



1           **An Experimental Investigation of Precipitation Utilization of plants in Arid Regions**

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17 **Abstract:**

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

34 **Keywords:** Ulan Buh Desert, Arid area, Tamarisk, Reverse sap flow, Atmospheric moisture

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.



## 40 1. Introduction

41 Plants absorb water from the soil and transport it up to the leaves to participate in photosynthesis  
42 or transpiration(Berry et al., 2019; Arif et al., 2020). This water transport process is usually  
43 described as the soil-vegetation-atmosphere continuum (SPAC) and is the primary framework for  
44 studying the transport of water through the plant body system. The physical basis for the SPAC  
45 system is that water moved from high water potential to low water potential(Fricke, 2019; Philip,  
46 1966). A dry atmosphere has a very low water potential status, while the soil filled with water has  
47 a high-water potential, so water moves from the soil, along the plant body transport system, to the  
48 atmosphere. Researches have shown that leaves could also absorb water(Aung et al., 2018;  
49 Holanda et al., 2019), especially Crassulaceae vegetation(Delf, 1912; Hietz et al., 1999), thus water  
50 might flow in a reverse direction in the SPAC system if the atmosphere is relatively wet with a  
51 relatively high water potential, thus water flows from the atmosphere through the shoot to the stem,  
52 and then to the soil.

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



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

71 Although researchers have made great progresses in understanding absorption of atmospheric  
72 water by leaves(Dubbert and Werner, 2019), there are still several critical knowledge gaps on the  
73 subject. For example, vegetation is capable of transpiring water at night without sunlight, and the  
74 mechanism of doing so is not entirely understood(Beyer et al., 2020). Most of the current  
75 researches on the subject concern with soil water from gaseous and precipitation, and the water  
76 balance formula is used to calculate the water vegetation consumption(Domínguez-Niño et al.,  
77 2020). However, soil water in arid regions is mostly from condensation (liquid water) and  
78 precipitation(Coopman et al., 2021; Assouline and Kamai, 2019), while atmospheric water  
79 absorbed by vegetation is less studied and the mechanism of such a process is unclear as well.  
80 Precipitation amount less than 5 mm/d will only infiltrate into the shallow soil layer whose depth  
81 is usually less than 5 cm in sandy land, thus such precipitation events do not contribute to the soil  
82 moisture of the plant root layer (which is usually deeper than 5 cm) and is considered ineffective  
83 to desert plants(Cheng et al., 2020a). However, some researchers have found that cacti could utilize  
84 water from precipitation events as small as 2.5 mm/d with succulent stems(Mackay et al., 2020).  
85 Indeed, increasing evidence shows that desert plant is more closely related to individual strong  
86 precipitation pulses rather than the total precipitation amount(Heffelfinger et al., 2018; Zhang et  
87 al., 2019). However, some other researchers have found that shrubs like *Nitraria* and *Elaeagnus*  
88 respond physiologically to light precipitation(Luo and Zhao, 2019). Such researches mainly focus  
89 on the utilization of light precipitation by the shallow-rooted plants through the root system or the  
90 effects of precipitation pulses on the physiology (e.g. photosynthesis, transpiration) and  
91 morphology of desert plants(Ouyang et al., 2020), but they do not address the issue concerning  
92 direct absorption of precipitated water through the leaves.

