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Original Research

The Influencing Factors of Dew Absorbed by Leaves

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Abstract

Dew commonly condenses on plant leaf and can be directly taken up by leaves. The factors affecting dew absorption on leaves are complex. Indoor pot experiments on *Zygocactus truncatus*, *Chlorophytum comosum*, and *Juniperus formosana* were conducted under different air temperatures and wind speeds by using the deuterium (D) stable isotope tracer method. The proportion of dew uptake by leaf (F_u) of different plants was revealed, and the influence of different meteorological conditions and leaf microstructure on dew absorption was identified. Results showed that much of the dew returns to the atmosphere during evaporation, and only 6%–35% can be absorbed by the plant leaves. The capacity of dew uptake by leaves showed considerable differences between thress plants, and the amount of dew absorbed by *Zygocactus truncatus* leaves (25.96%±2.69% – 34.81%±4.61%) was significantly higher than that by *Chlorophytum comosum* (20.50%±1.89% – 23.39%±4.35%) (P = 2.19E^{-10}) and *Juniperus formosana* (6.26%±0.69% – 11.95%±1.35%) (P = 1.06E^{-30}). F_u varied according to different plants with the increase in air temperature and decreased gradually with the increase in wind speed. Leaves of compound or sickle-leaved plants with dense stomatal and tomentum are more able to absorb dew than those of coniferous plants with high wax content. In relation to external meteorological factors, the amount of absorbed dew depends on the plant type and leaf microscopic structure. This study is helpful in comprehensively evaluating the effect of dew evaporation on ecological environment and has importance for the application of dew resources.

Keywords: leaf microstructure, meteorological factors, dew, stable isotope, evaporation process

Introduction

Dew condensation on plant leaves at night is a common and frequently occurring meteorological phenomenon. Dew generally evaporates to the atmosphere but can also be absorbed and utilized directly by plant leaves [1] or drip onto the soil surface [2]. Evidence suggests that dew formation benefits plant growth. Dew can be absorbed directly through foliar uptake and improve plant water status, which is especially relevant in plants exposed to prolonged drought [3]. In the arid region, dew is redistributed among plant organs and affects seedlings' early growth characteristics through the growth rate, plant height, stem diameter, and leaf count [4]. During the dry

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summer months in many Mediterranean-type climate regions, coastal shrub species have high photosynthetic rates and allow for CO_2 assimilation through leaf water uptake [5]. Dew also can suppress transpiration in leaves [6]. According to Binks et al. [7] and Cynthia et al. [8] the contribution by foliar water uptake to annual transpiration has a median value of 8.2% and 30%, respectively. Holanda et al. [9] showed that leaf wetting by dew is relevant for physiology and lead lifespan.

The factors affecting dew absorption by plants are complex. Stone et al. [10] and Zhang et al. [3] found that biomass accumulation is controlled by dew and soil water conditions. In addition, the effect of leaf morphology on dew absorption is controversial. Emery et al. [5] studied Mediterranean-type shrub species and found that the stomatal crypts in *Ceanothus megacarpus* reduce the contact between stomata and condensed water droplets on the leaves, thus making it difficult for plants to take up water. In addition to stomatal crypts, *Ceanothus megacarpus* has trichomes that may increase hydrophobicity and the distance between water droplet and leaf interior. However, some evidence suggests that stomata [11, 12] or trichomes [1] contribute to leaf water uptake. A positive correlation might occur between the hydroscopicity of pteridophytes and the trichome density of leaves [13]. Therefore, the specific effects of microscopic characteristics of plant leaves on dew absorption should be further studied. In addition, dew frequently appears on plant leaves. The change of meteorological factors during dew evaporation might influence the dew absorption by plants; however, the related reports are limited. Understanding the effect of meteorological factors and microstructures on dew absorption by leaves is urgent.

