieve contact angles of 150-160°, while sparsely pubescent leaves have contact angles of approximately 120° [?]. Structural variations in trichomes (such as presence of wax) significantly affect wettability [?]; waxy trichome adaxial surfaces are extremely hydrophobic, while non-waxy trichome surfaces only temporarily repel water. *Leymus chinensis* trichomes without wax have contact angles of only 50°, whereas waxy trichome surfaces exhibit extremely strong water repellency with contact angles of 150-160° [?].

Natural leaf surfaces are not smooth but result from the combined effects of hydrophobic substances and surface roughness, which alter wetting properties. Wenzel [?] and Cassie and Baxter [?] improved upon Young' s equation by incorporating contact angle and surface roughness, proposing models for non-smooth surfaces. Due to surface roughness, actual solid-liquid contact area exceeds apparent geometric area, increasing hydrophobicity (or hydrophilicity), assuming liquid always fills surface grooves (Wenzel model) [?]. The Cassie-Baxter model proposes that droplet behavior on rough surfaces is complex; when surface microstructures are smaller than droplet size and highly hydrophobic, droplets cannot fill surface grooves, trapping air beneath them [?].

2.3 Physical Mechanisms of Condensed Water Formation

Condensed water formation is a phase transition process where gaseous water transforms to liquid upon contact with object surfaces [?]. This process includes several physical phenomena: heterogeneous nucleation, self-similar growth, nuclei implantation, and droplet coalescence [?]. Nucleation forms thermodynamically stable nanoscale droplets [?], with the primary condition being surface temperature at or below dew point [?]. Appropriate low temperatures are crucial for condensation deposition. When ambient temperature falls below dew point, atmospheric water vapor pressure decreases, increasing condensed water formation. Desert nighttime temperatures can drop to around 10°C, leading to substantial condensation [?]. Additionally, condensation requires sufficient atmospheric water vapor content; higher vapor content accelerates condensation formation [?].

3 Absorption and Utilization of Condensed Water by Desert Plant Trichomes

Among plant accessory structures, trichomes represent the strongest defense system, with complex three-dimensional networks helping plants adapt to harsh environments [?]. Trichomes consist of single or multiple cells distributed on angiosperm surfaces, exhibiting diverse morphologies and structures. Non-glandular trichomes commonly include conical, needle-like, and leaf-like forms that reduce water loss, enhance temperature tolerance, and protect against UV radiation, insects, and herbivores [?]. Furthermore, desert plants facilitate condensed water formation and absorption through trichomes, improving leaf water status [?].

3.1 Structural Characteristics of Trichomes

In the hyperarid Namib Desert, many plants have fibrous trichomes on leaf surfaces that help obtain water by promoting condensed water formation and absorption [?]. Researchers studying conical trichome structures under drought conditions have explored how twisted structures form in conical trichomes, revealing characteristics of water collection, microfibril storage, and release. Conical trichomes contain internal microfibril structures visible under scanning electron microscopy [Figure 5: see original paper]. Vertical sections show sponge-like microfibril textures [Figure 5: see original paper]. When droplets attach to trichomes, they immediately become conical [Figure 5: see original paper]; under drought conditions, conical trichomes reversibly transform into vertically twisted compressed structures [Figure 5: see original paper], returning to conical form upon rehydration [Figure 5: see original paper]. This variable structure facilitates rapid water absorption, storage, and transport to mesophyll cells [**?**].

Most cacti (*Opuntia stricta*) grow in desert regions or extremely dry environments like the Atacama Desert. To adapt, cacti have evolved efficient condensed water collection systems relying primarily on needle-like trichome structures on leaf surfaces. All cactus stems have thickened, succulent portions suitable for water storage [Figure 6: see original paper]; during evolution, cacti lost true leaves to reduce evaporation, retaining only needle-like trichome structures [Figure 6: see original paper]. A single cactus spine has specialized structures including a conical tip [Figure 6: see original paper], wide groove sections [Figure 6: see original paper], narrower groove sections [Figure 6: see original paper], and barbed structures [Figure 6: see original paper]. These structures drive directional droplet movement, with arrows indicating water droplet movement direction [Figure 6: see original paper].

