



1 An Experimental Investigation of Precipitation Utilization of plants in Arid Regions 2 Yiben Cheng¹, Wei Feng², Hongbin Zhan³, Huijie Xiao¹, Zhiming Xin⁴, Wenbin Yang⁵ 3 4 ¹ School of soil and water conservation, Beijing Forestry University, Beijing, China, 100083 5 6 ² Xilingol Vocational College, Xilingol, China, 026000 ³ Department of Geology and Geophysics, Texas A&M University, College Station, Texas, USA, 7 77843 8 ⁴ The Sand Forestry Experimental Centre, Chinese Academy of Forestry, Dengkou, Inner 9 Mongolia, China, 015200 10 ⁵ Low-coverage sand control company, Hohhot, Inner Mongolia, China, 010000 11 12 Correspondence: 13 Yiben Cheng (chengyiben@bjfu.edu.cn) 14 Huijie Xiao (herr xiao@hotmail.com) 15 Zhiming Xin (xzmlkn@163.com) 16





Abstract:

What is the water source for ecological restoration plants in arid region is still up to debate. To 18 address this issue, we conducted an in-situ experiment in the Ulan Buh Desert of China. We 19 selected Tamarisk, a common drought-salt-tolerance species in the desert for ecological restoration 20 21 as our research subject, used a new designed lysimeter to monitor precipitation infiltration, a sap 22 flow system to track reverse sap flow that occurred in shoot, branch, and stem during the precipitation event, and observed the precipitation redistribution process of the Tamarisk plot. The 23 24 results showed that Tamarisk indeed directly absorb precipitation water, when precipitation occurs, the main stem, lateral branch, and shoot all show the signs of reversed sap flow, and the reversed 25 sap flow accounted for 21.5% of the annual sap flow in the shoot and branch, and 13.6% in the 26 27 stem. Precipitation event in desert was dominated by light precipitation events, which accounted for 81% of the annual precipitation events. It was found that light precipitation can be directly 28 29 absorbed by the Tamarisk leaves, especially in nighttime or cloudy days. Even when the 30 precipitation is absent, it was found that desert plants can still absorb unsaturated atmospheric vapor, as reversed sap flow was observed when the atmospheric relative humidity reached 75%. 31 This study indicated that the effect of light precipitation on desert plants was significant and should 32 33 not be overlooked in terms of managing the ecological and hydrological systems in arid regions.



35 Highlights:

- 36 (1) Light precipitation is the important water source of Tamarisk in arid areas.
- 37 (2) Tamarisk leaves can directly absorb precipitation and transmits the water to branch and stem.
- 38 (3) Increased RH can also result in leaf atmospheric water absorption when RH is above 75 %.
- 39 (4) Direct precipitation absorption accounts for 21.5% of Tamarisk annual water consumptions.





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1. Introduction

Plants absorb water from the soil and transport it up to the leaves to participate in photosynthesis or transpiration (Berry et al., 2019; Arif et al., 2020). This water transport process is usually described as the soil-vegetation-atmosphere continuum (SPAC) and is the primary framework for studying the transport of water through the plant-body system. The physical basis for the SPAC system is that water moved from high water potential to low water potential (Fricke, 2019; Philip, 1966). A dry atmosphere has a very low water potential status, while the soil filled with water has a high-water potential, so water moves from the soil, along the plant body transport system, to the atmosphere. Researches have shown that leaves could also absorb water (Aung et al., 2018; Holanda et al., 2019), especially Crassulaceae vegetation (Delf, 1912; Hietz et al., 1999), thus water might flow in a reverse direction in the SPAC system if the atmosphere is relatively wet with a relatively high water potential, thus water flows from the atmosphere through the shoot to the stem, and then to the soil.

For water from the atmosphere to enter the plant leaves (Dacey, 1980), the water potential of the leaves should be lower than the atmospheric water potential (Scholander et al., 1964). It is found that tropical montane forests are able to absorb water from the air during the dry season(Gotsch et al., 2014; Hu and Riveros-Iregui, 2016; Jones et al., 2011), because tropical areas are prone to the presence of rainy and foggy weather (Los et al., 2021). When a foggy day appears, the liquid water column adheres to the leaf surface, this leads to a situation that the external water potential of the leaf is higher than the internal water potential of the leaf, thus water can be drawn from the air into the leaf. Sufficient evidences have shown that a variety of pathways exist for atmospheric water transporting into the leaf, from the cuticle (Schreel and Steppe, 2020), stomata, and water channel protein(Drake et al., 2019). Water transport in plants also relies on water potential gradients in different parts of the plant's body(Sheil, 2018). When the water potential of the leaves is higher than the stem, water flows from the leaves to the stem. In fact, water in the leaves and stem could flow freely and replenish each other when certain parts of the plant body are dehydrated(Ganthaler et al., 2022). When the soil moisture is high, the water potential of the soil rises so the root system could absorb water from the soil and transfer the soil moisture to the stem and leaves for photosynthesis and transpiration(Wang et al., 2014). Scientists have also found that the plant root system is able to transfer water to the soil system in the reverse direction when the soil layer is



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70 extremely dry(Caldwell et al., 1998; Sprenger et al., 2019).

Although researchers have made great progresses in understanding absorption of atmospheric water by leaves(Dubbert and Werner, 2019), there are still several critical knowledge gaps on the subject. For example, vegetation is capable of transpiring water at night without sunlight, and the mechanism of doing so is not entirely understood(Beyer et al., 2020). Most of the current researches on the subject concern with soil water from gaseous and precipitation, and the water balance formula is used to calculate the water vegetation consumption(Domínguez-Niño et al., 2020). However, soil water in arid regions is mostly from condensation (liquid water) and precipitation(Coopman et al., 2021; Assouline and Kamai, 2019), while atmospheric water absorbed by vegetation is less studied and the mechanism of such a process is unclear as well. Precipitation amount less than 5 mm/d will only infiltrate into the shallow soil layer whose depth is usually less than 5 cm in sandy land, thus such precipitation events do not contribute to the soil moisture of the plant root layer (which is usually deeper than 5 cm) and is considered ineffective to desert plants (Cheng et al., 2020a). However, some researchers have found that cacti could utilize water from precipitation events as small as 2.5 mm/d with succulent stems(Mackay et al., 2020). Indeed, increasing evidence shows that desert plant is more closely related to individual strong precipitation pulses rather than the total precipitation amount (Heffelfinger et al., 2018; Zhang et al., 2019). However, some other researchers have found that shrubs like Nitraria and Elaeagnus respond physiologically to light precipitation (Luo and Zhao, 2019). Such researches mainly focus on the utilization of light precipitation by the shallow-rooted plants through the root system or the effects of precipitation pulses on the physiology (e.g. photosynthesis, transpiration) and morphology of desert plants(Ouyang et al., 2020), but they do not address the issue concerning direct absorption of precipitated water through the leaves.