Hydrogen and oxygen isotope fractionation occurs in the water vapor cycle. Water bodies at different stages of the dew cycle have characteristic ^{18}O and D, which can be used as tracer elements to reveal specific information about the water cycle [14]. With the use of isotope tracer method, the contribution ratio of atmospheric water vapor, soil evaporation, and plant transpiration water vapor to dew uptake was determined quantitatively [15, 16]. Some researchers used deuterium (D) tracing method and found that all δD values of leaves sprayed by heavy water (D_2O) largely exceeded that of the control leaves, it demonstrated dew can be directly absorbed by leaves [17-19]. In addition to these qualitative studies, a few scholars have quantitatively studied the proportion of dew in leaf water. Zhang et al. [3] found that under mild soil water conditions, the contribution rate of dew to the water content of *Populus euphratica* leaves was 3.1%-12.4%. However, current works focused on the proportion of dew in leaf water, and only a few reports were dedicated to the water transport pathway during dew evaporation.

In this work, artificial dew (diluted heavy water) was used as a tracer and sprayed in pot to reveal the dew absorption by different plants. For each pot, artificial dew was assumed to be evenly distributed in the leaves, and no difference can be found in the ability of the leaves to absorb water. The objectives of this study are as follows: 1) quantify the contribution of dew in leaf water (F_w) and proportion of dew uptaken by leaves (F_u) to different plant leaves, and to 2) investigate the influence of different meteorological factors and leaf microstructure on dew absorption by plant leaves. This research is helpful to comprehensively evaluate the effect of dew evaporation on ecological environment and has importance for the application of dew resources.

Material and Methods

Plant Selection

Pot experiment was performed in the laboratory of Jilin Jianzhu University from July to August, 2020. Three common plants widely distributed in Northern China, namely, *Zygocactus truncatus* (*Z. truncatus*) (P_1), *Chlorophytum comosum* (*C. comosum*) (P_2), and *Juniperus formosana* (*J. formosana*) (P_3) were selected to compare the influence of different plant leaf structures on dew absorption. Their leaflet traits are shown in Table 1. Each of the three species was plotted in 80 pots, and 240 one-year-old *C. comosum*, *Z. truncatus*, and *J. formosana* seedlings were planted in pots in April, 2020. For each type of seedling, 75 out of the 80 pots were randomly selected.

Experimental Design

Artificial dew (labeled water) was prepared by diluting source with the heavy water (99.9% at % D) and distilled water (δD = -55‰) down to a target of

Table 1. Leaf or leaflet traits of the three selected plant species.

Species	Leaf size (cm^2)	Texture	Trichomes	Shape	Margin	Amount of leaves per individual
Z. truncatus	5.5±1.8	Smooth	Large (few); Short (numerous)	Compound	Lobate	250-300
C. comosum	11±3.7	Rough with multiple veins	None	Sickle	Smooth	60-120
J. formosana	0.4±0.1	Smooth, water repellent	None	Acicular	Smooth	3500-3800

δD = 480‰. All the three plant pots were planted in the soil with the same composition and irrigated with distilled water (D = -55‰). During the experiment, the soil moisture gradient was maintained at 75%. The leaves area to be sprayed can be determined by the average leaf area and the number of leaves. The amount of artificial dew (δD = 480‰) also can be calculated. The artificial dew was sprayed onto the level of 0.1 mm simulated to the natural amount of dew. There was no difference among the amount of artificial dew on each plant's leaves. The experiment was designed as a two-factor experiment (Fig. 1). One factor was air temperature with three levels: 15ºC (T_1), 20ºC (T_2), and 25ºC (T_3) under breezeless environment. Another factor was wind speed with three levels: 0 $m \cdot s^{-1}$ (W_1), 1 $m \cdot s^{-1}$ (W_2), and 2 $m \cdot s^{-1}$ (W_3) under 20ºC. Air conditioner and fans were used to regulate indoor air temperature and wind speed. Three replicates were prepared for each group, and each experiment was conducted five times. Each plant was only sprayed artificial dew one time without any repeated application to avoid the residual effects of heavy water on leaf isotopes.

