

Article

Physiological Responses and Ecological Benefits of Water Uptake by *Populus euphratica* Leaves in Arid Areas

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Abstract: The absorption of atmospheric water by plants through their leaves, known as leaf water uptake, plays a crucial role in sustaining plant growth and survival in arid regions. Condensate is one of the important sources of water for plants in arid zones and plays an important role in alleviating the physiological state of plant water. In order to clarify the ecological role of the leaf absorption of condensation water, we took the dominant species of the desert Dugay forest plant, *Populus euphratica*, as the research object, and based on in situ leaf humidification field experiments, we comprehensively analyzed the effect of condensation water on the physiological state of *P. euphratica* and the ecological benefit of leaf water absorption on the arid zone by determining the parameters of the physiological indexes of the leaf, the leaf wettability, and the water-absorbing capacity of the leaf. The results showed that *P. euphratica* leaves have a water-absorbing ability on both sides, and under the condensation water treatment, the water potential of dawn leaves in the TR group (-1.75 ± 0.12 MPa) was significantly higher than that in the CK group (-1.41 ± 0.13 MPa); the net photosynthetic rate of leaves in the TR group ($13.08 \pm 0.68 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was significantly higher than that in the CK group ($10.42 \pm 0.57 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$); the proline content of the TR group ($22.82 \pm 0.8 \mu\text{g}\cdot\text{g}^{-1}$) was significantly lower than that of the CK group ($68.67 \pm 6.14 \mu\text{g}\cdot\text{g}^{-1}$); and the leaf photosynthetic capacity, leaf osmotic adjustment, and stress tolerance affected by condensation water were significantly different ($p < 0.05$). A leaf's water-absorbing ability is mainly affected by leaf wettability, the proline content, and other influencing factors. The mean FWU rate was positively correlated with the mean transpiration rate. Within the Ebinur Lake watershed, the water absorption rate of *P. euphratica* leaves accounts for 10.92% of the maximum transpiration rate (T_r); in 2022, the total summer leaf surface water uptake by *P. euphratica* was about 220.5 mol, a value that represents about 0.25% of the average annual evapotranspiration from Ebinur Lake. This study helps to improve the understanding of the impact of condensation water on the physiological ecology of the desert plant *P. euphratica* and provides a scientific basis for the ecological benefits of leaf water absorption in arid regions.

Keywords: arid zone; leaf wettability; foliar water uptake capacity; physiological regulation; *Populus euphratica*



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1. Introduction

Moisture is the most important environmental limiting factor in arid zones and an important ecological factor affecting the growth of trees in desert ecosystems [1]. As an important supplementary water source to alleviate the water shortage condition of plants, condensation water plays an important ecological role [2,3]. The frequent occurrence of condensation under arid conditions significantly affects the photosynthesis, water relations, and growth of desert plants [4–6]. During condensation events, leaves can directly absorb and utilize condensation water on the leaf surface, and the leaf temperature and

stomatal conductance will decrease, resulting in a reduction in the transpiration water consumption by plants [7,8]. Leaf wetting can affect plant function through different mechanisms. Wet leaves also provide sufficient water for photosynthesis as well as the root absorption of nutrients from the soil, and changes in the microclimate near the leaf surface, including an elevated atmospheric humidity, can reduce stomatal transpiration rates [8]. Although there have been many studies on the ecological role of condensation water on desert plants [9], there is still incomplete information on the effect of condensation water on the growth of woody plants and the ecological benefits of condensation water.

Since Hales (1727) first proposed the doctrine of leaf water uptake [10], Stone reported that the drought-tolerant American yellow pine (*Pinus ponderosa*) sustains itself by absorbing condensation and rainwater through the needle leaf blades when soil moisture is extremely scarce [11]. When the leaf blade is in a moist state, its internal water potential is lower than the external water potential, resulting in the phenomenon of leaf water uptake (foliar water uptake, FWU) [12]. Leaf water uptake is a widespread physiological phenomenon in natural ecosystems [13] and is one of the most important strategies for plants to maintain their water balance [14]. In some plants, the leaf water uptake rate and water uptake together determine whether the plant can utilize water efficiently [15–18]. Observations in cloud forests have shown that condensation water, calculated using hydrogen and oxygen isotope tracing, contributes up to 31% of the water source of the European spruce (*Picea abies*) [19], and that stem flow reversals from condensation water absorption account for 9% of dry season transpiration [20]. It has also been found that the total water absorbed from leaf surfaces by shrubs and herbaceous vegetation in the Patagonian steppe during spring and summer was 50 mol, which accounted for 11.6% of the total evapotranspiration of the site [21]. Precisely because of the variability in the water inputs in different habitats, it is necessary to carry out a study on the potential evapotranspiration of condensed water absorbed by the leaves of woody plants in the dry season in arid zones.

Water resources are very scarce in the Ebinur Lake basin in Xinjiang due to the scarcity and uneven distribution of precipitation [22,23]. Therefore, it is important to study the water uptake by plant leaves within this watershed to deepen the understanding of plant water use mechanisms in arid regions. In this study, *Populus euphratica*, a typical desert plant in the Ebinur Lake Basin, was used as the research object to explore the following issues, through simulated condensation water experiments and on the basis of leaf water potential, photosynthetic parameters, oxidative metabolism, and stress resistance, as well as leaf water uptake capacity and leaf wettability indicators: (1) What are the main influencing factors of water absorption indexes? (2) What are the ecological benefits of leaf humidification?

2. Materials and Methods

2.1. Overview of the Study Area

The study area was located within the Xinjiang Ebinur Lake Wetland National Nature Reserve (44°43′–45°12′ N, 82°35′–83°40′ E), with an area of 2670.85 km², adjacent to the bank of the Aqixu River in Jinghe County, which is the lowest depression and saltwater pooling zone on the southwestern margin of the Junggar Basin. The reserve is affected by a typical mesothermal continental arid climate, with an average annual temperature of 6–8 °C, an average annual precipitation of 90.8 mm [24], and an annual evapotranspiration of more than 1600 mm [25]. Rainfall is unevenly distributed annually, with summer precipitation accounting for 34.0% to 66.6% of the annual precipitation. Due to the complex topography and harsh climatic conditions, a unique desert–wetland–Gobi composite landscape is formed in the watershed. The region is characterized by high dune mobility and low vegetation, with an average moisture content of 7.9% in the topsoil and a pH value of 7.55. The main soil types are grey-brown desert soils, grey desert soils, salt soils, and wind-sand soils [26]. The plants are dominated by drought-tolerant desert plants, mainly the trees *Populus euphratica*, *Haloxylon ammodendron*, *Tamarix chinensis*, etc.