3.2 Water Absorption Characteristics of Trichomes

Directional water transport results from hydrophobic-hydrophilic bilayer structures [**?**], as heterogeneous surface tension can induce a driving force for directional water transport [**?**]. Advanced bioimaging techniques confirm cacti effectively absorb condensed water. Due to high temperatures and low humidity in desert regions with relatively high evaporation rates, trichome hydrophobicity increases adhesion and reduces transpiration rates. Cactus stems can be considered bilayer materials composed of hydrophobic trichomes and hydrophilic mucilage, driving spontaneous droplet penetration from the hydrophobic trichome layer to the hydrophilic layer. When droplets form on trichome surfaces, water is rapidly absorbed into the stem while reverse transport is restricted, causing droplets to spread into hydrophilic regions [**?**].

3.3 Mechanisms Driving Condensed Water Absorption by Trichomes

Cactus spine structures can be considered conical bodies with linear grooves on their surfaces. Most collected condensed water is absorbed through trichomes, with small amounts lost through evaporation via inflow pathways. Cactus survival strategies are illustrated in [Figure 7: see original paper]. At sunrise, droplets condense on spines and are absorbed through trichome clusters (downward direction, blue arrows), while mucilage in cactus stems reduces evaporative water loss (upward, red arrows) [**?**].

3.3.1 Laplace Pressure Difference Laplace pressure difference arises from pressure differentials formed by droplets on individual hairs or spines with varying curvature radii, providing driving force for droplet movement from spine tips to bases against gravity [Figure 8: see original paper] [**?**]. This conical geometry creates different local radii at droplet ends, generating Laplace pressure differences calculable by:

$$\Delta P_{Laplace} = \int_{R_0}^{R} \frac{2\gamma \sin\alpha}{(R + R_0)^2} dz$$

where R and R_0 represent local radii at spine ends, γ is water surface tension, α is spine half-cone angle, and dz is spine radius increment [Figure 8: see original paper].

3.3.2 Surface Free Energy Gradient Surface free energy gradients also generate driving forces (F) [**?**], enabling apical droplets to move basally. Cactus spine microgrooves exhibit width gradients, with rougher, sparser structures near the base. The driving force from surface free energy gradients is expressed as:

$$F = \int_{tip}^{base} \gamma(\cos\theta_A - \cos\theta_R) dl$$

where γ is roughness coefficient, θ_A is advancing contact angle, θ_R is receding contact angle, and dl is the differential length from spine tip to base [**?**].

4 Research Methods for Retention and Absorption of Condensed Water on Plant Surfaces

Advanced technologies have gradually elucidated mechanisms of water-leaf surface interactions. Current methodologies include leaf anatomical methods, heat pulse and isotope tracing techniques, leaf pressure chamber methods, environmental scanning electron microscopy, and fluorescence tracing methods.

4.1 Anatomical Methods

Leaves are primary organs for photosynthesis and transpiration, with surface and internal structural characteristics highly sensitive to environmental factors like water and temperature [**?**]. Schreel et al. [**?**] observed through ultrathin sections and transmission electron microscopy that leaf epidermal cell walls have cuticle layers while trichome cell walls lack them. Brighigna et al. [**?**] used anatomical methods to study *Tillandsia usneoides* trichome ultrastructure under water stress, revealing the cellular system for trichome formation and water absorption, and confirming that nutrient transport is facilitated by hydrophilic substances produced during cytoplasmic secretion.

4.2 Heat Pulse and Isotope Tracing Techniques

Heat pulse and isotope tracing are common techniques in ecophysiological research. Heat pulse methods enable simple, real-time, accurate measurement of canopy transpiration water consumption with minimal disturbance to plant growth [?]. Isotope tracing uses labeled compounds to track element and compound migration, transformation, and accumulation in organisms and environmental media, analyzing plant leaf and stem water content through hydrogen and oxygen stable isotopes [?]. Burgess et al. [?] used heat pulse technology to observe sap flow reversal in *Sequoia sempervirens* under sufficient condensation conditions, while isotope tracing confirmed direct leaf absorption of condensed water. These techniques will become primary methods for future in-depth research on foliar water absorption in arid regions.