Sample Collection and Analysis

All leaf samples were taken immediately after the dew had completely evaporated in each experiment to prevent the absorbed dew from being transported from leaves to the stem or xylem. A total of 10-15 canopy and bottom leaves of *C. comosum*, *Z. truncates* and 200-250 leaves of *J. formosana* were randomly collected, and the leaves were immediately sealed and refrigerated. An automatic vacuum condensation extraction system (LI-2100, LICA United Technology Limited, China) was used to heat and distill water in the leaves in an ultra-low-pressure environment and extract water in a low-temperature environment. The principles of ultra-low-pressure vacuum distillation and freezing were applied. Water was collected through condensation at a low air temperature without fractional distillation, and 10-15 mLwas extracted at a time. The δD in each sample were measured using a liquid water isotope analyzer (LGR, LWIA-24d; USA). The precision of δD between the samples and the Vienna Standard Mean Ocean Water was below ±0.6‰.

The dew contribution rate in the leaf water can be calculated through a mass balance method. The formula is as follows:

$$F_w + F_i = 1 \quad (1)$$

$$\delta D_{lw} = \delta D_d F_w + \delta D_i F_i \quad (2)$$

where F_w and F_i (%) are the contribution of dew and irrigation water in leaf water, respectively; and δD_{lw}, δD_d, and δD_i is the D value of leaf water, dew, and irrigation water (distilled water), respectively.

$$F_u = \frac{V_{leaf} \times F_w}{S_{leaf} \times A} \times 100\% \quad (3)$$

where F_u (%) is the contribution of dew uptake by leaf, V_{leaf} (ml) is the volume of extraction water by collected leaves, S_{leaf} (cm^2) is the area of collected leaves, and *A* (cm) is the amount of artificial dew on unit leaf area.

Analysis of Leaf Microstructures

Leaf microstructure was identified through scanning electron microscopy (FEI Quanta SEM, USA). Following the method of Muhammad et al. [20], drop contact angle (DCA) was measured using a Canon EOS550D camera (Japan) attached to a macro lens (MP-E 65MM 1:2.8). A 6 μL droplet of distilled water (broadleaves) and 2 μL droplet (needles) was placed on the leaf sample. The quantity of epicuticular waxes was weighed after the evaporation of the chloroform collected in a pre-weighted beaker.

Data Analysis

Statistical analyses were conducted using SPSS software version 16.0. Q-Q Probability Plots were

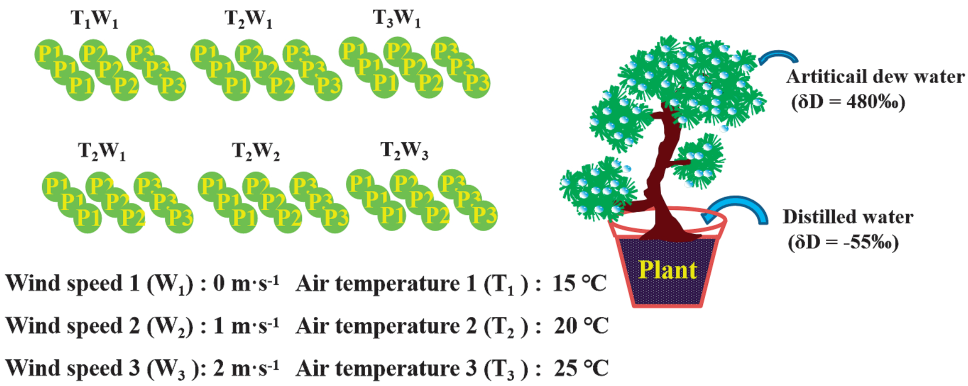

Fig. 1. Experimental diagram of six groups experiment under different meteorological factors (left) and potted plant spraying artificial dew (right).

employed to test the contribution of dew in leaf water (F_w) and proportion of dew uptake by leaves (F_u). The F_w and F_u of different plants under varied meteorological factors were subjected to one-way ANOVA. Significance was set at $P<0.05$. Least significant difference or Tamhane's T2 was used to determine significant differences.