To address the issue mentioned above, we have designed a sequence of multi-year in-situ experiments in a selected arid region in Northern China to find out whether leaves could absorb precipitation water or not. Specifically, we are trying to answer the following questions. 1) If leaves can absorb water, then at what time scale and under what conditions do the plants start to absorb precipitated water? 2) Does the water absorbed from precipitation can be transferred into the stem? 3) What is the exact amount of precipitated water that can be absorbed by leaves during the whole growing season? The answers to these questions can help us explain the ecological significance of



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100 precipitation events in the arid region, which are usually sporadic with highly variable intensities.

2. Materials and methods

To figure out the water source for the survival of Tamarisk in the research area, we set up in-site observation experiments on two spatial scales, one is used to observe the redistribution characteristics of precipitation in the plot scale, and the other is used to observe the absorption of atmospheric water by leaves on the individual plant scale. The soil moisture in the study site is normally less than 5%, and sometimes even below the measurement limit of the soil moisture probe (EC-5 probe measurement error range in sandy soils: ±3% volumetric water content), so it is impractical to use the soil moisture probe to monitor the soil moisture accurately. Therefore, the main observation target of this experiment is deep soil recharge (DSR), rather than the soil moisture, where DSR refers to the rate of downward soil recharge at the depth of 2 m. We use a newly designed lysimeter to monitor the amount of DSR to measure the replenishment effect of precipitation on the deep soil layer(Cheng et al., 2021a). The reason to observe DSR at the depth of 2 m is that the roots of the vegetation in the study area are mainly distributed within the 0-1.5 m depth, and the maximum height of capillary rising of the sandy soil at the site is about 0.5 meters, so the soil moisture at the 2 m depth will be difficult to be absorbed by the roots of Tamarisk. One point to note is that the deep soil moisture may replenish the shallow soil layer in the gaseous phase through upward vertical vapor flow. This factor is regarded as secondary and is not considered in this investigation. However, the vapor flow issue should not be overlooked without scrutiny and it requires specifically designed field experiments which will be the subject of a future investigation.

2.1 Research field

- The research field site is located at the northeastern edge of the Ulan Buh Desert (106°00'-107°20'E,
- 123 39°40'-41°00'N) of China, with an average elevation of 1050 m above mean sea level (AMSL).
- 124 The research area is flat and the soil type is mainly fine sand, and it has a semi-arid continental
- 125 climate with an average annual precipitation of 98 mm, an average annual temperature of 6.8
- 126 Celsius, and an annual sunshine duration of 3229.9 hr. The water table is approximately 9 meters
- below the ground surface(Cheng et al., 2017).





The main type of plants in the field site is native Tamarisk ramosissima, and the main types of other plantations are Haloxylon ammodendron, Hedysarum scoparium, Caragana korshinskii. Natural herbaceous vegetation mainly includes Artemisia ordosica, Nitraria tangutorum and so on. The experimental site is located in an artificial Tamarisk forest with a relatively flat terrain with minor undulation(Cheng et al., 2021b). The Tamarisk Forest is about 30 years old, and is planted with a row space of 3 m×2 m. The average base diameter of Tamarisk is 9.34 cm, the average height of Tamarisk is 2.95 m, and the average crown width of Tamarisk is 2.69 m×2.32 m. After excavation, we find that the deepest root depth of native plants is about 6 m, but most of the roots

of artificial vegetation are concentrated in 0-1.5 m depths.

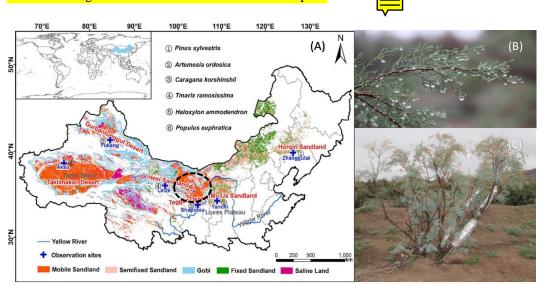


Figure 1. A) The map showing the species distribution of artificial forests in northern China (Ma et al., 2019), Tamarisk as a shrub with low water consumption is widely planted in the arid areas of China; B) This diagram shows precipitation and condensation water hanging on Tamarisk branches in the morning in the site; C) This diagram shows the observed in-situ Tamarisk, where sap flow sensors are wrapped at the main stem, lateral branches, shoot, respectively.

2.2 Deep soil recharge observation

To calculate the proportion of atmospheric water (precipitation) absorbed by Tamarisk to the total water consumption in a growing season, we have carried out a Tamarisk water balance observation experiment through in-situ observations of precipitation, soil moisture, and DSR. To monitor DSR,