4.3 Leaf Pressure Chamber Method

The leaf pressure chamber method is widely used to measure plant water potential due to its simplicity and stable measurements [?]. Water typically moves along water potential gradients (ψ) [?]. Waseem et al. [?] conducted three treatments on *Caragana korshinskii* under drought stress: well-watered, drought stress with condensation, and drought stress without condensation. Results showed trichome density on both adaxial and abaxial leaf surfaces increased by approximately 30-40% in drought-stressed plants compared to well-watered plants. Using leaf water potential (ψ) as a physiological indicator, plants with condensation showed water potential approximately 2.6 MPa higher than those without condensation, proving trichomes are important water absorption structures.

4.4 Environmental Scanning Electron Microscopy

To observe true morphologies of hydrated samples, environmental scanning electron microscopy (ESEM) and cryogenic scanning electron microscopy (Cryo-SEM) were developed based on SEM principles [?]. These techniques minimize water loss in hydrated samples through differential pressure aperture technology or by forming vitreous ice from liquid water under cryogenic conditions, preserving surface morphology [?]. Researchers used ESEM for in situ studies of dynamic microdroplet suspension behavior on fresh lotus leaves at micro- and nanoscales. During droplet condensation, droplets formed wettable micro-nanostructure gradients along nanoscale papillae surfaces, driving directional droplet movement. This research revealed the mechanism of dew formation on lotus leaves and explained self-cleaning principles from micro- and nanoscale perspectives [?].

4.5 Fluorescence Tracing Method

Fluorescence microscopy utilizes characteristic wavelength light to generate fluorescence in specimens for microscopic examination [?]. Pina et al. [?] used fluorescence tracing to study condensed water absorption by *Combretum leprosum* leaves in Brazil' s semi-arid region, revealing that water absorbed by hydrophilic trichomes could enter mesophyll cells through palisade tissue, proving trichomes can both absorb water and balance internal water distribution.

5 Outlook

This review summarizes research progress on water accumulation mechanisms in arid plants, outlining condensed water formation mechanisms and effects on plants, with emphasis on leaf surface wettability theory and the critical role of trichomes in retaining condensed water. We discuss how trichome presence affects desert plant survival and adaptation, providing insights for drought resistance mechanisms. Building on previous studies, our research group has investigated *Salsola ferganica* trichome structural characteristics and their influence on leaf surface wettability using multiple methods. Microstructural observations suggest *S. ferganica* trichomes may help capture atmospheric moisture, while surface physicochemical properties—including hydrophobic functional groups, hydrophilic pectin, and low crystallinity—may enhance droplet adhesion and improve water acquisition for survival under harsh conditions [**?**]. However, further research is needed to determine how nanoscale structure and chemical composition affect wettability.

Due to technical limitations, progress in trichome function and plant interaction mechanisms has been relatively slow. Future studies should employ precision instruments for in-depth exploration at tissue, cellular, physiological, biochemical, and molecular levels to investigate efficient condensed water utilization mechanisms by desert plant trichomes. Additionally, integrating theory with practice through biomimetic applications—such as developing efficient fog harvesters inspired by plant trichomes—will positively impact water utilization in arid regions.

References

[1] Eckardt F D, Soderberg K, Coop L J, et al. The nature of moisture at Gobabeb, in the central Namib Desert[J]. Journal of Arid Environments, 2013, 93(36): 7-19.

[2] Agam N, Berliner P R. Dew formation and water vapor adsorption in semi arid environments A review[J]. Journal of Arid Environments, 2006, 65(4): 572-590.

[3] Hill A J, Dawson T E, Shelef O, et al. The role of dew in Negev Desert plants[J]. Oecologia, 2015, 178(2): 317-327.

[4] Emery N C. Foliar uptake of fog in coastal California shrub species[J]. Oecologia, 2016, 182(3): 731-742.

[5] Fernández V, Bahamonde H A, Javier Peguero Pina J, et al. Physichemical

properties of plant cuticles and their functional and ecological significance[J]. Journal of Experimental Botany, 2017, 68(19): 5293-5306.