Results and Discussion

Leaf Absorption of Dew

All selected plants were able to use dew through their leaves. Fig. 2 shows that under 20ºC and breezeless condition, the F_w in *Z. truncatus*, *C. comosum*, and *J. formosana* leaves was 8.42%±0.15%, 8.26%±0.84%, and 6.68±0.77%, respectively. The contribution of dew to leaf water is not comparable to the large amounts previously reported. Hill et al. [21] stated that *S. inermis*, *A. sieberi*, and *H. scoparium* in Negev Desert used 56%, 63%, and 46% of their water from dew, respectively. Kim and Lee [12] found that the dew contribution to leaf water of rain-fed plants was 72% (±17%) and 94% (±11%) according to the ^{18}O and D tracers, respectively. During the dry season, 23%-59% of the water used by *P. tomentosa* seeding came from fog water in Xishuangbanna [22]. The dew in arid region can afford additional water for plant utilization. The amount of dew absorbed by plants differed significantly under different levels of drought stress [23, 24]. Dew provides substantial amounts of water, which is especially relevant in water-stressed plants [25], and can be used efficiently under moist soil with moderate drought [3, 26]. Waseem et al. [27] observed dew absorption amends leaf hydraulic functions during dehydration. When exposed to dew, drought-stressed plants increase their leaf relative water content and net photosynthetic rate [28-30]. The amount of dew absorbed by different plants depends on plant variety, survival strategy, and soil moisture conditions. Dew has a short-term effect on plant survival in drought circumstances [28]. Dew contributes 9%-16% to stem water in Wet Scrub, and this percentage increases to 14%-20% in Dry Scrub [31]. Foliar could absorb much dew water especially during drought when the water stress is great. When a leaf experiences a water deficit, it creates a driving gradient for its water uptake [32]. When the soil is not subjected to any water stress, dew is only a supplementary water source.

Effect of Air Temperature and Wind Speed on Dew Absorption

When meteorological conditions changed, F_w and F_u also changed. The F_w to the three plants was the lowest at 15ºC (Fig. 2), and the F_w of *Z. truncatus*, *C. comosum*, and *J. formosana* leaves was 8.48%±0.68%, 7.10%±0.92%, and 4.30%±0.62%, respectively. For *Z. truncatus*, F_w increased with air temperature to 8.72%±0.42% and 10.52%±1.39% under 20ºC and 25ºC, respectively. Meanwhile, F_w was 7.88%±0.51% (*C. comosum*) and 5.46%±0.81% (*J. formosana*) at 25ºC, which were slightly lower than those at 20ºC.

The F_u of the three plant varies with air temperature and was the lowest at 15ºC (Fig. 3). When the air temperature increased from 15ºC to 25ºC, the F_u of *Z. truncatus* increased significantly (P = 0.00057) from 26.53%±2.18% to 34.81%±4.61%. At high air temperature, the adaptability of *Z. truncatus* was strong, and its leaf absorption capacity was enhanced. The F_u of *C. comosum* was 23.39%±4.35% at 20ºC, and this value was not significantly different from that at 15ºC (P = 0.475) and 25ºC (P = 0.887). The proportion of dew absorbed by *J. formosana* at 20ºC was 11.95%±1.35%, which was significantly higher than that at 15ºC (6.26%±0.69%) (P = 0.013) and had no significant difference from that at 25ºC (10.22%±3.02%) (P = 0.432). The effect of air temperature on the dew uptake capacity of plants was not consistent and was not observed for species such as *Z. truncatus* with strong adaptability to air temperature change. The F_w and F_u of different plants do not increase with air temperature, and the leaves easily absorb dew at 20ºC for *C. comosum* and *J. formosana* and 25ºC for *Z. truncatus*. This phenomenon occurred because 20ºC or 25ºC is the most suitable air temperature for plant growth because it accelerates the metabolic rate of plants and promotes the absorption of dew on leaves. High air temperature is widely considered as the dominant factor contributing to the increase in evaporation [33]. High air temperature (>20ºC) also increases dew evaporation and decreases near surface relative humidity [34]. Evaporation reduces the contact time between the leaves and dew, thus consequently decreasing dew absorption.