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a new lysimeter is used in this research(Cheng et al., 2020b). This new lysimeter is assembled with two parts: a balanced part and a measurement part. As shown in Figure 2, the function of the balance part is to ensure that the soil moisture infiltrating into this part can be completely transported to the downward measurement part. The balance part uses a cylinder with an impervious sidewall to wrap the undisturbed in-situ soil column. The length of the soil column is determined based on the local soil particle size, and the capillary rise (which is less than 50 cm for the fine sandy soil of the site). The advantage of this design is that when the soil at depth B (in Figure 2) reaches the saturated state, the capillary rise can at most reach depth A (see Figure 2), thus the soil moisture cannot overflow from the top of the soil column at the depth A. When there is soil moisture infiltrating into the water balance part at depth A, the soil moisture at depth B would discharge into the underneath measurement part. The amount of water discharged from the upper balance part into the lower measuring part is calculated using a rain gauge made by the American Spectrum company with an accuracy of 0.2 mm. After the installation, we irrigate the sandy soil in the balance part to make sure it reaches the saturation state. After this step, the excess soil moisture would be discharged from the lower boundary of the balance part to make sure the balance part maintains the saturation state. The function of the measuring part is to record the amount of water discharged from the upper balance part. The vegetation roots in the research site are mainly distributed at a depth of 0-1.5 m depth, and the upper interface of the lysimeter is installed at a depth of 200 cm to measure the DSR generated by precipitation. The installation of this new lysimeter would inevitably alter the structure of the in-situ sandy soil, so we need to install this instrument in advance, backfill the excavation with in-situ soil, and allow the soil to settle for six months to one year to approximate its pre-installation status before taking the measurement data(Cheng et al., 2018).

$$ET = P - \Delta SWS - DSR - R \tag{1}$$

$$\Delta SWS = SWS_E - SWS_B \tag{2}$$

$$SWS = \sum_{i=1}^{n} D_i * SVC_i$$
 (3)

Where ET is evapotranspiration, P is precipitation, SWS is soil water storage, SWS_E is soil water storage at the end of the year, SWS_B is soil water storage before the year, DSR is deep soil recharge,



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R is runoff, there is no runoff in the plot, D_i is soil depth of the i layer, and SWC_i is soil volumetric water content of the i layer.

2.3 Sap flow observation

2.3.1 In-situ observation site

The sap flow meter uses a thermal dissipation probe to measure the heat transfer rate, then converts the thermal transfer rate to the instantaneous sap flow velocity in the trunk, Long-term observation of the sap flow of plants could provide information about water exchange between plants and the atmosphere and one can use this information to monitor the impact of reforesting ecosystems on environmental changes(Cheng et al., 2022). In this research, 4 Tamarisk plants are selected as experimental plants, and the continuous sap flow data are monitored for a total duration of 150 days, covering the entire growing season of Tamarisk, roughly represent the stand structure at the site. After the experiment, both Tamarisk trees are cut down and all the leaves are collected for further analysis. We use a SF-3 HPV sap flow monitoring system (East 30, USA), which has a central heater needle and two thermistors-needle up and down, can be used in shoot as small as 0.5 cm in diameter. To avoid thermal radiation and precipitation from interfering with data interpretation, we wrap the probe with soft foam plastic first and then wrap it further with tin foil plastic film. For the installation of the probe, one can refer to the SF-3 Sap Flow System Manual, and the data are collected with CR-300 (Campbell, USA) at an interval of 6 min. The diameter of a Tamarisk is measured by a vernier caliper. Sap velocities are calculated according to Eq. (1)(Burgess et al., 2001; Campbell et al., 1991):

$$V_{sap} = \frac{2k}{C_w(r_u + r_d)} \ln\left(\frac{\Delta T_u}{\Delta T_d}\right) \tag{4}$$

Where k is the sapwood thermal connectivity, set to $0.5 \text{Wm}^{-1} \text{K}^{-1}$, C_w is the special heat capacity of water, r is the distance of heating needle to measuring needle, ΔT is the temperature difference before and after the heating, u and d stand for location up and down of the heater sensor.

We also need to correct the sap velocity as the bark been damaged during the drilling process and affect the sap flow results, the correction formula and sap flow calculation formulas are as follows:





$$V_c = bV_{sap} + cV_{sap}^2 + dV_{sap}^3$$
 (5)

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$$A_{sap} = \pi (d - d_{bark})^2 - \pi (d - d_{bark} - d_{sap})^2$$
 (6)

$$F_{sap} = A_{sap} * V_c \tag{7}$$

Where V_c (ms⁻¹) is the corrected V_{sap} , and b, c and d are the correction coefficients, we set b=1.8558, c=-0.0018sm⁻¹, d=0.0003s²m⁻² in line with former researcher(Burgess et al., 2001; Mennekes et al., 2021), A_{sap} is sapwood area, calculated using the power law function, d is measuring point diameter, d_{bark} is bark thickness, d_{sap} is sapwood thickness.

2.3.2 Determination of leaf absorption of atmospheric water



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Figure 2. A) This diagram shows the in-situ Tamarisk, with sap flow probes wrapped on the main stem, lateral branches, and shoots. B) This diagram shows the experimental setup, with the Tamarisk placed in a semi-enclosed transparent controlled-climate room, where artificial precipitation experiments can be carried out from above or-closed for atmospheric water vapor absorption experiments.

When the atmospheric relative humidity (RH) reaches a certain level, Tamarisk leaves start to absorb atmospheric water, and such a condition is named the critical condition in this research,





where the critical condition refers to Tamarisk leaves begin to absorb water and reversed sap flow was monitored. As shown in Figure 2(A and B), we have designed an in-situ control room that can simulate humidification under in-situ conditions. By regulating the RH values of the control room, we can determine the critical condition when Tamarisk to absorb atmospheric water. As shown in Figure 2B, a plastic film is laid on the lower part of the control room (ground surface) to prevent water from infiltrating into the soil layer during humidification.

2.4 Calculation of atmospheric water absorption

2.4.1 Reverse flow measurement



Figure 3. The canopy width (length, width, and height) of the target branch is measured in situ, based on the captured images.

The sap flow meter could measure the direction and the amount of sap flow in different scenarios, but one should be noted that there is always uncertainty or measurement bias when the sap flow meter measures the sap flow. This is because the sap flow meter only measures the sap flow through the measuring part, but there is a certain portion of immobile water stored in leaves or branches absorbed by roots or leaves, and the sap flow meter is incapable of measuring such immobile water. The reversed sap flow (water uptake) of the branches is converted into uptake per unit area using Eq. 8, this amount of water absorbed per unit area can be compared to the amount of one precipitation event. As shown in Figure 2B, to accurately calculate the amount of





atmospheric water absorbed by Tamarisk leaves, we have used a method of repeated sampling and weighing to establish the relationship between the amount of atmospheric water absorbed and the weight of the unit leaf dry matter.

$$AWA = \frac{SF}{BCHA} \tag{8}$$

Where *AWA* is Atmospheric water absorption, *SF* is reversed sap flux, *BCHA* is branch crown horizontal area.