[6] Burgess S S O, Dawson T E. The contribution of fog to the water relations of *Sequoia sempervirens* (D. Don): Foliar uptake and prevention of dehydration[J]. Plant, Cell & Environment, 2004, 27(8): 1023-1034.

[7] Ohrui T, Nobira H, Sakata Y, et al. Foliar trichome and aquaporin aided water uptake in a drought resistant epiphyte *Tillandsia ionantha* Planchon[J]. Planta, 2007, 227(1): 47-56.

[8] Martin C E, Willert V D J. Leaf epidermal hydathodes and the ecophysiological consequences of foliar water uptake in species of *Crassula* from the Namib Desert in Southern Africa[J]. Plant Biology, 2000, 2(2): 229-242.

[9] Berry Z C, Emery N C, Gotsch S G, et al. Foliar water uptake: Processes, pathways, and integration into plant water budgets[J]. Plant, Cell & Environment, 2019, 42(2): 410-423.

[10] Bickford C P. Ecophysiology of leaf trichomes[J]. Functional Plant Biology, 2016, 43(9): 807-814.

[11] Schreel J D M, Leroux O, Goossens W, et al. Identifying the pathways for foliar water uptake in beech (*Fagus sylvatica* L.): A major role for trichomes[J]. The Plant Journal, 2020, 103(2): 769-780.

[12] Brewer C A, Smith W K, Vogelmann T C. Functional interaction between leaf trichomes, leaf wettability and the optical properties of water droplets[J]. Plant, Cell & Environment, 1991, 14(9): 955-962.

[13] Masrahi Y S. Glochids microstructure and dew harvesting ability *Opuntia stricta* (Cactaceae)[J]. Journal of King Saud University Science, 2020, 32(8): 3307-3312.

[14] Zhuang Yanli, Zhao Wenzhi. Experimental study of effects of artificial dew on *Bassia dasyphylla* and *Agriophyllum squarrosum* leaves[J]. Journal of Desert Research, 2010, 30(5): 1068-1074.

[15] Gürsoy M, Harris M T, Downing J O, et al. Bioinspired fog capture and channel mechanism based on the arid climate plant *Salsola crassa*[J]. Colloids and Surfaces A: Physicochemical and Engineering Aspects, 2017, 529(25): 195-202.

[16] Baier W. Studies on dew formation under semi-arid conditions[J]. Agricultural Meteorology, 1966, 3(1-2): 103-112.

[17] Ebner M, Miranda T, Roth Nebelsick A. Efficient fog harvesting by *Stipagrostis sabulicola* (Namib dune bushman grass)[J]. Journal of Arid Environments, 2011, 75(6): 524-531.

[18] Mares M A. Encyclopedia of Deserts[M]. Norman: University of Oklahoma Press, 2017: 383-384.

[19] Lancaster J, Lancaster N, Seely M K. Climate of the central Namib Desert[J]. Madoqua, 1984, 14(1): 5-61.

[20] Shanyengana E S, Henschel J R, Seely M K, et al. Exploring fog as a supplementary water source in Namibia[J]. Atmospheric Research, 2002, 64(1-4): 251-259.

[21] Hiatt C, Fernandez D, Potter C. Measurements of fog water deposition on the California Central Coast[J]. Atmospheric and Climate Sciences, 2012, 2(4): 525.

[22] Hao X, Li C, Guo B, et al. Dew formation and its long term trend in a desert riparian forest ecosystem on the eastern edge of the Taklimakan Desert in China[J]. Journal of Hydrology, 2012, 472(50): 90-98.

[23] Hayes M A, Chapman S, Jesse A, et al. Foliar water uptake by coastal wetland plants: A novel water acquisition mechanism in arid and humid subtropical mangroves[J]. Journal of Ecology, 2020, 108(6): 2625-2637.

[24] Williams H F. Absorption of water by the leaves of common mesophytes[J]. Journal of the Elisha Mitchell Scientific Society, 1932, 48(1): 83-100.