The δD and F_w of the three plants showed a decreasing trend with the increase in wind speed (Fig. 2). Under breezeless condition, the proportion of dew in *Z. truncatus*, *C. comosum*, and *J. formosana* leaves was 8.72%±0.42%, 8.26%±0.84% and 6.68±0.77%, respectively, which decreased to 7.64%±0.50%, 6.84%±0.45%, and 5.04±0.61%, respectively, at the wind speed of $2 m·s^{-1}$. The F_u of the three plants tended to decrease with the increase in wind speed but did not decrease significantly. With *C. comosum* as an example, the F_u was 23.39%±4.35%, 22.24%±1.94%, and 20.50%±1.89% at the breezeless, $1 m·s^{-1}$, and $2 m·s^{-1}$ wind speed, respectively, and no significant difference in F_u was observed under breezeless and $1 m·s^{-1}$ (P = 0.550), or $2 m·s^{-1}$ wind speeds (P = 0.148). Wind is the most important driver for evaporation, and high wind speed enhances the evaporation rate [35]. On windy mornings, the dew that condensed on leaves depletes quickly and reduces the time for dew station on leaves [36], leading to the reduction of dew absorbed by plants.

As shown Fig. 3, much of the dew returned to the atmosphere through evaporation, and only

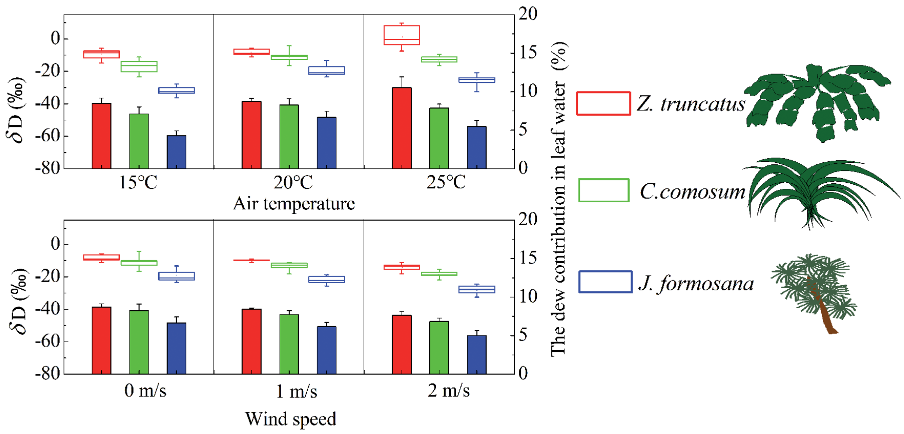

Fig. 2. δD value (box) and contribution rate of dew (bar) (mean±SE, n = 5) to different plants under various air temperatures (15ºC, 20ºC, and 25ºC) and wind speed (0 m·s^{-1}, 1 m·s^{-1}, and 2 m·s^{-1}).

6%-35% of the dew was absorbed by plant leaves. Under the experimental conditions, the F_u of different plants varied greatly. The F_u of *Z. truncatus* (25.96%±2.69% – 34.81%±4.61%) was significantly higher than that of *C. comosum* (20.50%±1.89% – 23.39%±4.35%) and *J. formosana* (6.26%±0.69% – 11.95%±1.35%). Under different air temperature and wind speed conditions, the F_u of *Z. truncatus* was higher than that of *C. comosum* (P = 2.19E^{-10}) and *J. formosana* (P = 1.06E^{-30}), and F_u of *C. comosum* was also higher than that of *J. formosana* (P = 2.22E^{-19}). Therefore, meteorological factors and plant species are the effect factors on dew absorption, but plant species are the main factors. Meteorological factors have varying effects on the dew absorption of different plant species.