To find the critical condition for the leaves to absorb atmospheric water, we need to continuously adjust the RH values in the control room. If the RH is kept high for a sufficiently long time, the Tamarisk leaves will continuously absorb atmospheric water. At the end of the experiment, we will cut down the whole Tamarisk, and the branches installed with the sap flow meter are picked and weighed, thus the water retained in the leaves can be measured. A point to note is that the condensed water attached to the leaves should be removed from time to time because this portion of water can be easily mistaken for the water absorbed by the leaves. For this purpose, we use absorbent filter paper to remove the attached water on leaves to minimize the impact on the structure of the leaves. After the measurement, the leaves of the whole Tamarisk are collected and brought back to the Desert Ecohydrology Laboratory which is located in Beijing Forestry University for drying and weighing.

2.4.2 Calculation of leaf water absorption

The atmospheric water absorbed by the leaves includes the moisture stored in the leaves absorbed by the leaves and the moisture transported downward through the sap flow after absorption by the leaves (the so-called reversed sap flow). To measure the atmospheric water absorbed by the leaves and stored in the leaves, we have selected 20 Tamarisk plants at different growing stages in the experimental plot and divide them into two groups (ten plants per group), one group with humidification, and one group without humidification. From May to September of 2019, we continuously monitored the sap flow for a week per month and measured the atmospheric water absorption and reverse sap flow of Tamarisk under humidified conditions. After the experiment, all the Tamarisk branches were cut off, and the Tamarisk leaves on the branches were collected and brought back to the Desert Ecohydrology Laboratory for drying. The dry matter was weighed





and the water absorption of the leaves after humidification was calculated, as shown in Eqs. 9 and 10. Comparing the difference between the moisture content of the leaves in the humidified and non-humidified groups, one can deduce how much atmospheric water has been stored in leaves per unit of dry mass. To convert the water absorption of Tamarisk at a single plant scale to the water absorption of Tamarisk per unit crown size, we cut down the Tamarisk after the experiment and collected all the leaves, which were dried and weighed, and when combined with the crown width, one can calculate the absorption of atmospheric water by the Tamarisk per unit area. The main water sources in the arid region are precipitation and condensation water. Precipitation is a water source that can be consistently monitored, in this research, we will focus on calculating the uptake of precipitation by leaves.

$$LWC_B = \frac{W_B - W_{Dry-B}}{W_B} \times 100 \tag{9}$$

 $LWC_A = \frac{W_A - W_{Dry - A}}{W_A} \times 100 \tag{10}$

where LWC_B and LWC_A are leaf water contents (in percentages) before and after precipitation,

respectively; W_B and W_A are leaf fresh weights (g) before and after precipitation, respectively,

and W_(Dry-B) and W_(Dry-A) are leaf dry weights (g) before and after precipitation,

respectively.

2.5 Air relative humidity observation

To facilitate the computation, this research needs precipitation data and atmospheric relative humidity data from the experimental site. We have established a HOBO H21 small automatic weather station on the experimental site to record temperature, precipitation, atmospheric relative humidity (RH) in and out of the control room, and other environmental information. The precipitation sensor is a rain gauge (S-RGB-M002, Meter, USA), and the air temperature and humidity sensor are S-THB-M002 (Onset, USA). Vapor pressure deficit (VPD) is the difference between the actual amount of moisture in the air and the maximum (saturated) amount of moisture of the air at a given site of concern. Once the air becomes saturated, water will condense to form dew or films of water over leaves. We like to use VPD as an index to investigate the water absorption through vegetation leaves in this study. This is based on the hypothesis that a greater









water stress will lead to a greater ability of the leaves to absorb water. VPD is calculated as follows:

$$VPD = a * Exp\left(\frac{bT}{T+c}\right)(1-RH)$$
 (11)

- Where a, b, c are coefficients, set as 0.611, 17.502 and 240.97, respectively (Campbell and Norman,
- 2000), *I* is atmospheric temperature at 2 m height, *RH* is the relative humidity.
- **3. Results**

3.1 Time for vegetation to absorb atmospheric water

As shown in Figure 4, we have observed the sap flow for the main stem, lateral branch, and shoot of Tamarisk separately. In this study, when counting the sap flow amount, the lateral branch and shoot are counted as the branch. We find that the day and night sap flow rates of Tamarisk in the in-situ condition vary significantly, showing a decrease in sap flow rate at night, which may be due to the lower transpiration at night. We also find that the sap flow does not converge to zero until midnight, indicating that even when the photosynthesis ceases at night, Tamarisk can still carry out physiological activities and continue to absorb soil water for transpiration. After midnight, the reversal sap flow starts in the shoots first, and some moments later, the reversed sap flow is also observed in the branch and main stem. On the fourth day of the observation period, as shown in Figure 3, when precipitation occurs at the night, the main stem, lateral branch, and shoot all show the signs of reversed sap flow, meaning that precipitation is transported from the leaves to the main stem. This is a piece of evidence showing that desert vegetation (like Tamarisk) can absorb atmospheric water directly from the precipitation and transfer water to the stem. Whether the water transferred to the stem will continue to transfer to the soil is an open question that requires further investigation.



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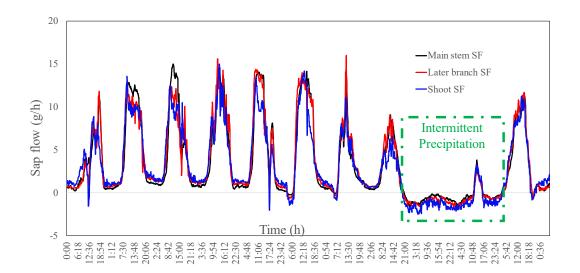


Figure 4. Changes of in-situ Tamarisk sap flow in the main steam, lateral branch, and shoot. SFR stands for sap flow rate.