2.2. Sample Plot Design

In July 2022, a sample plot was selected to be set up within the desert habitat 2 km to the north of the Dongdaqiao management station in the Ebinur Lake Wetland National Nature Reserve. A large sample square of 100×100 m was set up in this sample plot, and three mature and healthy *P. euphratica* plants with similar habitats and individual sizes of 30 cm diameter at breast height and about 6 m in height were selected and labelled as the test plants within the sample square. The test area was gently sloping, there was no rainfall in the week prior to the test treatments, and the weather during the test was sunny, with an average daily temperature of 23.6°C .

2.3. Test Methods

2.3.1. In Situ Field Control Test

The in situ field control test was conducted at the mature stage (July 2022) of *P. euphratica* growth. As shown in Figure 1, two parts of different branches of the same main stem of each *P. euphratica* were treated separately, as follows: for 4 branches low in the canopy, the branches treated with water sprayed from a small spray can as condensation were recorded as TR, while the branches not treated with condensation were recorded as CK or the control.

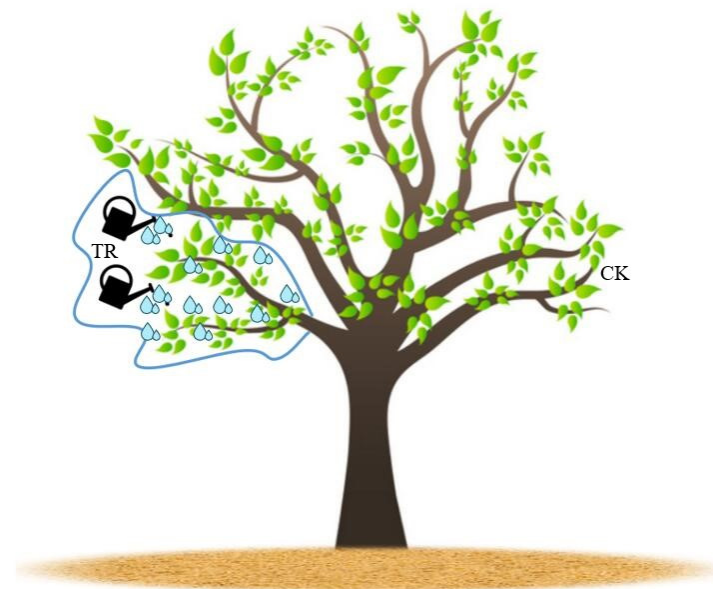


Figure 1. Schematic diagram of control experiment.

2.3.2. Measurement of Leaf Water Potential at Dawn and Noon

To evaluate the effect of leaf water uptake on the leaf water potential (Ψ_{Leaf}), the leaf water potential (Ψ_{initial}) of *P. euphratica* TR and CK plants was measured at dawn (06:00) and noon (14:00) on July 7 using a pressure chamber (PMS System, Corvallis, OR, USA). Then, distilled water was sprayed on four branches of each of the three *P. euphratica* plants and the branches were kept wet for 1 h (spray treatment); other branches of the same *P. euphratica* plant were kept dry (control treatment). The leaf water potential (Ψ_{final}) was measured after 1 h. The leaf water potential (Ψ_{final}) was measured 1 h after spraying. Twelve replicates were set up for each treatment.

$$\Delta\Psi_{\text{Leaf}} = \Psi_{\text{final}} - \Psi_{\text{initial}} \quad (1)$$

2.3.3. Measurement of Photosynthetic Parameters

Using an Li-6400XT portable photosynthesizer (LICOR, Lincoln, NE, USA) equipped with a 2×3 cm standard transparent leaf chamber and an LED light source (6400-02B), the gas exchange characteristics of *P. euphratica* leaves from different treatments were

measured at 12:00 noon under sunny weather conditions (3 July). The measurement conditions were kept as follows: the CO₂ concentration was 400 ± 5 ppm and the PPFD was $1200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. For the measurement, four mature and healthy leaves were selected from each of the three *P. euphratica* plants on each *P. euphratica* TR and CK branch, and 12 replicates were set up for each treatment. The light source was natural, with the stable input of the atmospheric CO₂ concentration controlled by a buffer bottle device. The measured parameters mainly included the following: the net photosynthetic chemical rate (P_n , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), the transpiration rate (T_r , $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), the intercellular CO₂ concentration (C_i , $\mu\text{mol}\cdot\text{mol}^{-1}$), the stomatal conductance (g_s , $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and the related index water use efficiency (WUE, $\mu\text{mol}\cdot\text{mmol}^{-1}$). The WUE was calculated as follows:

$$\text{WUE} = P_n / T_r \quad (2)$$

2.3.4. Measurement of Osmoregulatory and Antioxidant Enzymes

For the determination of antioxidant enzymes (catalase: CAT, superoxide dismutase: SOD, and proline: PRO) and osmoregulatory substances (soluble sugars: SS and malondialdehyde: MDA), 0.5 g of fresh plant samples was weighed and placed into a mortar and pestle, and then liquid nitrogen was added (enough to cover the tissues completely) to grind the tissues and break them up. Then, 2 mL of pre-cooled phosphate buffer and 0.1 g of polyvinyl were added. After that, 2 mL of pre-cooled phosphate buffer and 0.1 g of polyvinylpyrrolidone (PVP) were added and the mixture was ground on ice. The sample was then transferred into a centrifuge tube; the mortar was washed with 2 mL of buffer, which was transferred into the centrifuge tube; and the sample was centrifuged for 20 min at 15,000 r/min under 4 °C. The supernatant was the crude enzyme extraction solution. The crude enzyme extract was divided into tubes for the determination of osmoregulatory substances and antioxidant enzyme activities, and the determination methods are shown in Table 1.

Table 1. Methods for determination of osmoregulation and antioxidant enzymes.

Oxidative Metabolism	Abbreviation	Method
Malondialdehyde	MDA	enzyme marker
Superoxide dismutase	SOD	enzyme marker
Catalase	CAT	spectrophotometer
Soluble sugar	SS	enzyme marker
Proline	PRO	enzyme marker

2.3.5. Water Droplet Experiment

Three healthy *P. euphratica* plants were selected as replicates within the sample plot, and four leaves were collected from each tree for a total of 12 healthy and intact leaves, which were placed horizontally on the sampling table using double-sided adhesive tape, with six of them facing upwards on the front side and the remaining six facing upwards on the back side. Then, a pipette gun (range of 5–100 μL , precision of 1 μL) was used to titrate water droplets onto the leaf surface (the tip of the gun at the beginning of the titration was perpendicular to and in contact with the leaf surface, and was gradually lifted up during the titration; the tip of the gun was separated from the upper surface of the droplets at the end of the titration). Different water droplet volumes were measured for each leaf (5 μL , 15 μL , and 30 μL for each of the two leaves, adaxial and abaxial) and three equal water droplets per leaf were used as 1 parallel experiment for this treatment. Finally, immediately after the water droplets touched the leaf surface, a side view of the water droplets was taken with a macro camera (Nikon Corp., Tokyo, Japan).