Effect of Leaf Microstructure on Dew Absorption

All three species absorbed dew through their leaves, but the capacity differed among them (Figs 2 and 3). The amount of dew absorbed by *Z. truncatus* leaves was higher than that of *C. comosum* and *J. formosana*. Under the same soil, moisture, and meteorological conditions, the difference is mainly due to the leaf shapes and microstructure of the three plants. Holanda et al. [9] reported that the species' morphoanatomical traits may be related to the difference in their dew usage. The three plants have different leaf shapes, and all leaves have wax (Fig. 4 d, e, and f). The surface wax layer content of *J. formosana* (1.25±0.09 g·m^{-2}) and *C. comosum* (0.79±0.09 g·m^{-2}) was higher than that of *Z. truncatus* (0.49±0.11 g·m^{-2}). In addition, the drop contact angle (DCA) of *J. formosana* (119.6°±10.5°) and *C. comosum* (109.6°±6.5°) was higher than that of *Z. truncatus* (82.8°±12.3°). This finding indicated that *J. formosana* is more hydrophobic than *C. comosum* and *Z. truncatus*. The lipid-rich wax acts as a barrier for the bidirectional transport of substances between the plant and the surrounding environment [37], and the wax layer can create an air layer between the leaves and the water to prevent the dew from entering the leaves.

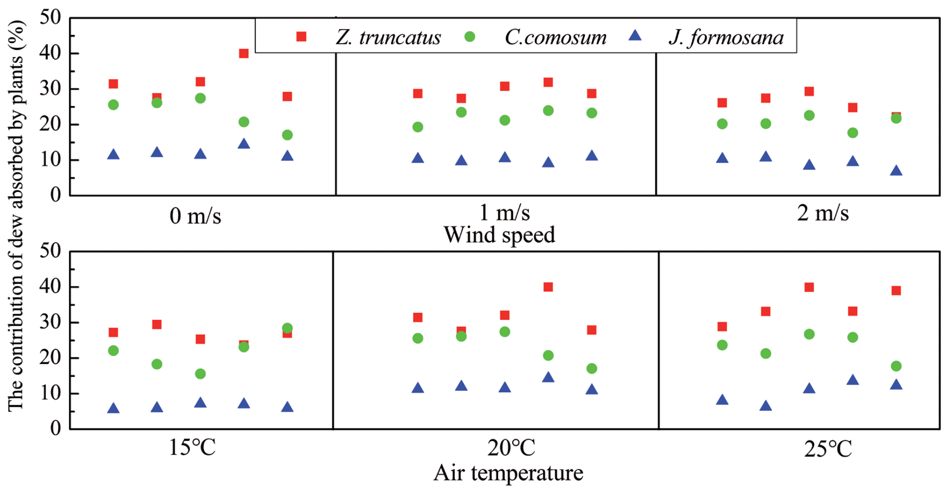

Fig. 3. F_u of different plant species under various air temperature(15ºC, 20ºC, and 25ºC) and wind speed (0 m·s^{-1}, 1 m·s^{-1}, and 2 m·s^{-1}).

The three plants all have the stomata distributed on the leaves. The stomatal pore diameter of *Z. truncatus*, *C. comosum*, and *J. formosana* was 40.90, 41.53, and 37.19 μm, respectively (Fig. 4(d, k, l)), and the stomatal pore density was 22±8.8, 64±20.5, and 35±10.5·mm^{-2}, respectively. No significant difference in stomatal size was found among the three plants, and he stomatal density of *C. comosum* was higher than that of the other two plants. Plants utilize water that condenses on leaf possibly through stomatal pores [29, 38]. Larcher et al. [11] found that leaf water absorption is positively related to stomatal density. Stomata constitute a major pathway for dew uptake, thus explaining why all three plants can absorb dew despite of their waxy structures.