Through the above-mentioned in-situ experimental observations, we have found that the Tamarisk is able to absorb precipitation moisture, especially at night, and reversed sap flows can be formed at the shoot, branch, and stem. To accurately obtain the critical condition of precipitation moisture absorption by Tamarisk, we have carried out a control experiment to find out at what point the Tamarisk leaves could absorb atmospheric moisture. To serve this purpose, we have used RH as an indicator to identify the critical condition of Tamarisk absorption of atmospheric water vapor under different RH conditions. The Tamarisk is enclosed in an in-situ controlled-climate room, as shown in Figure 2B, isolating the possibility of Tamarisk leaves absorbing water vapor from the atmosphere, and avoiding vapor water entering the soil during the humidification process. We start the experiment at night and start the water vapor input in the controlled-climate room to increase the RH values gradually in the controlled-climate room. As shown in Figure 5, the rate of sap flow decreases as the RH increases in the controlled-climate room, and when the RH reaches 75%, the shoot begins to show reversed sap flow, meaning that Tamarisk begins to absorb vapor. At the same time, dew has not yet appeared in the controlled-climate room, indicating that Tamarisk is able to directly absorb unsaturated vapor moisture. As the RH value increases further and reaches 90%, dew begins to appear in the controlled-climate room, and we then terminate the humidification process. Afterward, the dehumidification process starts in the controlled-climate



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room, and when the RH value of the controlled-climate room drops to 63%, the reversed sap flow of Tamarisk disappears. Because dew appears at RH of 90%, and some branches are still wet even when the RH drops to 63%, the RH value for the critical condition should be greater than 63%. Unfortunately, the equipment we used in-site can only observe the change of RH of the control room, cannot observe whether the internal organs of the leaf absorbed water. Thus, we determine the leaf absorbed atmospheric vapor by the direction of the sap flow at the shoot position. through several humidification experiment, so we determined the RH at 75% was the critical point, at this point a reversed sap flow appears on the shoot, means leaf start to absorb atmospheric moisture. one should note that real critical point is certainly lower than the RH of 75%, because there is a distance from leaf to the shoot sap flow prob, and reserved sap flow needs time to transfer, when the reverse sap flow was observed, the process of leaves absorbs atmospheric water vapor has already begun. In the future, detailed and refined observations with better equipment are needed to address this issue. When we found that tamarisk reverses sap flow appears the same at high RH conditions. To verify this phenomenon, we humidified the other two controlled tamarisk, one is at low humidifying intensity (controlled RH at 75%) and the other at high humidifying intensity (controlled RH above 90%). As shown in Figure 5(BC), reverse sap flow occurred under both conditions and the sap flow lasted for a long period, lasting for 8 and 7.5 hours until we ended of the humidification experiment. This is a direct evidence of tamarisk leaves can absorb atmospheric vapor under a certain condition of high relative humidity.







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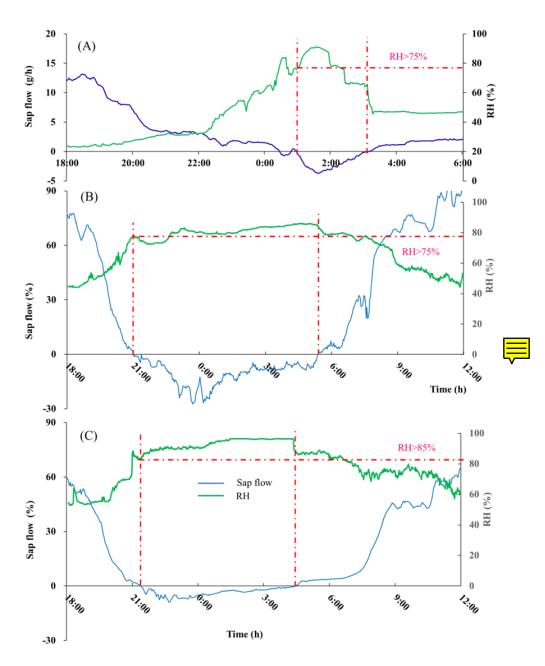


Figure 5. The occurrence time of reversed sap flow and corresponded RH, humidification process and dehumidification process. Humidifying the tamarisk 1 in the control room and finding reverse sap flow when the RH reached 75% (A); humidifying the tamarisk in the other two control rooms,



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357 (B) is RH around 80% with slight fluctuations for we manually control the humidifier, and (C) is 358 high intensity humidification, maintaining RH at around 90%.

3.2 Precipitation events that can cause water absorption in leaves

In the site of this study, a short period of precipitation (precipitation pulse) may not create a high enough RH value up to 63% over the entire experimental plot, but the liquid water drop adhered to the leaves may create a locally high enough RH within a small area (such as the leaf scale). Now the question is: Is this sufficient to create a reversed sap flow? To answer this question, we have observed the variation of sap flow at two different precipitation events (0.6 mm for 20 min for a short-duration precipitation and 12 mm for 3 hours for a long-duration precipitation event). It is interesting to observe that not only the long-duration precipitation initiates the reverse sap flow, the short-duration precipitation also does, as shown in Figure 6. When the light precipitation (0.6 mm for 20 min) occurs, the atmosphere RH is as low as 17-30%, the reversed sap flow has been observed in the shoot but not in the branch and stem. This observation indicates that at a light precipitation event, atmosphere RH do not need to reach 75%, precipitation can be absorbed and stored in the leaves without being transported to the stem. When the precipitation lasts for a longer time, as shown in Figure 6B, we find that the RH rises rapidly, reaching 95%, and the reversed sap flows have been observed in the stem, branch, and shoot. This shows that both light and heavy precipitations can create favorable conditions for the leaves to absorb precipitation moisture. Light precipitation in the arid region accounts for most of the annual precipitation (81%), and plants might rely on such high-frequency light precipitation events to absorb moisture through leaves.



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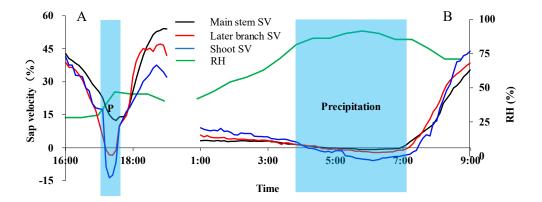


Figure 6. Effects of light and heavy precipitation events on reversed sap velocity (the ratio of the real-time sap velocity to the maximum sap velocity). A refers to a light precipitation during the day, B refers to a long precipitation during the night. SFR stands for sap flow rate.