The droplet–leaf contact angle (θ) is the angle between a straight line tangent to the droplet and passing through the point of contact between the droplet and the surface of the leaf blade; the larger θ is, the more repulsive it is to the leaf surface and the lower the leaf wettability, and the smaller θ is, the less repulsive it is to the leaf surface and the higher

the leaf wettability (Figure 2) [27–29]. Finally, the contact angle θ was calculated using the contact angle plug-in in ImageJ v.1.8.0 (NIH, Bethesda, MD, USA).

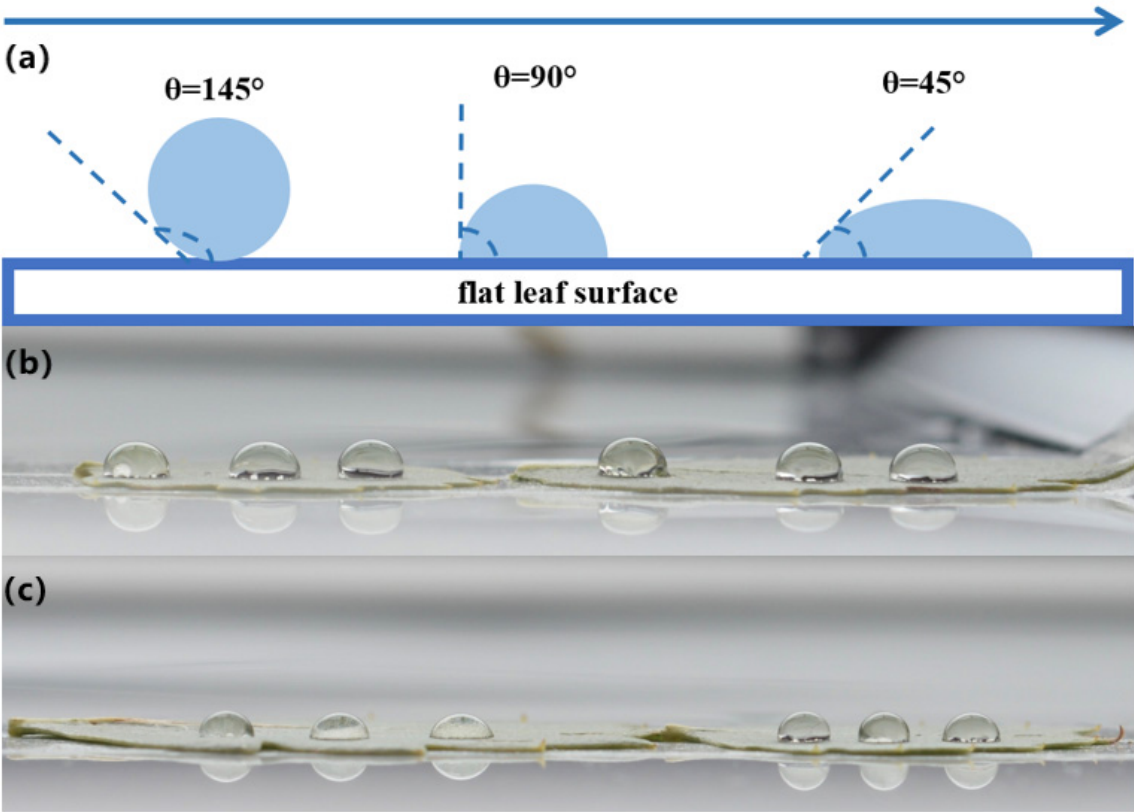


Figure 2. Schematic diagram and experimental diagram of contact angle between water droplets and blade surface. Note: (a) is the schematic diagram of the experiment, (b) is the experimental diagram of 30 μL of water droplets on the back of the leaf, and (c) is the experimental diagram of 30 μL of water droplets on the front of the leaf.

2.3.6. Determination of Water Absorption Parameters

Leaf blades were cut from twigs according to the method determined by Liang et al. [30], the leaf area (LA ; cm^2) was measured before the start of the experiment, and the petioles of the leaves were subsequently sealed with petroleum jelly. The leaf fresh weight (CW) was determined before and after sealing. After the fresh weight measurement, the leaves were completely submerged in deionized water in a dark environment, avoiding contact between water and the petiole, and weighed every 15 min for 2 h, then every 30 min for 2 h. Finally, the leaves were submerged in water again for 1 h and weighed to obtain the saturation weight, SW . The formula for the total foliar water uptake (mm) is as follows:

$$\text{Total FWU (mm)} = \Sigma \text{FWU} \times \text{LAI} \times \% \text{Cover} \times \text{accumulated LWD} \tag{3}$$

The main water absorption parameters were as follows (Table 2).

Table 2. Measurement of water absorption parameters.

Main Water Absorption Parameters	Unit	Formula
Foliar water uptake capacity ($\text{FWU}_{\text{capacity}}$)	$\text{mg} \cdot \text{cm}^{-2}$	$\text{FWU}_{\text{capacity}} = \frac{\text{SW} - \text{CW}}{\text{LA}}$
Cumulative leaf water uptake (ΔM)	$\text{mg} \cdot \text{mg}^{-1}$	$\Delta \text{M} = \frac{\text{SW} - \text{CW}}{\text{CW}}$
Leaf water absorption rate (k)	$\text{mg} \cdot \text{cm}^{-2} \cdot \text{min}^{-1}$	$k = \frac{\text{FWU}_{\text{capacity}}}{t}$

Note: SW is leaf saturation weight, CW is fresh weight, LA is leaf area, and t is time.

2.4. Data Processing

A two-way analysis of variance (ANOVA) was used to investigate the wettability of the leaves of the plants to be tested and a one-way ANOVA was used to analyze the variability in the water uptake and the photosynthetic, hydrodynamic, and oxidative metabolism parameters in the presence and absence of condensate. The LSD test was used for comparisons when the variances were aligned, and the Games–Howell test was used for comparisons when the variances were not aligned. Secondly, we used logistic and exponential equations to fit a model for the change pattern of leaf water uptake over time, with a confidence level of 0.95. We used R (version 4.3.1, <http://www.r-project.org/>) to carry out a principal component analysis of the influencing factors, and we explored the main influencing factors of FWU and the relationships. The one- and two-factor ANOVA were performed in SPSS 27.0 (IBM Corp., Armonk, NY, USA), and the logistic and exponential model fitting as well as the graphic production were performed in Origin 2023b (OriginLab, Northampton, MA, USA). The level of significance was $\alpha = 0.05$.