[25] Cernusak L A, Ubierna N, Jenkins M W, et al. Unsaturation of vapor pressure inside leaves of two conifer species[J]. Scientific Reports, 2018, 8(1): 1-7.

[26] Vesala T, Sevanto S, Grönholm T, et al. Effect of leaf water potential on internal humidity and CO_2 dissolution: Reverse transpiration and improved water use efficiency under negative pressure[J]. Frontiers in Plant Science, 2017, 8(8): 54-64.

[27] Simonin K A, Santiago L S, Dawson T E. Fog interception by *Sequoia sempervirens* (D. Don) crowns decouples physiology from soil water deficit[J]. Plant, Cell & Environment, 2009, 32(7): 882-892.

[28] Koch K, Bhushan B, Jung Y C, et al. Fabrication of artificial Lotus leaves and significance of hierarchical structure for superhydrophobicity and low adhesion[J]. Soft Matter, 2009, 5(7): 1386-1393.

[29] Lange O L, Lösch R, Schulze E D, et al. Responses of stomata to changes in humidity[J]. Planta, 1971, 100(1): 76-86.

[30] Brighigna L, Palandri M R, Giuffrida M, et al. Ultrastructural features of the *Tillandsia usneoides* L. absorbing trichome during conditions of moisture and aridity[J]. Caryologia, 1988, 41(2): 111-129.

[31] Cui L, Yingying M, Nina W, et al. The overlooked functions of trichomes: Water absorption and metal detoxication[J]. Plant, Cell & Environment, 2022, 46(3): 669-687.

[32] Stone E C. The ecological importance of dew[J]. The Quarterly Review of Biology, 1963, 38(4): 328-341.

[33] Monteith J L. Dew: Facts and fallacies[J]. The Water Relations of Plants, 1963: 37-56.

[34] Liu Zhidong, Lv Guanghui, Zhang Xueni, et al. Response of physiological and ecological indexes of ephemeral plant *Lappula semiglabra* with leaf hairs in Arid Area[J]. Arid Zone Research, 2017, 34(5): 1101-1108.

[35] Li Jie, Zhang Mingfang. Advances in regulation of plant trichome development[J]. Northern Horticulture, 2020, 44(23): 133-139.

[36] Cassie A B D, Baxter S. Wettability of porous surfaces[J]. Transactions of the Faraday Society, 1944, 40(40): 546-551.

[37] Williams C R, Kruger A, Gage K S, et al. Comparison of simultaneous rain drop size distributions estimated from two surface disdrometers and a UHF profiler[J]. Geophysical Research Letters, 2000, 27(12): 1763-1766.

[38] Wier K A, McCarthy T J. Condensation on ultrahydrophobic surfaces and its effect on droplet mobility: Ultrahydrophobic surfaces are not always water repellant[J]. Langmuir, 2006, 22(6): 2433-2436.

[39] Holder C D. The relationship between leaf hydrophobicity, water droplet retention, and leaf angle of common species in a semi-arid region of the western United States[J]. Agricultural and Forest Meteorology, 2012, 152(49): 11-16.

[40] Wang J, Wu Y, Cao Y, et al. Influence of surface roughness on contact angle hysteresis and spreading work[J]. Colloid and Polymer Science, 2020, 298(115): 1107-1112.

[41] Percy K E, Jensen K F, Mcquattie C J. Effects of ozone and acidic fog on red spruce needle epicuticular wax production, chemical composition, cuticular membrane ultrastructure and needle wettability[J]. New Phytologist, 1992, 122(1): 71-81.

[42] Fürstner R, Barthlott W, Neinhuis C, et al. Wetting and self cleaning properties of artificial superhydrophobic surfaces[J]. Langmuir, 2005, 21(3): 956-961.

[43] Kolyva F, Stratakis E, Rhizopoulou S, et al. Leaf surface characteristics and wetting in *Ceratonia siliqua* L.[J]. Flora Morphology, Distribution, Functional Ecology of Plants, 2012, 207(8): 551-556.

[44] Peschel S, Beyer M, Knoche M. Surface characteristics of sweet cherry fruit: Stomata number, distribution, functionality and surface wetting[J]. Scientia Horticulturae, 2003, 97(3-4): 265-278.