3.3 Environmental factors affect vapor absorption

The sap flow rate is much higher during the daytime than at nighttime at a given VPD value. The decrease of the sap flow rate in August of 2019 (Figure 7B) as compared to the sap flow rate in July of 2019 (Figure 7A) indicates that the physiological activity of Tamarisk started to diminish in August. As shown in Table 1, the average daytime sap flow rate of Tamarisk in August 2019 has a low Pearson correlation with VPD (R²=0.501, P<0.001) (Figure 6A), and the nighttime sap flow rate was better correlated with VPD during the same duration (R²=0.718, P<0.001), where R² is the coefficient of determination and P is the P-value used in the Pearson correlation analysis and it is the probability that you would have found the current result if the correlation coefficient was in fact zero (null hypothesis). Correlation coefficient R² which is between 0 and 1. The closer of the R² value to 1, the eloser of the linear regression prediction to true value, and the more representative the fitted formula. In July and August of 2019, the Tamarisk sap flow rates and VPD for daytime and nighttime were best fitted with two quadratically polynomial functions. Above observations may be explainable as follows. July is the time of budding for Tamarisk, but precipitation amount was relatively low for July of 2019, thus the Tamarisk leaves are forced to absorb more water vapor from the atmosphere as a means of maintaining physiological activities. In contrast, precipitation in August of 2019 was relatively abundant, thus the Tamarisk leaves do





not need to absorb more water from the atmosphere as the Tamarisk roots can uptake a greater amount of water from the relatively wetter soil to meet its physiological activities.



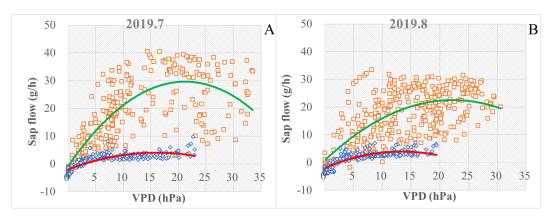




Figure 7. Relationship between the sap flow and water stress at different periods. Where daytime (denoted as orange color □) and nighttime (denoted as blue color □) data were plotted separately. Daytime refers to the duration from 7:00 am to 7:00 pm at the same day, and nighttime refers to the duration from 7:00 pm to 7:00 am of the following day. (A) The mean values of branch sap flows from 18 to 28 July 2019 in relation to VPD; (b) The mean values of branch sap flows from 20 August to 2 September 2019 in relation to VPD.

The absorption capacities of leaves at daytime and nighttime were also quite different from each other. According to Table 1, the absorption capacity of Tamarisk at nighttime was relatively high. This is probably because photosynthesis of Tamarisk ceases at nighttime, leading to less transpiration at nighttime. With the decrease of temperature at nighttime, RH tended to reach a higher level, even saturated and dewy. Our results have shown that when RH reached 75%, the leaves could absorb unsaturated atmospheric water directly. Sap flow is an indirect method to observe leaves absorb unsaturated atmospheric water better equipment with higher precision such as stain labeling and isotope tracing is needed for those measurements in the future.

Table 1 The best-fitted sap flow rates of Tamarisk branches versus VPD in July 2019 and August 2019 during both daytime and nighttime using quadratic functions. SF stands for sap flow rate (g/h) and R^2 is the coefficient of determination.



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Date	Time		R^2
2019.7	daytime	$SF = -0.044VPD^2 + 1.951VPD + 0.794$	0.501
	nighttime	$SF = -0.033 \text{ VPD}^2 + 0.893 \text{ VPD} - 2.013$	0.718
2019.8	daytime	$SF = -0.068 \text{ VPD}^2 + 2.868 \text{ VPD} - 0.758$	0.658
	nighttime	$SF = -0.024 \text{ VPD}^2 + 0.759 \text{ VPD} - 1.981$	0.703

3.4 Calculation of precipitation absorption and utilization

The Tamarisk leaves were the primary means for absorbing atmospheric water. If we obtained the relationship between the water absorption and the dry mass of leaves, we could estimate the total amount of precipitation absorbed by any Tamarisk leaves. As shown in Figure 8, we collected the dry leaves mass and water absorbed by leaves after 15 precipitation events in 2019, and found that the precipitation absorption and the dry mass of leaves was positively correlated, with a coefficient of determination (R²) of 0.9645. These 15 precipitation events were randomly distributed during the daytime and nighttime of July (a dry month) and August (a wet month) of 2019. The amount of precipitation absorbed by the Tamarisk leaves can be calculated by weighing the dry matter mass of the Tamarisk leaves, but this method needs to destroy of the plant. We want to calculate the amount of water absorbed by the Tamarisk leaves by measuring the reverse sap flow. In particular, how much precipitation will be absorbed by the Tamarisk leaves?



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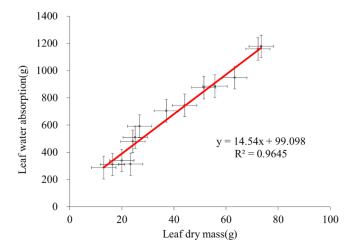


Figure 8. Relationship between dry leaf mass and its' absorption of atmospheric water