3. Results

3.1. Response of *Populus euphratica* Leaves to Changes in Condensation Water

3.1.1. Variability in Leaf Water Potential under Condensation Water Treatment

The leaf water potential reflects the water deficit of leaves. As can be seen in Figure 3, the differences between the dawn water potential (Ψ_{pd}) and the noon water potential (Ψ_{md}) of *P. euphratica* leaves under different condensation water treatments were significant ($p < 0.05$). The dawn leaf water potential of -1.75 ± 0.12 MPa under the condensation water treatment was significantly higher than that of the CK group, with -1.41 ± 0.13 MPa (Figure 3a), but the noonday leaf water potential under the condensation water treatment of -1.87 ± 0.17 MPa was slightly lower than the leaf water potential of -2.01 ± 0.22 MPa in the CK group (Figure 3b).

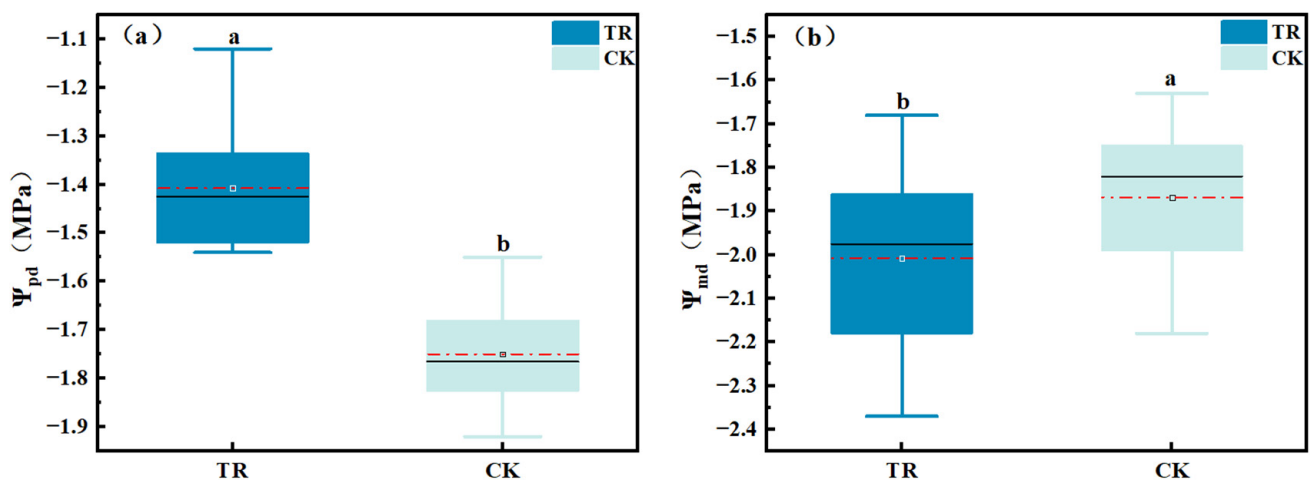


Figure 3. Difference in leaf hydraulic properties of *Populus euphratica*. Note: Blue and green colors are with and without condensate treatments, respectively; Ψ_{pd} in (a) and Ψ_{md} in (b) denote helioblast water potential and noonday water potential, respectively; and red dashed line and black solid line are mean and median lines, respectively. Figures containing different lowercase letters indicate significant differences ($p < 0.05$) between hydrodynamic parameters under different condensate treatments (mean $\pm$ standard error; $N = 12$).

3.1.2. Differences in Photosynthetic Parameters under Condensation Water Treatment

As can be seen in Figure 4, when simulating condensation water, the net photosynthetic rate of leaves in the TR group ($13.08 \pm 0.68 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was significantly higher than that in the CK group ($10.42 \pm 0.57 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and the stomatal conductance g_s of $0.31 \pm 0.02 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ under the TR treatment was not significantly different from $0.30 \pm 0.02 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ under the CK treatment ($p > 0.05$). P_n , T_r , and WUE were significantly higher under the TR treatment than in the CK group ($p < 0.05$), while C_i was significantly lower under the TR treatment than in the CK group (Figure 4a–e).

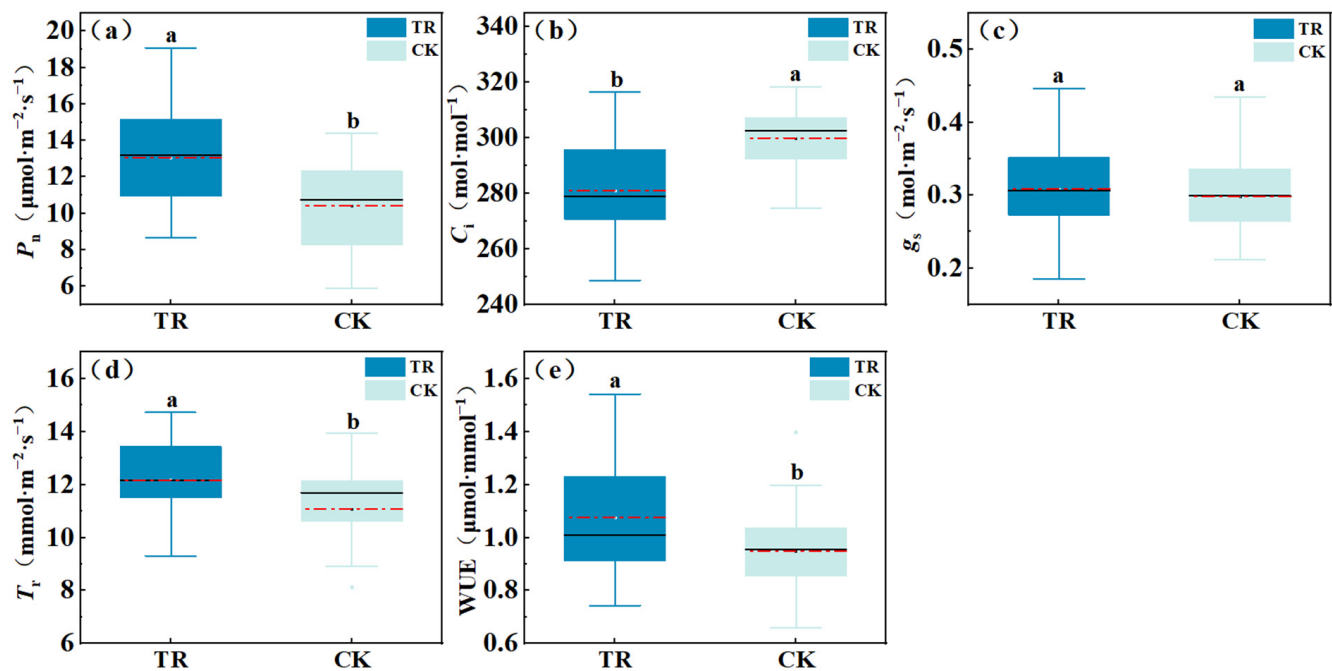


Figure 4. Difference in photosynthetic parameters of *Populus euphratica* leaves. Note: Blue and green colors are with and without condensation water treatments, respectively; P_n in (a), C_i in (b), g_s in (c), T_r in (d), and WUE in (e) are the net photosynthetic rate, intercellular carbon dioxide concentration, stomatal conductance, transpiration rate, and water use efficiency, respectively; and the red dashed line and the black solid line are the mean and median, respectively. Figures containing different lowercase letters indicate significant ($p < 0.05$) differences among photosynthetic parameters under different condensation treatments (mean $\pm$ standard error; $N = 12$).