[45] Young T. An essay on the cohesion of fluids[J]. Philosophical Transactions of the Royal Society of London, 1805, 95(1): 65-87.

[46] Wenzel R N. Resistance of solid surfaces to wetting by water[J]. Industrial & Engineering Chemistry, 1936, 28(8): 988-994.

[47] Barthlott W, Mail M, Bhushan B, et al. Plant surfaces: Structures and functions for biomimetic innovations[J]. Nano Micro Letters, 2017, 9(2): 23-63.

[48] Brewer C A, Smith W K. Patterns of leaf surface wetness for montane and subalpine plants[J]. Plant, Cell & Environment, 1997, 20(1): 1-11.

[49] Pandey S, Nagar P K. Leaf surface wetness and morphological characteristics of *Valeriana jatamansi* grown under open and shade habitats[J]. Biological Plantarum, 2002, 45(2): 291-294.

[50] Ren L Q, Wang S J, Tian X M, et al. Non-typical plant leaf surfaces and their anti-adhesion effects[J]. Journal of Bionics Engineering, 2007, 4(1): 33-40.

[51] Neinhuis C, Barthlott W. Characterization and distribution of water repellent, self cleaning plant surfaces[J]. Annals of Botany, 1997, 79(6): 667-677.

[52] Beysens D. The formation of dew[J]. Atmospheric Research, 1995, 39(1-3): 215-237.

[53] Narhe R D, Beysens D A. Nucleation and growth on a superhydrophobic grooved surface[J]. Physical Review Letters, 2004, 93(7): 076103.

[54] Pruppacher H R, Klett J D. Microstructure of atmospheric clouds and precipitation[J]. Physics Today, 1979, 32(6): 56-56.

[55] Agam N, Berliner P R. Dew formation and water vapor adsorption in semi-arid environments A review[J]. Journal of Arid Environments, 2006, 65(4): 572-590.

[56] Malek E, Mccurdy G, Giles B. Dew contribution to the annual water balances in semi-arid desert valleys[J]. Journal of Arid Environments, 1999, 42(2): 71-80.

[57] Jacobs A F G, Heusinkveld B G, Berkowicz S M. A simple model for potential dewfall in an arid region[J]. Atmospheric Research, 2002, 64(1-4): 285-295.

[58] Sadia H, Zulfiqar A, Bakar A M S, et al. Leaf prickle hairs and longitudinal grooves help wheat plants capture air moisture as a smart strategy for a changing climate[J]. Planta, 2021, 254(1): 19.

[59] Hülskamp M, Miséra S, Jürgens G. Genetic dissection of trichome cell development in Arabidopsis[J]. Cell, 1994, 76(3): 555-566.

[60] Bar M, Shtein I. Plant trichomes and the biomechanics of defense in various systems, with Solanaceae as a model[J]. Botany, 2019, 97(12): 651-660.

[61] Vogel S, Müller-Doblies U. Desert geophytes under dew and fog: "curly whirlies" of Namaqualand (South Africa)[J]. Flora Morphology, Distribution, Functional Ecology of Plants, 2011, 206(1): 3-31.

[62] Roth Nebelsick A, Ebner M, Miranda T, et al. Leaf surface structures enable the endemic namib desert grass *Stipagrostis sabulicola* to irrigate itself with fog water[J]. Journal of the Royal Society Interface, 2012, 9(73): 1965-1974.

[63] Ito F, Komatsubara S, Shigezawa N, et al. Mechanics of water collection in plants via morphology change of conical hairs[J]. Applied Physics Letters, 2015,

106(13): 133701.

[64] Ju J, Bai H, Zheng Y, et al. A multi-structural and multi-functional integrated fog collection system in cactus[J]. Nature Communications, 2012, 3(1): 1-6.

[65] Wu J, Wang N, Wang L, et al. Unidirectional water penetration composite fibrous film via electrospinning[J]. Soft Matter, 2012, 8(22): 5996-5999.

[66] Wang H, Ding J, Dai L, et al. Directional water transfer through fabrics induced by asymmetric wettability[J]. Journal of Materials Chemistry, 2010, 20(37): 7938-7940.