The reversed sap flow amount is positively correlated with precipitation events, but precipitation events did not necessarily result in a reversed sap flow in branch of Tamarisk. The occurrence of reversed sap flow was not only influenced by the amount of precipitation but-was also influenced by the duration of the precipitation event. Table 2 shows the reversed sap flow in the stem and branch of a Tamarisk under different precipitation events in July and August 2019. The reversed sap flow was normalized to mm per unit based on the Tamarisk canopy area, ratio of reversed sap flow to time. One can see that even for precipitation intensity as small as 0.5 mm/d, unsaturated atmospheric moisture can be absorbed by Tamarisk leaves. There is a relatively strong precipitation event occurred on August 2, 2019 with an intensity of 5.2 mm/d, but the reversed sap flow of Tamarisk was not remarkable. This is probably due to the relatively short duration of this precipitation event, and consequently the stem and branch sap flows accounted for only 0.5% and 1.1% of the precipitation amount, respectively. A light precipitation event occurred in the morning, July 24, 2019, but this precipitation event was not recorded by the in-situ rain gauges as the precipitation intensity was less than the 0.2 mm, lower than the minimum measurement range of the rain gauge. Surprisingly, Tamarisk stem and branch showed significant reversed sap flows during this precipitation period. There were two precipitation events recorded at weather stations on 18 and 22 July, 2019, and the reversed sap flow was only seen in Tamarisk shoot while the Tamarisk branch showed no or slight reversed sap flow. This is probably because the two precipitation events occurred at midday and late afternoon, during which the evapotranspiration





rates were relatively high. There was a continuous precipitation event (more than 12 hours) occurred in 27, July, 2019, and consequently, significant reversed sap flows were observed at the shoot, branch, and stem. In summary, the light precipitation could also lead to the reversed sap flow, which was also related to the duration of precipitation, and the timing of precipitation.

Table 2 Precipitation characteristics and precipitation prior by the Tamarisk leaves during the observation period in 2019

Date	Time	Duration	Precipitation	Sap flux(mm)		Reversed sap flux on	
						Precipitation%	
		(h)	(mm)	Stem	Branch	Stem	Branch
7/6	Midday	0.33	Under 0.2	0	0.004	0.000	0.020
7/18	Midday	0.5	0.2	0	0.006	0.000	0.030
7/20	Late afternoon	0.17	Under 0.2	0	0	0.000	0.000
7/22	Late afternoon	0.5	0.2	0	0.004	0.000	0.020
7/23	Afternoon	0.17	Under 0.2	0	0	0.000	0.000
7/24	Dawn	3	Under 0.2	0.002	0.01	0.010	0.050
7/25	Late afternoon	0.08	Under 0.2	0	0.006	0.000	0.030
7/27	Dawn and night	>12 h	23 (5.6; 10.4; 7.0)	5.93	9.802	0.258	0.426
8/2	Late afternoon	1.5	5.2	0.028	0.055	0.005	0.011
8/6	Afternoon	0.08	Under 0.2	0	0.004	0.000	0.020
8/12	Midnight to early morning	8	2	0.135	0.222	0.068	0.111
8/18	Afternoon	0.17	Under 0.2	0	0	0.000	0.000
8/25	Midmorning	1	0.4	0.002	0.006	0.005	0.015
8/27	Late afternoon	0.17	Under 0.2	0	0.004	0.000	0.020
8/30~9/1	Day and night	>12 h	22 (6; 7; 9)	1.312	1.608	0.060	0.073
Sum				7.409	11.731	0.136	0.215

3.5 Water absorption and consumption characteristics of Tamarisk

As shown in Figure 9A. The rainy season started in June and ended in September, and the mean multi-year annual precipitation was less than 100 mm(Cheng et al., 2018). As shown in Figure 9B, the sap flow rate of Tamarisk was in the rising trend from June to August, indicating that this was the fast-growing period of Tamarisk. After August, the sap flow rate decreased and Tamarisk gradually entered the hibernation period. July was the main period for Tamarisk to absorb vapor



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464 water absorbed from the atmosphere gradually decreased, as shown in Figure 9C. The timing of water consumption and timing of water vapor absorption by Tamarisk were different, the 465 maximum water consumption period of Tamarisk was in August, while solar radiation reached its 466 maximum in July, and transpiration was the strongest in July, 467 468 The DSR throughout the year is mostly concentrated in December-April. During the five-year experimental period, the DSR accounts for 5.77% of the precipitation over the same period. The 469 470 annual precipitation of the experimental site in 2020 is 84 mm, and the DSR of the same year is 5 mm. As shown in Figure 9D. Precipitation patterns and DSR at the plot revealed that precipitation 471 472 was mainly distributed in June and August, while Tamarisk was still budding in June and Tamarisk physiological activity began to weaken in August, thus the amount of atmospheric water absorbed 473 474 by Tamarisk leaves was small in these two months. A larger amount of precipitation occurred in August, and soil moisture became the main source to sustain the water need of Tamarisk, as shown 475 476 in Figure 9E. 477 In Ulan Buh Desert, light precipitation was the main type of precipitation events. Especially at the 478 beginning of the growing season, small amount of precipitation led to extremely dry soil-for, and

Tamarisk was forced to absorb water from light precipitation with leaves. When the rainy season

arrived, soil moisture was relatively abundant, but Tamarisk was also approaching dormancy with

less demand for water, thus the amounts of water obtained from both the soil and leaves were

dropped. To survive in a water deficit harsh environment, Tamarisk was able to mitigate its water

need by taking water from multiple means such as leaves and soil.

from atmosphere. As precipitation increased and Tamarisk growth slowed down, the amount of





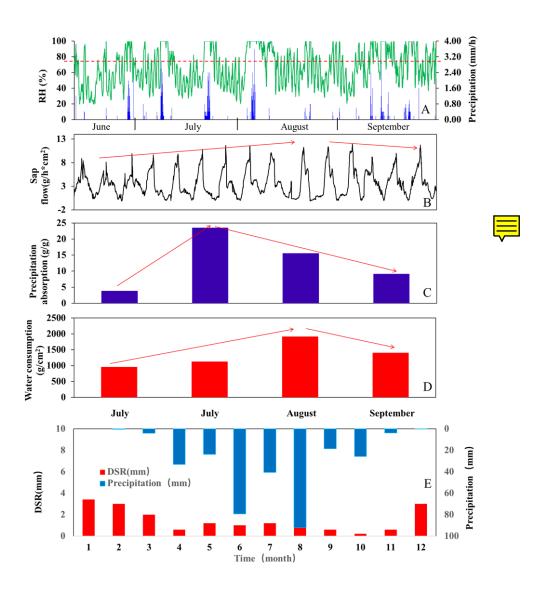


Figure 9. Water absorption and water consumption characteristics of Tamarisk during the growing season.