3.1.3. Differences in Osmoregulation and Antioxidant Enzymes under Condensation Water Treatment

As can be seen from Figure 5, the proline content ($22.82 \pm 0.8 \mu\text{g}\cdot\text{g}^{-1}$) was significantly lower in the leaves subjected to the condensation water treatment compared to that of the CK group ($68.67 \pm 6.14 \mu\text{g}\cdot\text{g}^{-1}$), and the leaf CAT content of $46.71 \pm 2.45 \mu\text{mol}\cdot\text{g}^{-1}$ in the TR group was not significantly different from $45.58 \pm 1.18 \mu\text{mol}\cdot\text{g}^{-1}$ in the CK group ($p > 0.05$) (Figure 5b). The leaf PRO content, MDA content, and SS content in the TR group were all significantly lower than those of the CK group ($p < 0.05$), while the leaf SOD contents of the TR group were significantly higher than those of the CK group ($p < 0.05$) (Figure 5a–e).

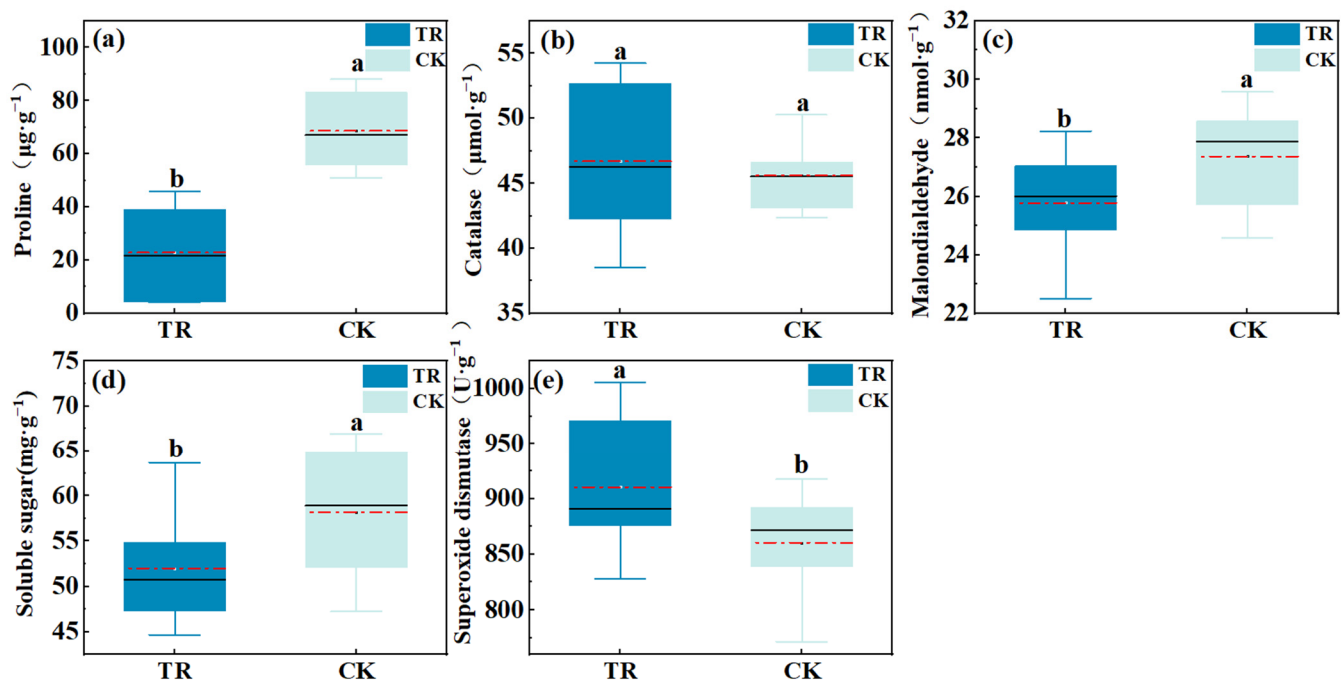


Figure 5. Differences in leaf permeability regulation and antioxidant parameters of *Populus euphratica*. Note: Blue and green colors are with and without condensate treatments, respectively; PRO in (a), CAT in (b), MDA in (c), SOD in (d), and SS in (e) refer to proline, catalase, malondialdehyde, superoxide dismutase, and soluble sugars, respectively; red dashed and black solid lines refer to mean and median, respectively. Figures containing different lowercase letters indicate significant ($p < 0.05$) differences between the oxidative metabolic parameters under different condensate treatments (mean $\pm$ standard error; $N = 12$).

3.2. Leaf Wettability

Variability Analysis of Contact Angle with Different Water Droplet Volume Sizes

The contact angle of the leaf blade's abaxial surface was found to be differential ($p < 0.05$) for all the different water droplet volume gradients, while the contact angle of the leaf blade's adaxial surface was only significantly different from the other water droplet volumes for a volume of $30\ \mu\text{L}$ ($p < 0.05$). The leaf blade's contact angle was not significantly different between the adaxial and abaxial surface ($p > 0.05$). At water volumes of $5\ \mu\text{L}$ and $15\ \mu\text{L}$, the contact angle of both the leaf's adaxial and abaxial surfaces was greater than 90° , and the leaf surface was hydrophobic. At a water volume of $30\ \mu\text{L}$, the contact angle of the adaxial surface was slightly less than 90° , showing weak hydrophilicity, while the abaxial surface was slightly higher than 90° , showing weak hydrophobicity. The hydrophilicity of the leaf blade's frontal surface tended to increase with an increase in the water droplet volume, while the hydrophilicity of the leaf blade's abaxial surface, with an increase in the water droplet volume, tended to decrease and then increase, and showed a better hydrophilicity than that for $5\ \mu\text{L}$ and $15\ \mu\text{L}$ when the water volume was $30\ \mu\text{L}$ ($p > 0.05$) (Figure 6).