In addition to its stomata pores, the *Z. truncatus* has a unique structure on its leaf edge (Fig. 4(g, j)). *Z. truncatus* is a member of *Opuntia* and has the microstructures of glochids (Fig. 4g) and trichomes (Fig. 4j) [39]. The droplets nucleate on the glochid tips and then move from the tip to the base of the glochid where they are distributed with dense trichome. These devices may contribute to optimized moisture harvesting. Therefore, *Z. truncatus* absorbs more dew than the other two plants. Leaves with dense trichome absorb much dew, which agrees well with previous studies. Schwerbrock and Leuschner [13] showed a positive relation between trichome density and foliar absorption. Yan et al. [4] also found the tree species with trichomes had the largest amount

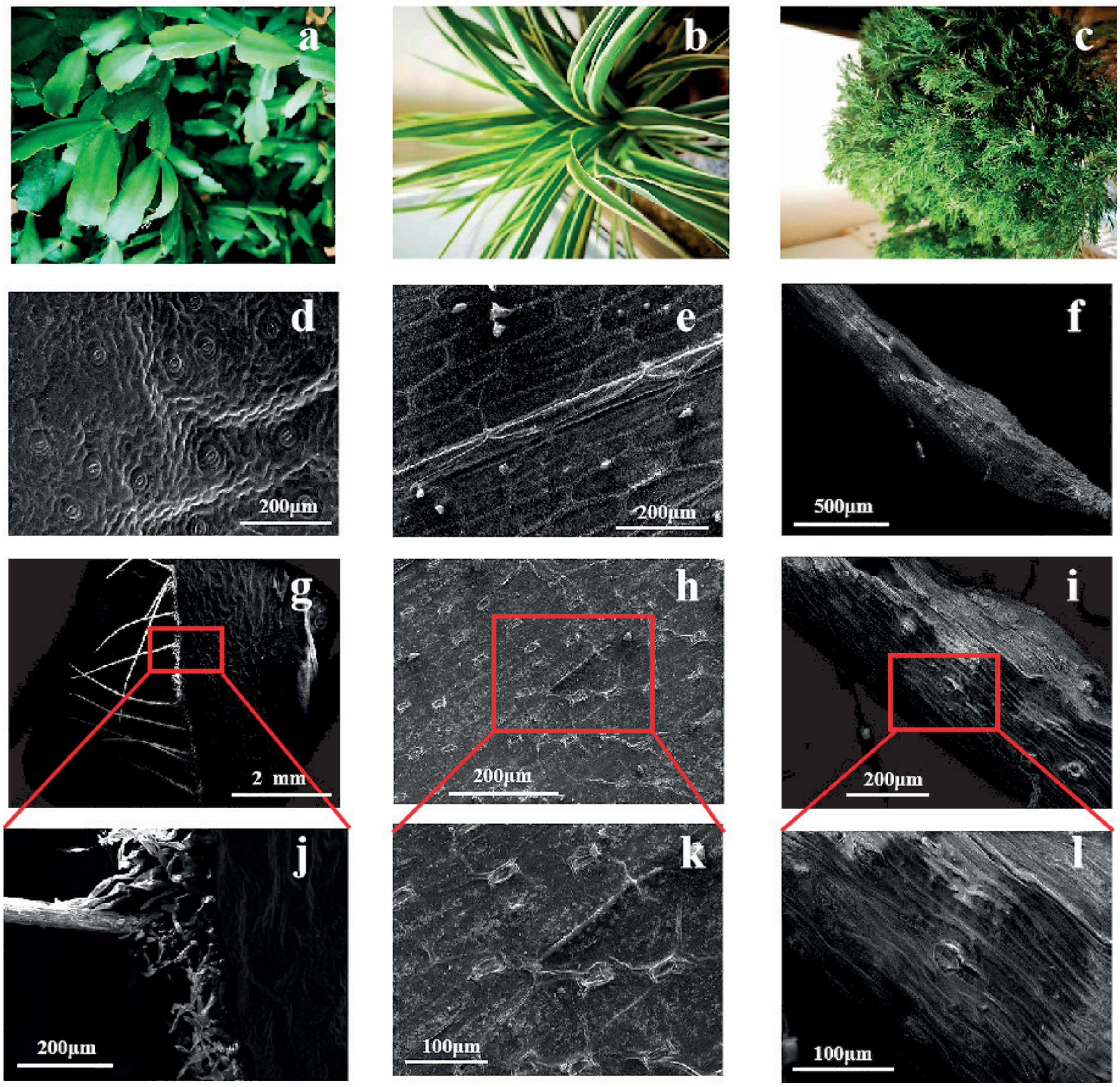

Fig. 4. Microstructure of different plant leaves with SEM.
(a: photograph of *Z. truncatus* b: photograph of *C.comosum* c: photograph of *J. formosana*; d: abaxial leaf surface of *Z. truncatus* (×500); e: adaxial leaf surface of *C.comosum* (×500); f: leaf surface of *J. formosana* (×200); g: leaf edge surface of *Z. truncatus* (×50); h: abaxial leaf surface of *C.comosum*. (×500); i: leaf surface of *J. formosana* (×500); j: one glochids dense mat of trichomes in the base of *Z. truncatus* (×500); k: abaxial leaf surface of *C.comosum*. (×1000); l: leaf surface of *J. formosana* (×1000)).

of adsorbed water compared to those without trichomes. This finding indicated that leaf trichome structure probably influences the foliar water uptake. Trichome is hydrophilic and has a strong adhesive force to facilitate dew absorption [40].

Although *C. comosum* and *J. formosana* do not have the trichome structure, they can absorb dew through their leaves. Although the tomentum on leaves is the location of dew absorption, the leaves without tomentum do not necessarily lack the ability to absorb dew. Gong et al. [41] found that tomentum-less leaves can also absorb dew. Trichome are not the factor that determines whether the leaves can absorb dew and instead help the leaves to absorb dew. Our studies indicated that external microstructures, such as stomatal pores and tomentum, might be advantageous in absorbing water from dew. Leaves with dense tomentum and stomata highly benefit from dew, and hydrophobicity leaves with waxy layer could prevent dew from entering the plant body to some extent.