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



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

## 101 **2. Materials and methods**

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

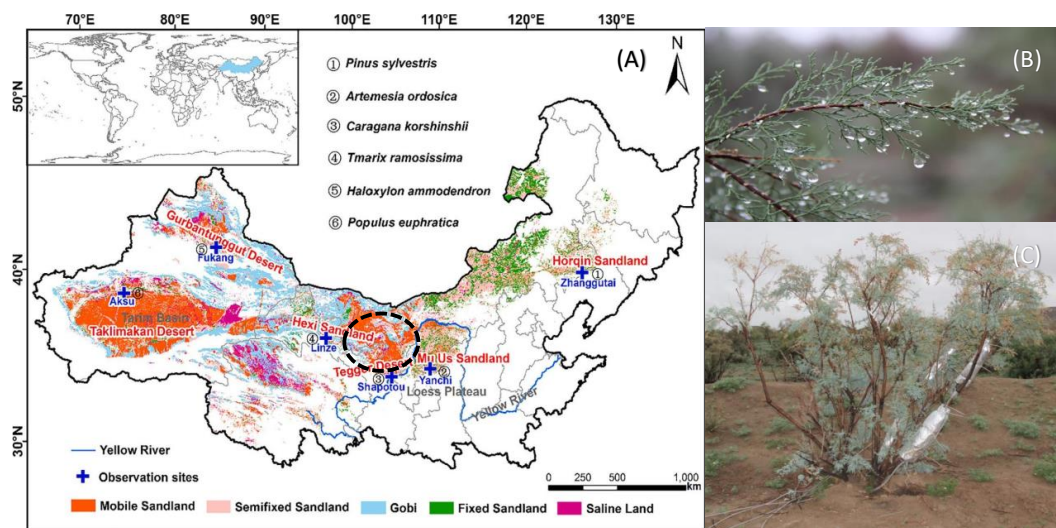
### 121 **2.1 Research field**

122 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  
127 below the ground surface(Cheng et al., 2017).



128 The main type of plants in the field site is native Tamarisk ramosissima, and the main types of  
129 other plantations are Haloxylon ammodendron, Hedysarum scoparium, Caragana korshinskii.  
130 Natural herbaceous vegetation mainly includes Artemisia ordosica, Nitraria tangutorum and so on.  
131 The experimental site is located in an artificial Tamarisk forest with a relatively flat terrain with  
132 minor undulation (Cheng et al., 2021b). The Tamarisk Forest is about 30 years old, and is planted  
133 with a row space of 3 m×2 m. The average base diameter of Tamarisk is 9.34 cm, the average  
134 height of Tamarisk is 2.95 m, and the average crown width of Tamarisk is 2.69 m×2.32 m. After  
135 excavation, we find that the deepest root depth of native plants is about 6 m, but most of the roots  
136 of artificial vegetation are concentrated in 0-1.5 m depths.

137



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

## 143 2.2 Deep soil recharge observation

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



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

170 
$$ET = P - \Delta SWS - DSR - R \quad (1)$$

171 
$$\Delta SWS = SWS_E - SWS_B \quad (2)$$

172 
$$SWS = \sum_{i=1}^n D_i * SVC_i \quad (3)$$

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



175 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  
176 water content of the  $i$  layer.

## 177 2.3 Sap flow observation

### 178 2.3.1 In-situ observation site

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

$$195 \quad V_{sap} = \frac{2k}{C_w(r_u + r_d)} \ln\left(\frac{\Delta T_u}{\Delta T_d}\right) \quad (4)$$

196 Where  $k$  is the sapwood thermal conductivity, set to  $0.5 \text{ W m}^{-1} \text{ K}^{-1}$ ,  $C_w$  is the specific heat capacity  
197 of water,  $r$  is the distance of heating needle to measuring needle,  $\Delta T$  is the temperature difference  
198 before and after the heating,  $u$  and  $d$  stand for location up and down of the heater sensor.

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





201 
$$V_c = bV_{sap} + cV_{sap}^2 + dV_{sap}^3 \quad (5)$$

202 
$$A_{sap} = \pi(d - d_{bark})^2 - \pi(d - d_{bark} - d_{sap})^2 \quad (6)$$

203 
$$F_{sap} = A_{sap} * V_c \quad (7)$$

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

208 **2.3.2 Determination of leaf absorption of atmospheric water**



209  
210 Figure 2. A) This diagram shows the in-situ Tamarisk, with sap flow probes wrapped on the main  
211 stem, lateral branches, and shoots. B) This diagram shows the experimental setup, with the  
212 Tamarisk placed in a semi-enclosed transparent controlled-climate room, where artificial  
213 precipitation experiments can be carried out from above or closed for atmospheric water vapor  
214 absorption experiments.

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



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

## 223 2.4 Calculation of atmospheric water absorption

### 224 2.4.1 Reverse flow measurement



225  
226 Figure 3. The canopy width (length, width, and height) of the target branch is measured in situ,  
227 based on the captured images.

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



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

$$239 \quad AWA = \frac{SF}{BCHA} \quad (8)$$

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

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

#### 253 **2.4.2 Calculation of leaf water absorption**

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



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

274 
$$LWC_B = \frac{W_B - W_{Dry-B}}{W_B} \times 100 \quad (9)$$

275

276 
$$LWC_A = \frac{W_A - W_{Dry-A}}{W_A} \times 100 \quad (10)$$

277 where LWC<sub>B</sub> and LWC<sub>A</sub> are leaf water contents (in percentages) before and after precipitation,  
278 respectively; W<sub>B</sub> and W<sub>A</sub> are leaf fresh weights (g) before and after precipitation, respectively,  
279 and W<sub>(Dry-B)</sub> and W<sub>(Dry-A)</sub> are leaf dry weights (g) before and after precipitation,  
280 respectively.