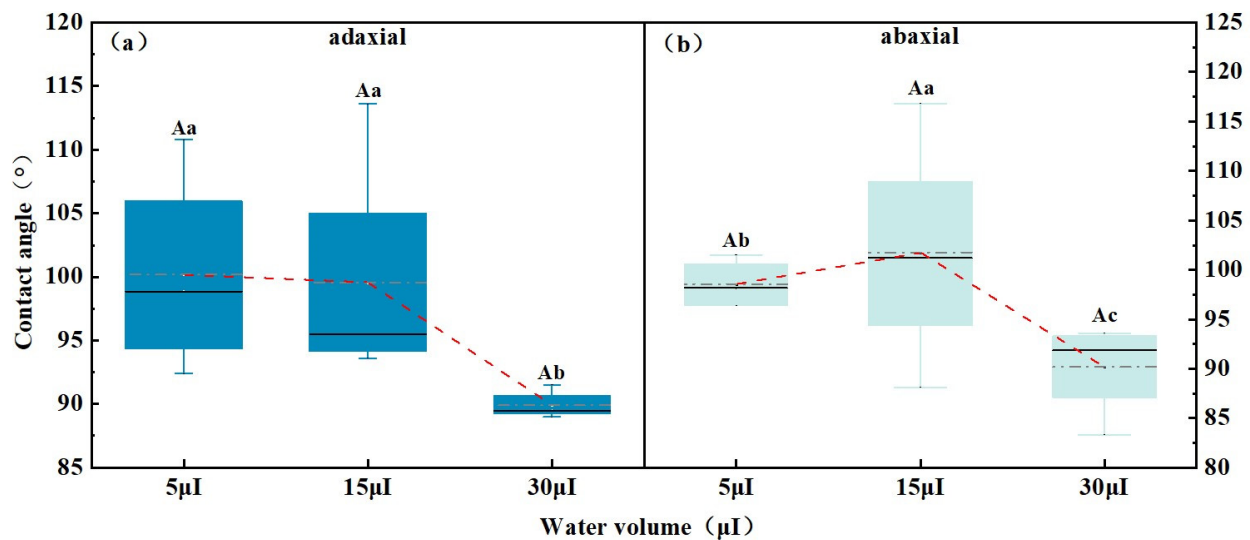


Figure 6. Difference in leaf contact angle under different water drop volumes. Note: (a) in blue and (b) in green show leaf adaxial and abaxial surfaces, respectively; the black dashed line and the black solid line in the box are the mean and median, respectively; and the red line shows the trend in the change in the mean contact angle with the increase in droplet volume. Different lowercase letters indicate significant ($p < 0.05$) differences in the leaf contact angle between different droplet volume treatments; different uppercase letters indicate significant ($p < 0.05$) differences in the leaf contact angle of the adaxial and abaxial surfaces between different droplet volume treatments (mean $\pm$ standard error; $N = 6$).

3.3. The Change Rule of Water Absorption Characteristics of *Populus euphratica* Leaves over Time

The *P. euphratica* pre-dawn leaf water potential (Ψ_{pd}) changed with time in a “J” type growth pattern; in the first 200 min, there was a rapid increase in the stage, followed by a flat trend (Figure 7a). The water uptake per unit area ($FWU_{capacity}$) of the *P. euphratica* leaves showed a logistic Steele curve growth pattern over time, which was divided into a slow-growth phase, a fast-rise phase, and a saturation phase, with a leveling-off trend after the first 100 min and 200 min, and the $FWU_{capacity}$ gradually reached its maximum value (Figure 7b). The leaf dynamic water content (ΔM) over time also showed a logistic Steele curve growth pattern; the curve showed an “S” type growth, and its change law and $FWU_{capacity}$ over time showed consistency (Figure 7c). The water uptake rate k of *P. euphratica* was higher at the beginning stage, when the relative water content of the leaves was lower; k showed a trend of increasing and then decreasing with time, and the water uptake rate decreased rapidly after 50 min. There was a trend of slow recovery at 180 min, but then it would continue to decline (Figure 7d).

3.4. Relationship among Water Uptake, Leaf Structure, and Hydrodynamic Parameters of *Populus euphratica* Leaves

In order to clarify the relationship between the water uptake of *P. euphratica* leaves and the leaf structural and hydrodynamic parameters, a principal component analysis (PCA) of the functional traits of *P. euphratica* leaves (Figure 8) showed that PC1 and PC2 explained 39.98% and 34.80% of the total variance, respectively. The leaf water uptake per unit area ($FWU_{capacity}$) was linearly and positively correlated with the leaf water uptake (ΔM), the intercellular carbon dioxide concentration (C_i), proline (PRO), and the noonday leaf water potential (Ψ_{md}), where the intercellular carbon dioxide concentration (C_i) and proline (PRO) were the main influencing factors of the leaf water uptake per unit area ($FWU_{capacity}$). The mean FWU rate was positively correlated with the mean transpiration rate.