4. Discussion

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4.1 The timing of absorbing atmospheric moisture

Whether desert areas plants leaves can actively absorb atmospheric moisture was a long-debated issue(Henschel and Seely, 2008; Marks et al., 1964). Some researchers believed that atmospheric



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water can be absorbed by leaves only after condensation(Mitchell et al., 2020). For example, elouds, dew could be absorbed by the leaves(Stone, 1957, 1963). The potential of unsaturated atmospheric water was low, thus it was difficult for leaves to directly absorb water from the atmosphere(Hill et al., 2015). In this research, we have taken an important step forward by controlling the RH value in the in-situ controlled-climate room between 60% and 90%, which was at an unsaturated state. Under such experimental conditions, we found that the leaves were able absorb the unsaturated atmospheric vapor-(75%). In the dehumidification experiments, we found that even with RH as low as 30%, leaves were still able to absorb moisture from droplets at the surfaces of leaves. This research showed that leaves in the arid regions had multiple means of obtaining water.

4.2 Characteristics of atmospheric water absorption by leaves

We demonstrated that there was no significant time lag between the appearance of reversed sap flow and the occurrence of precipitation events in shoots, indicating that Tamarisk leaves can rapidly absorb water when precipitation happened. Water absorbed by leaves can be transported downward to branches and stems. Some previous studies found that when fog appeared without apparent precipitation events, the reversed sap flow was lagged (Alvarado-Barrientos et al., 2014). However, when precipitation events occurred, the reversed sap flow appeared simultaneously(Smith et al., 1999). Previous studies also found that the reversed sap flow could occur soon after leaves were wet(Scholz et al., 2002). When continuous precipitation events occurred, photosynthesis and transpiration were suppressed, and the reversed sap flow occurred in both daytime and nighttime(Schreel et al., 2019). This phenomenon also occurred in the case of fog(Steppe et al., 2018), lasting more than 2 hours. A longer precipitation events not only produced a significant reversed sap flow, but also yielded a high absorption ratio of precipitation by leaves (He et al., 2020). Even when where was no precipitation, the RH value above 63% still can lead to the reversed sap flow, which occurred mostly at nighttime. During daytime when RH was as low as 30% or VPD was sufficiently high, shoot may experience the reversed sap flow when the leaves were wet after a light precipitation event.

4.2 The fate of the absorbed water

Although previous studies demonstrated the pathways by which leaves absorb precipitation, a







comprehensive understanding of the water absorption mechanism was missing. Some researchers have demonstrated that the water vapor absorbed by leaves entered the leaves, but it was not clear what specific organs it entered. It was also not clear whether the absorbed water vapor was absorbed in a liquid state or a gaseous state(Matsumoto et al., 2018). Our research controlled the RH value at 60%-90% to avoid condensate and demonstrated that unsaturated atmospheric vapor could also be absorbed by leaves, and part of the absorbed moisture was transferred to the stem. However, we were not able to confirm that the water absorbed by leaves could be further transported downward into the root system—or not.

4.3 The significance of absorbed atmospheric water for plants

Leaves were able to absorb unsaturated atmospheric water vapor and precipitation water directly. Unfortunately, we could not demonstrate that the water absorbed from the atmosphere could participate directly in the physiological activities of Tamarisk. We have tried to use hydrogen and oxygen isotopes to label precipitation and to see whether ¹⁸O would appear with photosynthesis but failed to draw any affirmative conclusions due to a few reasons. The first reason was that we could not completely isolate the labeled atmospheric water vapor from entering the soil, and the soil moisture absorbed by the vegetation was also involved in the physiological process, which could interfere with the experimental results. The second reason was that our in-situ controlled-climate room could generate a greenhouse effect, resulting in plant death.

5. Conclusion

Water is the most important limiting factor for plants in an arid region, and plants are often suffered from drought stress during their growth. To adapt to the arid environment, plants have developed certain ways to accommodate the harsh water-deficit environments, such as leaf degradation, thicker cuticle, depressed stomata, and developed horizontal root systems or deep root systems. Precipitation was the main source of water in the arid region and has an important influence on plant growth and physiological processes. However, light precipitation is difficult to infiltrate into the deep soil layer. Also due to usual intense evapotranspiration effect in arid regions, precipitated water stays in the shallow soil only for a short period of time. In this research, we have analyzed the characteristics of precipitation patterns of the research site, and investigated whether the Tamarisk leaves could directly absorb the intercepted precipitation or not. The results showed that





549 the precipitation in arid region was dominated by light precipitation events (with intensity below 550 0.5 mm/d). Our results showed that Tamarisk leaves could absorb unsaturated water vapor and precipitation directly. The reverse sap flow usually appeared in the shoots soon after precipitation, 551 552 and then in the branch and stem in turn. The rate of reverse sap flow was not only related to the amount of precipitation, but also related to the timing and duration of precipitation. Continuous 553 precipitation results in the escalated reversed sap flow. During the experiment, a single nighttime 554 light precipitation was surprisingly absorbed by the Tamarisk leaves by 42.6%. The Tamarisk 555 leaves can absorb precipitation moisture even when the precipitation intensity is less than 0.2 mm/d, 556 especially if the precipitation event occurs late at night or early in the morning. The reversed sap 557 flows at stem and branch accounts for 13.6% and 21.5% of the precipitation amount, respectively, 558 559 during an observation year. In summary, water absorption of Tamarisk leaves is very important for Tamarisk to survive in a harsh water-deficit desert environment. 560 561 Availability of data and material: All the data are available from the corresponding author on 562 reasonable request 563 **Competing interests:** The authors declare that they have no competing interests 564 Funding: This research was supported by the Project of Intergovernmental Cooperation in Science and Technology Innovation (2019YFE0116500). Research grants from the National Natural 565 Science Foundation of China (U224320, 31870706). The Major Science and Technology Project 566 in Inner Mongolia (2019ZD003). Grants from China Academy of Forestry (IDS2022JY-8, 567 568 IDS2022JY-9). 569 Acknowledgments: We gratefully acknowledge the Fundamental Research Funds for the Central Universities (2021ZY45) and the Beijing Municipal Education Commission for their financial 570 support through the Innovative Transdisciplinary Program "Ecological Restoration Engineering". 571 572 We thank the Desert Forestry Experimental Center of the Chinese Academy of Forestry and 573 Yanchi Research Station for providing the experimental site.







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