## 281 **2.5 Air relative humidity observation**

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



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

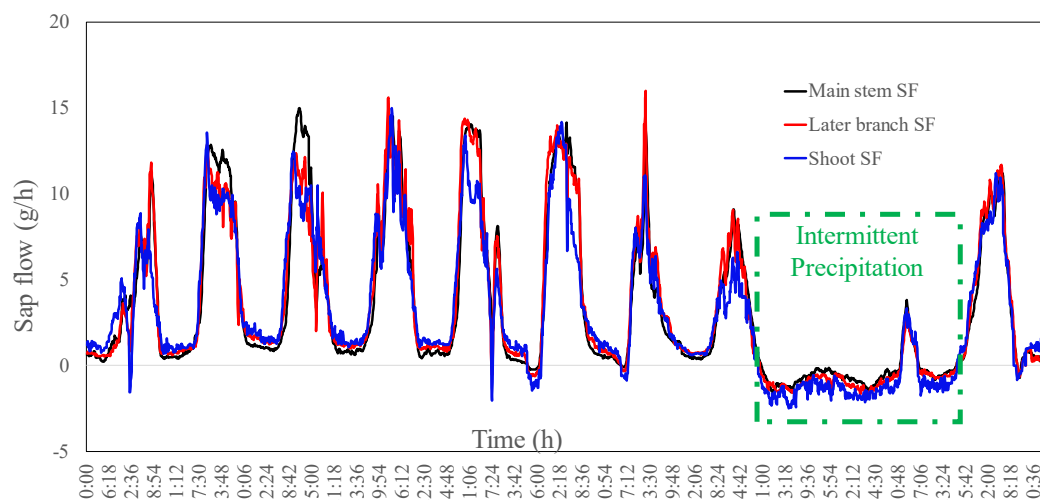
$$293 \quad VPD = a * \text{Exp}\left(\frac{bT}{T + c}\right) (1 - RH) \quad (11)$$

294 Where  $a$ ,  $b$ ,  $c$  are coefficients, set as 0.611, 17.502 and 240.97, respectively (Campbell and Norman,  
295 2000),  $T$  is atmospheric temperature at 2 m height,  $RH$  is the relative humidity.

### 296 **3. Results**

#### 297 **3.1 Time for vegetation to absorb atmospheric water**

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



313

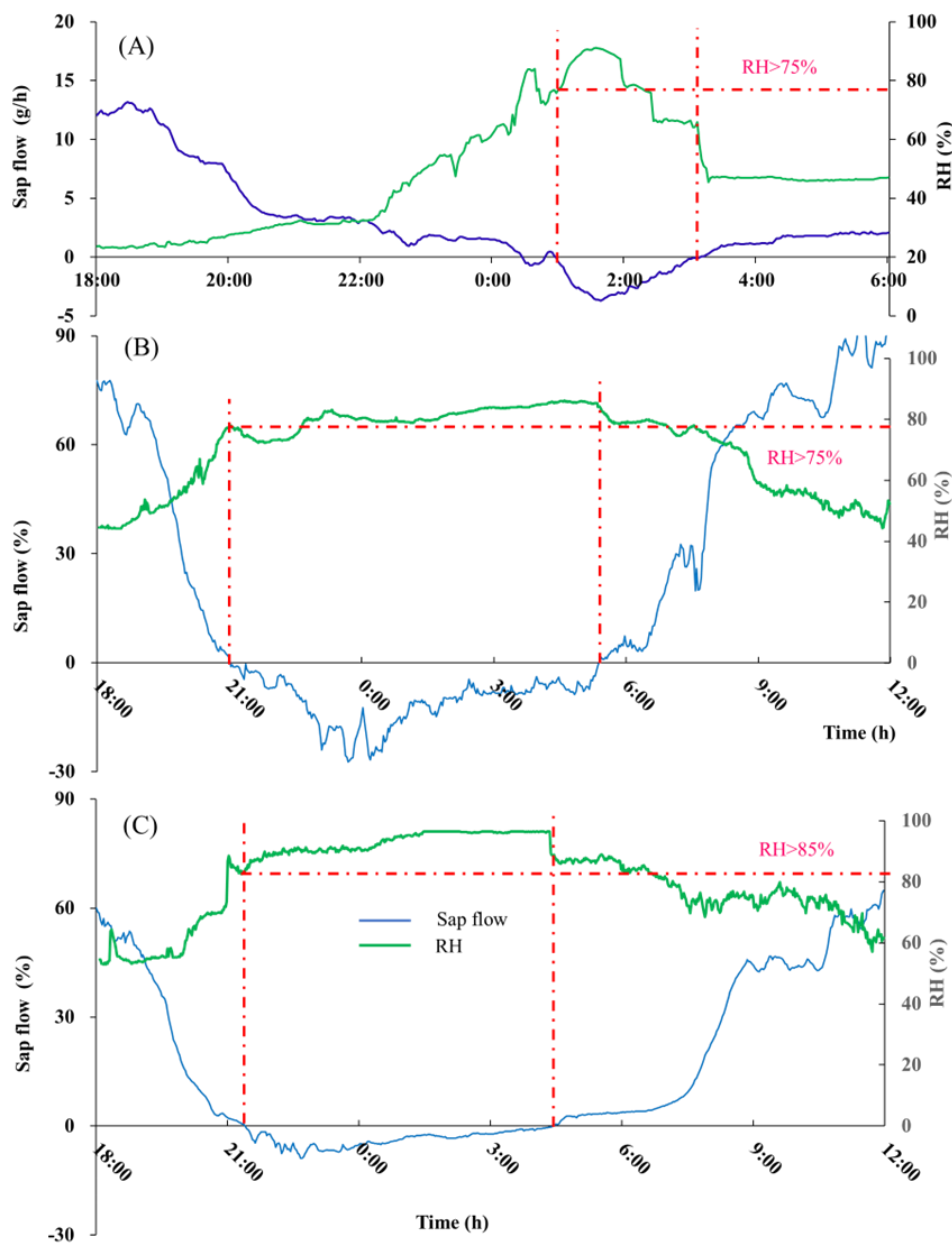
314 Figure 4. Changes of in-situ Tamarisk sap flow in the main stem, lateral branch, and shoot. SFR  
315 stands for sap flow rate.