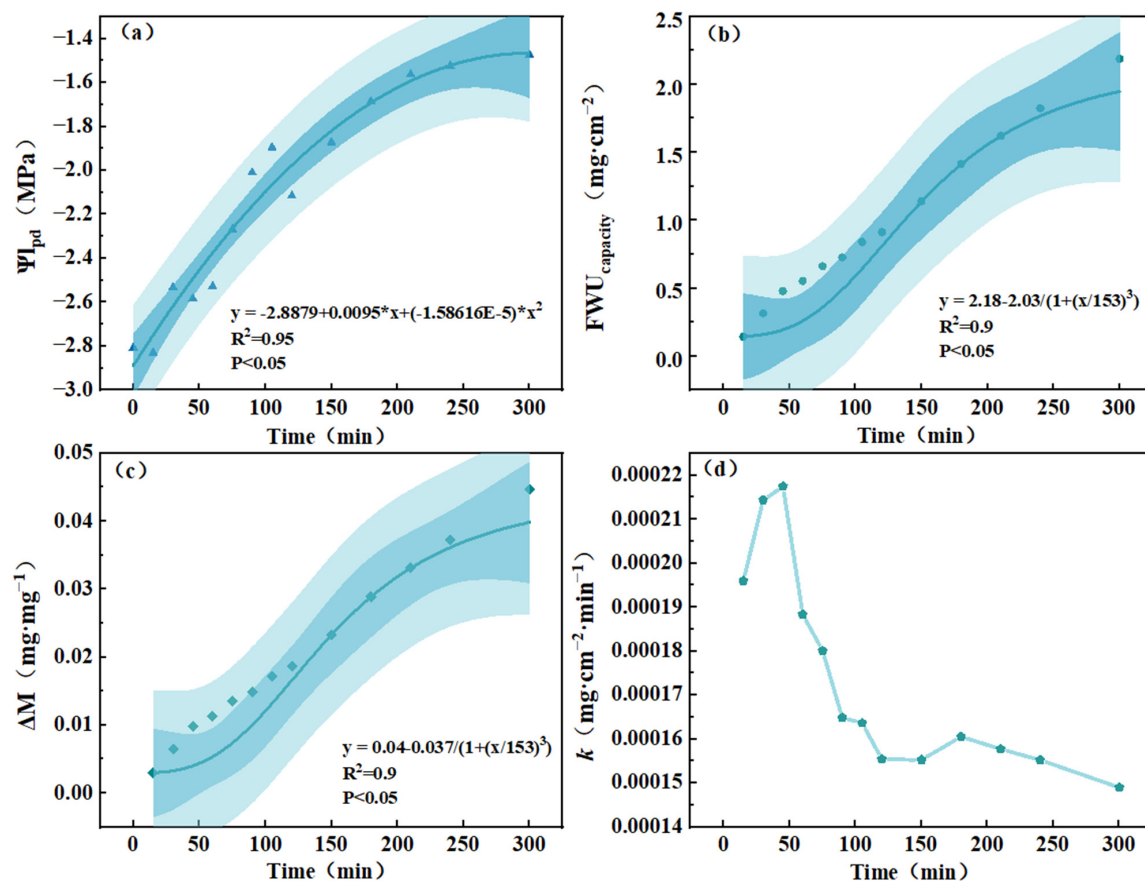


Figure 7. Changes in water absorption characteristics of *Populus euphratica* leaves with time. Note: (a–d) indicate the variation patterns of the dawn leaf water potential, the leaf water uptake per unit area ($FWU_{capacity}$), the leaf water uptake (ΔM), and the water uptake rate (k) over time, respectively; the blue area indicates the average confidence value of the model (95% confidence interval); and the green area indicates the average prediction value of the model (95% prediction interval) ($p < 0.05$, $N = 4$).

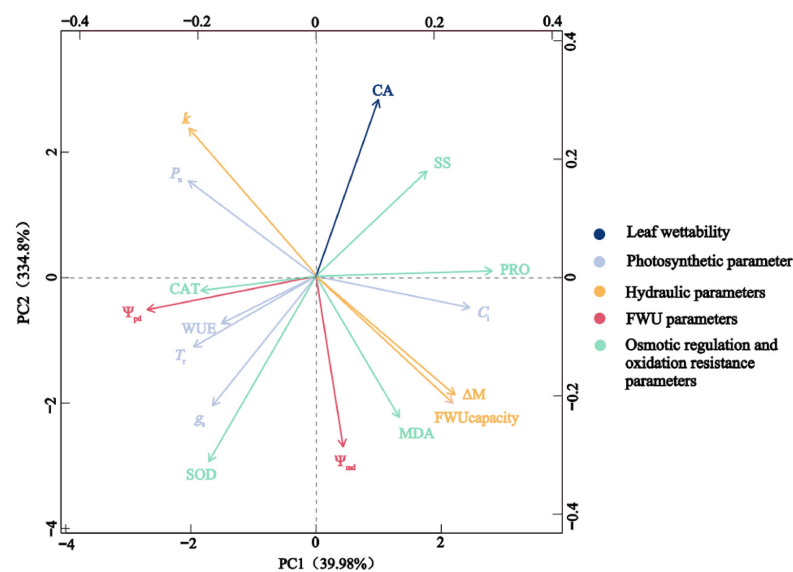


Figure 8. Principal component analysis of different factors. Note: the FWU parameters (FWU) include ΔM , $FWU_{capacity}$, and k ; the hydraulic parameters (HP) include Ψ_{pd} and Ψ_{md} ; leaf wettability (LW) denotes CA; the photosynthetic parameters (PP) include P_n , C_i , g_s , T_r , and WUE; and the stress resistance parameters (SRPs) include PRO, CAT, MDA, SOD, and SS. Light blue, green, yellow, red, and dark blue denote PP, SRP, FWU, HP, and LW, respectively ($p < 0.05$).

4. Discussion

4.1. Physiological Water Pattern of *P. euphratica* Leaves under Condensate Treatment

Moisture is a limiting factor for plant growth in arid zones [31]. Scarce condensation water can briefly compensate for the limitation imposed on plants suffering from various unfavorable factors such as a water deficit, so condensation water recharge becomes an important guarantee for plant survival [32,33]. It was found that the leaf water potential of *P. euphratica* leaves showed significant variability after the condensation water treatment (Figure 3). Leaf water potential is an important physiological indicator reflecting the degree of water deficit in plants, and it is widely used as a criterion for evaluating leaf water uptake in the study of leaf water uptake phenomena [34–36]. The results of the study simulating condensation water infiltration showed a significant physiological response of *P. euphratica* leaves. Compared with the control group, the increase in condensation water significantly increased the water potential of the dawn leaves in the *P. euphratica* treatment group, which was lower than the external atmospheric water potential, i.e., an approximate “reverse transpiration” [10]. The results showed that *P. euphratica* was able to fully utilize leaf water absorption to improve its physiological water status, and its reflective results were consistent with those of Li Luchen et al. [8]. Plants that are adapted to arid environments tend to close their stomata to avoid the loss of water by transpiration and to increase the concentration of osmotically active solutes, such as soluble sugars, in the leaves [37,38]. This behavior limits stomatal access to water and, thus, negatively affects FWU. To avoid transpiration in the control leaves (CK), it was observed (Figure 3) that the water potential of the dawn leaves after humidification was higher than the leaf water potential of the control leaves, which indicated that their stomata were effectively kept open during the wetting period. Therefore, the smaller decrease in the noon leaf water potential may have been due to the effect caused by FWU.

P. euphratica leaves are very sensitive to photosynthetic physiology under the influence of condensation water [39]. It has been pointed out that light and temperature are the main influencing factors of the net photosynthetic rate [40], while the water use efficiency (WUE) reflects the ability of plants to utilize water efficiently, and it is one of the effective indexes for assessing the drought tolerance of plants. In other words, under the same conditions, the higher the water utilization efficiency of a plant, the stronger its drought tolerance [41]. The results of this study (Figure 4) indicated that sufficient water ensured the net photosynthetic rate of *P. euphratica*, which was significantly increased in the presence of condensation water compared to the absence of condensation water, thus improving the water use efficiency and increasing the difference between the water use efficiency and the absence of condensation water, which contributes to a more efficient use of limited water resources. This result is similar to that of the study by Hengfang Wang et al. [42] on the effect of condensation water on salt spike wood. Most of the studies concluded that FWU moisturizes the leaves while leading to a decrease in transpiration [43,44], which suggests that plants have a trade-off strategy between replenishing water and diminishing photosynthesis, and such a strategy also changes with the environment; for example, higher parts of the leaves can receive more light energy, which increases photosynthesis, and the surroundings of leaves covered with condensation water may produce a low-temperature and high-humidity environment, which in turn also promote transpiration, and these may be the reasons for the increase in the transpiration rate in this study.