Conclusions

Indoor pot experiment on the three plants commonly found in northern cities of China revealed that all their leaves can absorb dew, but the capacity differed among species. The F_u of *Z. truncates* (25.96%±2.69% – 34.81%±4.61%) was higher than that of *C. comosum* (20.50%±1.89% – 23.39%±4.35%) (P = 2.19E^{-10}) and *J. formosana* (6.26%±0.69% – 11.95%±1.35%) (P = 1.06E^{-30}) under different air temperature and wind speed conditions. Approximately 65%-94% dew condenses at night and returns to the atmosphere through evaporation, and the remaining dew was absorbed by plant leaves. The dew absorption capacity of the leaves of the three plants did not increase with the air temperature. For *C. comosum* and *J. formosana*, the dew absorption capacity at 20ºC was higher than that at 15ºC and 25ºC. *Z. truncatus* absorbed more dew at 25ºC compared with the other two species. All three plants showed a decrease in dew absorption with the increase in wind speed. The F_u varied depending on the plant species due to the different leaf microstructures. Although the three plants exhibited foliar uptake capacity, the *Z. truncatus* with trichome and stomatal pores showed higher dew uptake capacity than *C. comosum* and *J. formosana*. The water-absorbing ability of the hydrophilic *Z. truncatus* and *C. comosum* was higher than that of the hydrophobic *J. formosana*. The tomentum and stomata on the leaf surface are beneficial to the water entering into the plant and are accessory structures for water absorption. This paper provides a theoretical basis f or further discussion of the ecological importance of dew. Further discussion is needed on the nutrients in dew absorbed by plants.

Acknowledgments

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Conflict of Interest

The authors declare no conflict of interest.

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