316 Through the above-mentioned in-situ experimental observations, we have found that the Tamarisk  
317 is able to absorb precipitation moisture, especially at night, and reversed sap flows can be formed  
318 at the shoot, branch, and stem. To accurately obtain the critical condition of precipitation moisture  
319 absorption by Tamarisk, we have carried out a control experiment to find out at what point the  
320 Tamarisk leaves could absorb atmospheric moisture. To serve this purpose, we have used RH as  
321 an indicator to identify the critical condition of Tamarisk absorption of atmospheric water vapor  
322 under different RH conditions. The Tamarisk is enclosed in an in-situ controlled-climate room, as  
323 shown in Figure 2B, isolating the possibility of Tamarisk leaves absorbing water vapor from the  
324 atmosphere, and avoiding vapor water entering the soil during the humidification process. We start  
325 the experiment at night and start the water vapor input in the controlled-climate room to increase  
326 the RH values gradually in the controlled-climate room. As shown in Figure 5, the rate of sap flow  
327 decreases as the RH increases in the controlled-climate room, and when the RH reaches 75%, the  
328 shoot begins to show reversed sap flow, meaning that Tamarisk begins to absorb vapor. At the  
329 same time, dew has not yet appeared in the controlled-climate room, indicating that Tamarisk is  
330 able to directly absorb unsaturated vapor moisture. As the RH value increases further and reaches  
331 90%, dew begins to appear in the controlled-climate room, and we then terminate the  
332 humidification process. Afterward, the dehumidification process starts in the controlled-climate



333 room, and when the RH value of the controlled-climate room drops to 63%, the reversed sap flow  
334 of Tamarisk disappears. Because dew appears at RH of 90%, and some branches are still wet even  
335 when the RH drops to 63%, the RH value for the critical condition should be greater than 63%.  
336 Unfortunately, the equipment we used in-site can only observe the change of RH of the control  
337 room, cannot observe whether the internal organs of the leaf absorbed water. Thus, we determine  
338 the leaf absorbed atmospheric vapor by the direction of the sap flow at the shoot position. through  
339 several humidification experiment, so we determined the RH at 75% was the critical point, at this  
340 point a reversed sap flow appears on the shoot, means leaf start to absorb atmospheric moisture.  
341 one should note that real critical point is certainly lower than the RH of 75%, because there is a  
342 distance from leaf to the shoot sap flow prob, and reserved sap flow needs time to transfer, when  
343 the reverse sap flow was observed, the process of leaves absorbs atmospheric water vapor has  
344 already begun. In the future, detailed and refined observations with better equipment are needed  
345 to address this issue.