When subjected to environmental stress, plant cells accumulate large amounts of reactive oxygen species (ROS), and when ROS exceed a certain threshold, membrane oxidation occurs, which can even lead to plant death [45]. Changes in the activities of superoxide dismutase (SOD) and catalase (CAT), as scavengers of reactive oxygen species in plant cells, are closely related to the degree of membrane lipid peroxidation, and are one of the most important indicators of plant stress tolerance [46]. Although the results of this experiment showed that condensate had no significant effect on CAT (see Figure 5), the activity of SOD was significantly increased under the condensate treatment, which suggests that condensate can improve the water stress situation of leaves and enhance the

resilience of *P. euphratica*. Malondialdehyde is a secondary product of cellular membrane lipid peroxidation that can be used to measure the level of membrane lipid peroxidation and the degree of plasma membrane damage, and it is an important indicator for determining the repair capacity of plants [47]. In this study (see Figure 5), the malondialdehyde (MDA) content in the condensate-treated group was lower than that in the control group (CK), indicating that, under the action of condensate, the production and removal of reactive oxygen species in the plant body gradually restored the dynamic equilibrium, which mitigated the degree of cellular membrane lipid peroxidation and ultimately led to a significant reduction in the MDA content of *P. euphratica* leaves. Soluble sugar and proline are osmotic regulating substances; their content can reflect the strength of plant stress tolerance to a certain extent [48]. Numerous studies have shown that, under drought stress, the drought tolerance of plants varies with an increase or decrease in the proline content [49,50]. In this study, we found that the condensation water treatment decreased the soluble sugar and proline contents, which indicated that the *P. euphratica* leaves had some adaptive enhancement of both their osmotic regulation and antioxidant capacity under condensation water.

4.2. Patterns of Leaf Wettability and Water Uptake Characteristics

Leaf water uptake can keep the leaf moist for more than 3 h continuously. Similar to other arid ecosystems [51–53], *P. euphratica* has the ability to absorb water from the leaf surface during these wetting events. In this study, we found that the water droplet contact angle was not differentiated between the adaxial and abaxial surfaces of the leaf blade, indicating that both the adaxial and abaxial surfaces of the *P. euphratica* leaf blade have approximately the same water absorption capacity.

The amount of water absorbed per unit area and the water absorption capacity of *P. euphratica* leaves showed a logistic Steele curve growth pattern over time, which may be mainly related to the leaf surface wettability [54]. As can be seen in Figure 6, the presence of a cuticle (hydrophobic) affected the leaf surface wettability at the initial stage of water absorption, resulting in a low initial rate of water absorption. With the prolongation of water uptake, the water absorbed by the leaf promoted epidermal rehydration, which accelerated the rate of water uptake. As the amount of water absorbed by the leaf increased, the leaf water absorption gradually approached saturation, the rate of water absorption gradually decreased and eventually approached zero, and the leaf no longer absorbed water. This conclusion is consistent with the findings of Guzmán-Delgado et al. [55]. At the same time, the leaf water potential gradually increased with time, the water uptake slowed down, and the rate of increase in the water potential slowed down. Leaf wettability is again related to leaf structure.

4.3. Contribution of FWU to Ecosystem Evapotranspiration

Few studies have assessed the relationship between FWU rates and transpiration rates [56,57]. It has been found that, in epiphytes of tropical montane cloud forests, FWU accounts for about 30% of the water transpired during the dry season [14] and about 70% during the wet season [15].

The water uptake rate of *P. euphratica* leaves accounted for 10.92% of the maximum transpiration rate. According to the Jinghe County meteorological data, rainfall events occurred on 22 days from May to September in summer 2022, and the summer precipitation (131 mm) accounted for 73.1% of the annual precipitation (179.1 mm). During this period, the number of days on which condensation was observed to occur was 56 days, and taking into account both rainfall events and condensation events, the cumulative length of time that the surface of *P. euphratica* leaves were wet (LWD) in summer was approximately 267 h, of which the LWD of rainfall events was approximately 4.5 h and the LWD of condensation events was approximately 3 h. According to the MOD15A2H dataset, the poplar leaf area index (LAI) for the summer of 2022, from May to September, was approximately 2.12. Considering the percentage of cover of *P. euphratica* forest (16.5%) [58], as well as the

average FWU (0.0425 g), the leaf area index (2.11), and the leaf wetting accumulation time in LWD (267 h) over a 3 h period, and with reference to Equation (3) [59], it was estimated that the total amount of water absorbed by *P. euphratica* from the surface of the leaves in the summer of 2022 was about 220 mol per unit of ground (Equation (3)). This value represents 0.25% of the average annual evapotranspiration from Ebinur Lake.

Evergreen species can be limited by a reduced hydraulic conductivity of the root system during the hot summer months, when the FWU can still meet some of the water requirements as an auxiliary water source [59]. In this case, FWU may have a more significant role. Despite the lower involvement of FWU relative to the water uptake by plant roots, it still plays an important role in restoring plant leaf water potential. Considering that high-intensity evaporation and sustained strong winds in arid-zone ecosystems can lead to the rapid evaporation of surface water from *P. euphratica* leaves, the rapid response of *P. euphratica* leaves to wettability in the Ebinur Lake watershed may be one of the important dominant strategies.

5. Conclusions

Condensed water increased the water potential of *P. euphratica* leaves, enhanced the photosynthetic capacity, and improved osmotic regulation and stress tolerance. This indicates that condensation water, as an important supplementary water source, can greatly alleviate the effect of drought conditions on the physiological water status of *P. euphratica* leaves. The water droplet contact angle was not significantly different between the leaf's adaxial and abaxial surfaces, indicating that *P. euphratica* leaves have approximately the same water absorption capacity on both the adaxial and abaxial surfaces, which is mainly affected by leaf wettability, proline, and so on. The average leaf water absorption rate was positively correlated with the average transpiration rate, the water absorption rate of *P. euphratica* leaves was about one-tenth of the maximum transpiration rate, and the total amount of water absorbed by *P. euphratica* from the surface of leaves in summer accounted for about 6.6% of the total transpiration of the vegetation system in the Ebinur Lake Hu Basin, which indicates that the atmospheric water source represented by the condensate water played an important role in the regional water cycle. The results of this study provide a new basis for the effect of condensation water on the physiological state of *P. euphratica* and the ecological benefits of leaf water absorption in the desert region.

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