[67] Malik F T, Clement R M, Gethin D T, et al. Hierarchical structures of cactus spines that aid in the directional movement of dew droplets[J]. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 2016, 374(2073): 20160110.

[68] Kim K, Kim H, Ho Park S, et al. Hydraulic strategy of cactus trichome for absorption and storage of water under arid environment[J]. Frontiers in Plant Science, 2017, 8(8): 1777-1785.

[69] Lorenceau E, Quéré D. Drops on a conical wire[J]. Journal of Fluid Mechanics, 2004, 510(49): 29-45.

[70] Bai F, Wu J, Gong G, et al. Biomimetic cactus spine with hierarchical groove structure for efficient fog collection[J]. Advanced Science, 2015, 2(7): 1500047.

[71] Ren F, Li G, Zhang Z, et al. A single-layer Janus membrane with dual-gradient conical micropore arrays for self-driving fog collection[J]. Journal of Materials Chemistry A, 2017, 5(35): 18403-18411.

[72] Escalona J M, Bota J, Medrano H. Distribution of leaf photosynthesis and transpiration within grapevine canopies under different drought conditions[J]. VITIS Journal of Grapevine Research, 2003, 42(2): 57-64.

[73] Schreel J D M, Leroux O, Goossens W, et al. Identifying the pathways for foliar water uptake in beech (*Fagus sylvatica* L.): A major role for trichomes[J]. The Plant Journal, 2020, 103(2): 769-780.

[74] Wullschleger S D, Meinzer F C, Vertessy R A. A review of whole-plant water use studies in tree[J]. Tree Physiology, 1998, 18(8-9): 499-512.

[75] Yang Q, Xiao H, Zhao L, et al. Stable isotope techniques in plant water sources: A review[J]. Sciences in Cold and Arid Regions, 2010, 2(2): 112-122.

[76] Burgess S S O, Adams M A, Turner N C, et al. An improved heat pulse method to measure low and reverse rates of sap flow in woody plants[J]. Tree Physiology, 2001, 21(9): 589-598.

[77] Meron M, Grimes D W, Phene C J, et al. Pressure chamber procedures for leaf water potential measurements of cotton[J]. Irrigation Science, 1987, 8(3): 215-222.

[78] Dainty J. The Discovery of Water Potential[J]. Discoveries in Plant Biology, 1998, 2: 271-285.

[79] Waseem M, Nie Z F, Yao G Q, et al. Dew absorption by leaf trichomes in *Caragana korshinskii*: An alternative water acquisition strategy for withstanding drought in arid environments[J]. Physiologia Plantarum, 2021, 1(1): 10-15.

[80] Stabentheiner E, Zankel A, Pölt P. Environmental scanning electron microscopy—a versatile tool in studying plants[J]. Protoplasma, 2010, 246(1-4): 89-99.

[81] Craig S, Beaton C D. A simple Cryo-SEM method for delicate plant tissues[J]. Journal of Microscopy, 1996, 182(2): 102-105.

[82] Zheng Y, Han D, Zhai J, et al. In situ investigation on dynamic suspending of microdroplet on lotus leaf and gradient of wettable micro- and nanostructure from water condensation[J]. Applied Physics Letters, 2008, 92(8): 084106.

[83] James B. Handbook of Biological Confocal Microscopy[M]. Berlin: Springer Science & Business Media, 2006.

[84] Hepler P K, Gunning B E S. Confocal fluorescence microscopy of plant cells[J]. Protoplasma, 1998, 201(3-4): 121-157.

[85] Pina A L C B, Zandavalli R B, Oliveira R S, et al. Dew absorption by the leaf trichomes of *Combretum leprosum* in the Brazilian semiarid region[J]. Functional Plant Biology, 2016, 43(9): 851-861.

[86] Yanxia L, Hanat A, Haiyan L. Characterization of leaf trichomes and their influence on surface wettability of *Salsola ferganica*, an annual halophyte in the desert[J]. Physiologia Plantarum, 2023, 173(3): e13905.

Note: Figure translations are in progress. See original paper for figures.