346 When we found that tamarisk reverses sap flow appears the same at high RH conditions. To verify  
347 this phenomenon, we humidified the other two controlled tamarisk, one is at low humidifying  
348 intensity (controlled RH at 75%) and the other at high humidifying intensity (controlled RH above  
349 90%). As shown in Figure 5(BC), reverse sap flow occurred under both conditions and the sap  
350 flow lasted for a long period, lasting for 8 and 7.5 hours until we ended of the humidification  
351 experiment. This is a direct evidence of tamarisk leaves can absorb atmospheric vapor under a  
352 certain condition of high relative humidity.



353

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

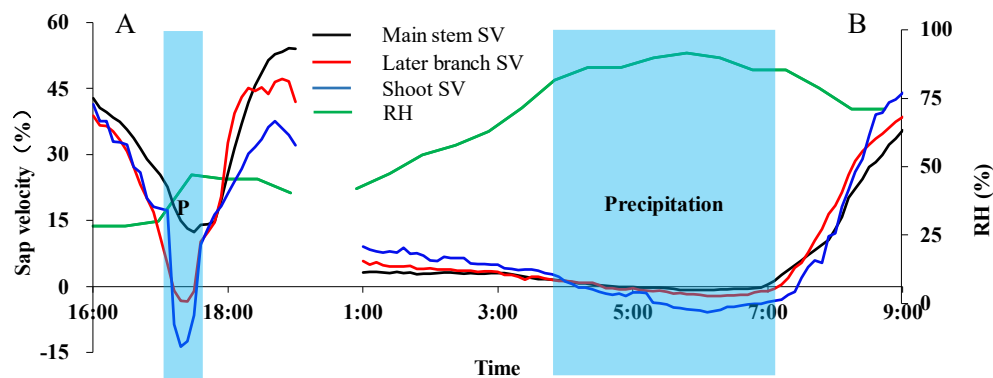




357 (B) is RH around 80% with slight fluctuations for we manually control the humidifier, and (C) is  
358 high intensity humidification, maintaining RH at around 90%.

### 359 **3.2 Precipitation events that can cause water absorption in leaves**

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



377

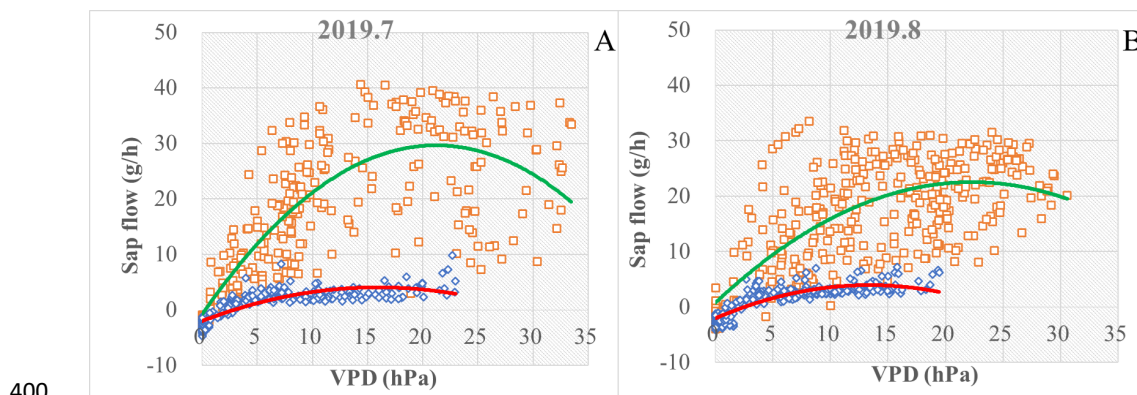
378 Figure 6. Effects of light and heavy precipitation events on reversed sap velocity (the ratio of the  
379 real-time sap velocity to the maximum sap velocity). A refers to a light precipitation during the  
380 day, B refers to a long precipitation during the night. SFR stands for sap flow rate.

### 381 3.3 Environmental factors affect vapor absorption

382 The sap flow rate is much higher during the daytime than at nighttime at a given VPD value. The  
383 decrease of the sap flow rate in August of 2019 (Figure 7B) as compared to the sap flow rate in  
384 July of 2019 (Figure 7A) indicates that the physiological activity of Tamarisk started to diminish  
385 in August. As shown in Table 1, the average daytime sap flow rate of Tamarisk in August 2019  
386 has a low Pearson correlation with VPD ( $R^2=0.501$ ,  $P<0.001$ ) (Figure 6A), and the nighttime sap  
387 flow rate was better correlated with VPD during the same duration ( $R^2=0.718$ ,  $P<0.001$ ), where  
388  $R^2$  is the coefficient of determination and P is the P-value used in the Pearson correlation analysis  
389 and it is the probability that you would have found the current result if the correlation coefficient  
390 was in fact zero (null hypothesis). Correlation coefficient  $R^2$  which is between 0 and 1. The closer  
391 of the  $R^2$  value to 1, the closer of the linear regression prediction to true value, and the more  
392 representative the fitted formula. In July and August of 2019, the Tamarisk sap flow rates and VPD  
393 for daytime and nighttime were best fitted with two quadratically polynomial functions. Above  
394 observations may be explainable as follows. July is the time of budding for Tamarisk, but  
395 precipitation amount was relatively low for July of 2019, thus the Tamarisk leaves are forced to  
396 absorb more water vapor from the atmosphere as a means of maintaining physiological activities.  
397 In contrast, precipitation in August of 2019 was relatively abundant, thus the Tamarisk leaves do



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



400

401 Figure 7. Relationship between the sap flow and water stress at different periods. Where daytime  
402 (denoted as orange color  $\square$ ) and nighttime (denoted as blue color  $\square$ ) data were plotted separately.  
403 Daytime refers to the duration from 7:00 am to 7:00 pm at the same day, and nighttime refers to  
404 the duration from 7:00 pm to 7:00 am of the following day. (A) The mean values of branch sap  
405 flows from 18 to 28 July 2019 in relation to VPD; (b) The mean values of branch sap flows from  
406 20 August to 2 September 2019 in relation to VPD.

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

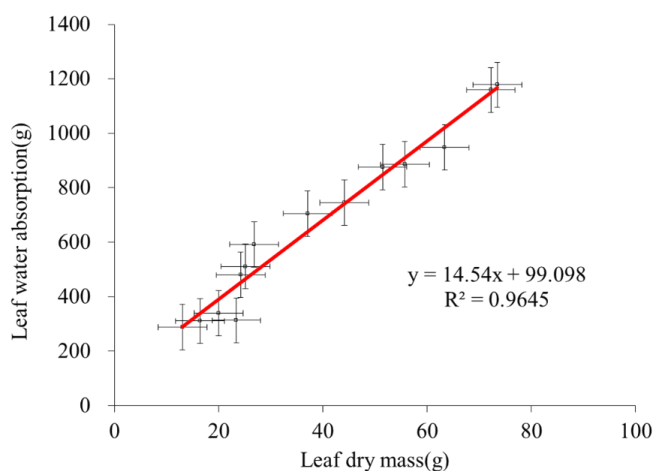
415 Table 1 The best-fitted sap flow rates of Tamarisk branches versus VPD in July 2019 and August  
416 2019 during both daytime and nighttime using quadratic functions. SF stands for sap flow rate (g/h)  
417 and  $R^2$  is the coefficient of determination.



Date	Time		R <sup>2</sup>
2019.7	daytime	SF = -0.044VPD <sup>2</sup> + 1.951 VPD + 0.794	0.501
	nighttime	SF = -0.033 VPD <sup>2</sup> + 0.893 VPD - 2.013	0.718
2019.8	daytime	SF = -0.068 VPD <sup>2</sup> + 2.868 VPD - 0.758	0.658
	nighttime	SF = -0.024 VPD <sup>2</sup> + 0.759 VPD - 1.981	0.703

#### 418 3.4 Calculation of precipitation absorption and utilization

419 The Tamarisk leaves were the primary means for absorbing atmospheric water. If we obtained the  
420 relationship between the water absorption and the dry mass of leaves, we could estimate the total  
421 amount of precipitation absorbed by any Tamarisk leaves. As shown in Figure 8, we collected the  
422 dry leaves mass and water absorbed by leaves after 15 precipitation events in 2019, and found that  
423 the precipitation absorption and the dry mass of leaves was positively correlated, with a coefficient  
424 of determination (R<sup>2</sup>) of 0.9645. These 15 precipitation events were randomly distributed during  
425 the daytime and nighttime of July (a dry month) and August (a wet month) of 2019. The amount  
426 of precipitation absorbed by the Tamarisk leaves can be calculated by weighing the dry matter  
427 mass of the Tamarisk leaves, but this method needs to destroy of the plant. We want to calculate  
428 the amount of water absorbed by the Tamarisk leaves by measuring the reverse sap flow. In  
429 particular, how much precipitation will be absorbed by the Tamarisk leaves?



430

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

432 The reversed sap flow amount is positively correlated with precipitation events, but precipitation  
433 events did not necessarily result in a reversed sap flow in branch of Tamarisk. The occurrence of  
434 reversed sap flow was not only influenced by the amount of precipitation but was also influenced  
435 by the duration of the precipitation event. Table 2 shows the reversed sap flow in the stem and  
436 branch of a Tamarisk under different precipitation events in July and August 2019. The reversed  
437 sap flow was normalized to mm per unit based on the Tamarisk canopy area, ratio of reversed sap  
438 flow to time. One can see that even for precipitation intensity as small as 0.5 mm/d, unsaturated  
439 atmospheric moisture can be absorbed by Tamarisk leaves. There is a relatively strong  
440 precipitation event occurred on August 2, 2019 with an intensity of 5.2 mm/d, but the reversed sap  
441 flow of Tamarisk was not remarkable. This is probably due to the relatively short duration of this  
442 precipitation event, and consequently the stem and branch sap flows accounted for only 0.5% and  
443 1.1% of the precipitation amount, respectively. A light precipitation event occurred in the morning,  
444 July 24, 2019, but this precipitation event was not recorded by the in-situ rain gauges as the  
445 precipitation intensity was less than the 0.2 mm, lower than the minimum measurement range of  
446 the rain gauge. Surprisingly, Tamarisk stem and branch showed significant reversed sap flows  
447 during this precipitation period. There were two precipitation events recorded at weather stations  
448 on 18 and 22 July, 2019, and the reversed sap flow was only seen in Tamarisk shoot while the  
449 Tamarisk branch showed no or slight reversed sap flow. This is probably because the two  
450 precipitation events occurred at midday and late afternoon, during which the evapotranspiration



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

455 Table 2 Precipitation characteristics and precipitation absorption by the Tamarisk leaves during  
 456 the observation period in 2019

Date	Time	Duration (h)	Precipitation (mm)	Sap flux(mm)		Reversed sap flux on Precipitation%	
				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

457 **3.5 Water absorption and consumption characteristics of Tamarisk**

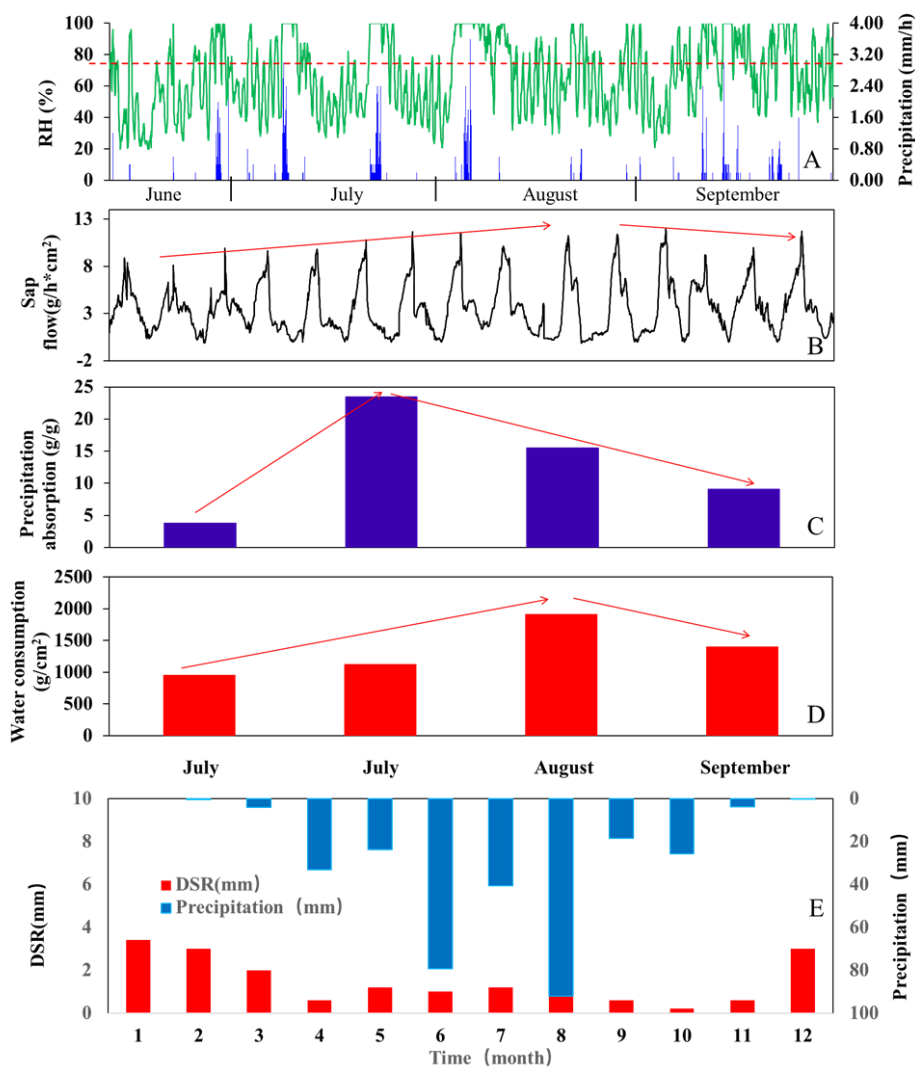
458 As shown in Figure 9A. The rainy season started in June and ended in September, and the mean  
 459 multi-year annual precipitation was less than 100 mm(Cheng et al., 2018). As shown in Figure 9B,  
 460 the sap flow rate of Tamarisk was in the rising trend from June to August, indicating that this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



463 from atmosphere. As precipitation increased and Tamarisk growth slowed down, the amount of  
464 water absorbed from the atmosphere gradually decreased, as shown in Figure 9C. The timing of  
465 water consumption and timing of water vapor absorption by Tamarisk were different, the  
466 maximum water consumption period of Tamarisk was in August, while solar radiation reached its  
467 maximum in July, and transpiration was the strongest in July,

468 The DSR throughout the year is mostly concentrated in December-April. During the five-year  
469 experimental period, the DSR accounts for 5.77% of the precipitation over the same period. The  
470 annual precipitation of the experimental site in 2020 is 84 mm, and the DSR of the same year is 5  
471 mm. As shown in Figure 9D. Precipitation patterns and DSR at the plot revealed that precipitation  
472 was mainly distributed in June and August, while Tamarisk was still budding in June and Tamarisk  
473 physiological activity began to weaken in August, thus the amount of atmospheric water absorbed  
474 by Tamarisk leaves was small in these two months. A larger amount of precipitation occurred in  
475 August, and soil moisture became the main source to sustain the water need of Tamarisk, as shown  
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  
479 Tamarisk was forced to absorb water from light precipitation with leaves. When the rainy season  
480 arrived, soil moisture was relatively abundant, but Tamarisk was also approaching dormancy with  
481 less demand for water, thus the amounts of water obtained from both the soil and leaves were  
482 dropped. To survive in a water deficit harsh environment, Tamarisk was able to mitigate its water  
483 need by taking water from multiple means such as leaves and soil.



484

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

#### 487 4. Discussion

##### 488 4.1 The timing of absorbing atmospheric moisture

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





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

#### 501 **4.2 Characteristics of atmospheric water absorption by leaves**

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

#### 518 **4.2 The fate of the absorbed water**

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



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

#### 528 **4.3 The significance of absorbed atmospheric water for plants**

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

#### 538 **5. Conclusion**

539 Water is the most important limiting factor for plants in an arid region, and plants are often suffered  
540 from drought stress during their growth. To adapt to the arid environment, plants have developed  
541 certain ways to accommodate the harsh water-deficit environments, such as leaf degradation,  
542 thicker cuticle, depressed stomata, and developed horizontal root systems or deep root systems.  
543 Precipitation was the main source of water in the arid region and has an important influence on  
544 plant growth and physiological processes. However, light precipitation is difficult to infiltrate into  
545 the deep soil layer. Also due to usual intense evapotranspiration effect in arid regions, precipitated  
546 water stays in the shallow soil only for a short period of time. In this research, we have analyzed  
547 the characteristics of precipitation patterns of the research site, and investigated whether the  
548 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  
551 precipitation directly. The reverse sap flow usually appeared in the shoots soon after precipitation,  
552 and then in the branch and stem in turn. The rate of reverse sap flow was not only related to the  
553 amount of precipitation, but also related to the timing and duration of precipitation. Continuous  
554 precipitation results in the escalated reversed sap flow. During the experiment, a single nighttime  
555 light precipitation was surprisingly absorbed by the Tamarisk leaves by 42.6%. The Tamarisk  
556 leaves can absorb precipitation moisture even when the precipitation intensity is less than 0.2 mm/d,  
557 especially if the precipitation event occurs late at night or early in the morning. The reversed sap  
558 flows at stem and branch accounts for 13.6% and 21.5% of the precipitation amount, respectively,  
559 during an observation year. In summary, water absorption of Tamarisk leaves is very important  
560 for Tamarisk to survive in a harsh water-deficit desert environment.

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

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