



# 毛乌素沙地两种典型灌木叶片凝结水吸收能力及吸水途径

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**摘要** 凝结水是半干旱地区生态系统重要的水源, 已有研究表明, 一些沙生植物可以通过叶片吸收凝结水以改善其水分状况。该研究以毛乌素沙地典型沙生灌木黑沙蒿(又称油蒿)(*Artemisia ordosica*)和北沙柳(*Salix psammophila*)为研究对象, 研究这两种植物的叶片是否具有吸收凝结水的能力, 并探究叶片吸水的途径及运移的通道。分别将黑沙蒿与北沙柳失水和未失水离体枝条置入人工模拟加湿室中, 使用高丰度氘水标记的凝结水进行浸润实验, 比对浸润前后枝条质量、叶片水及茎水氢同位素丰度变化, 确定黑沙蒿和北沙柳的叶片吸水能力; 并将盆栽黑沙蒿和北沙柳整株置入人工模拟加湿室, 使用荧光标记的凝结水进行浸润实验, 比对浸润前后叶片、小枝荧光显像, 确定黑沙蒿和北沙柳叶片吸收和运移凝结水的途径。结果显示: (1) 黑沙蒿和北沙柳未失水枝条在浸润前后质量无显著差异, 黑沙蒿和北沙柳失水离体枝条在凝结水浸润后质量显著提高了2.04%和6.74%, 叶片水氘丰度提高了170.10‰和104.09‰, 茎水氘丰度提高了10.52‰和12.72‰; (2) 荧光标记凝结水浸润后, 荧光示踪剂分布在黑沙蒿和北沙柳叶片的角质层、气孔、海绵组织、栅栏组织和维管束中, 黑沙蒿叶片的厚角组织中也发现了荧光示踪剂, 两种灌木小枝的表皮、韧皮部、木质部和髓中均观察到荧光。以上结果表明, 毛乌素沙地两种典型灌木叶片均具有吸收凝结水的能力, 水分亏缺植株的吸水能力更强; 两种灌木叶片通过气孔或角质层吸收凝结水, 并通过叶肉运移至维管束乃至小枝。黑沙蒿与北沙柳叶片具有的吸水功能可能是其适应干旱期水分亏缺的重要水分利用策略。

**关键词** 黑沙蒿; 北沙柳; 叶片吸水; 凝结水; 水分利用策略

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## Foliar condensate absorption and its pathways of two typical shrub species in the Mu Us Desert

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### Abstract

**Aims** Condensate is an important water source for plants in the ecosystems of drylands. Previous studies have found that some desert plants can absorb condensate via leaves. This study aimed to determine the capacity of the foliar condensate absorption of typical shrub species (*Artemisia ordosica* and *Salix psammophila*) in the Mu Us Desert, and to explore the pathways of foliar condensate absorption and transport.

**Methods** The dehydrated and non-dehydrated detached shoots of *A. ordosica* and *S. psammophila* were placed in an artificial chamber and exposed to deuterium labelled condensate, and the foliar condensate absorption was determined by comparing the differences of shoot masses and isotopic signals between pre- and post-immersion. The potted whole plants of *A. ordosica* and *S. psammophila* were placed in an artificial chamber and exposed to fluorescent tracer solution, and the pathways of foliar water uptake and transport were determined by comparing the differences of fluorescent tracing in leaves and twigs between pre- and post-immersion.

**Important findings** (1) After the deuterium labelled dew exposure, no significant differences were found in shoot masses between pre- and post-immersion of non-dehydrated detached shoots of *A. ordosica* and *S. psammophila*. However, the dehydrated shoot masses significantly increased by 2.04% and 6.74% in *A. ordosica* and

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*S. psammophila*, respectively; the  $\delta D$  (stable isotope ratio of hydrogen) of leaf water increased by 170.10‰ and 104.09‰ in *A. ordosica* and *S. psammophila*, respectively; and the  $\delta D$  of xylem water increased by 10.52‰ and 12.72‰ in *A. ordosica* and *S. psammophila*, respectively. (2) After the fluorescent tracer solution exposure, fluorescence was observed in the cuticles, stomata, spongy mesophyll, palisade cells and vascular bundle of the leaves of *A. ordosica* and *S. psammophila*. The fluorescence was also found in collenchyma of the leaves of *A. ordosica*. In addition, the fluorescence was observed in phloem, xylem, and pith of twigs of two shrub species. This study found that two typical shrub species in the Mu Us Desert had the capacity to absorb condensate via their leaves, and the plants undergoing water stress had the higher capacity of foliar condensate absorption. The leaves of *A. ordosica* and *S. psammophila* absorbed condensate through cuticles or stomata, and the absorbed water was transported to vascular bundle and even twigs. Foliar condensate absorption may be an important water use strategy to survive for *A. ordosica* and *S. psammophila* during dry periods.

**Key words** *Artemisia ordosica*; *Salix psammophila*; foliar condensate absorption; condensate; water use strategy

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水分是荒漠生态系统最主要的环境限制要素。凝结水是干旱半干旱区重要的补充性水源,发挥着不可忽视的作用(Zhang *et al.*, 2009; Hao *et al.*, 2012)。在有些地区,如纳米布沙漠,凝结水量可超过年降水量(Mitchell *et al.*, 2020)。而在以色列内盖夫沙漠、美国内华达沙漠、中国毛乌素沙地,凝结水量可达年降水量的7.2%–16.2% (Zangvil, 1996; Malek *et al.*, 1999; 郭晓楠, 2017)。在凝结水事件中,土壤表层水分可以得到一定改善(刘文杰等, 2001),叶片温度及气孔导度降低,致使植物蒸腾耗水减少(Zhuang & Ratchiffe, 2012; 李鹭辰等, 2021),叶片还可以直接吸收利用叶片表面的凝结水。

自Hales (1727)首次提出叶片吸水以来,已经在200多种植物、6个主要生态系统中发现此种现象(Berry *et al.*, 2019)。作为一种广泛存在的功能,叶片吸水可显著改善植物水分状况。对两种常绿灌木的研究结果表明,具有叶片吸水功能的植物种经历长期干旱后,凝结水的输入使叶片组织相对含水量和小枝水势均有大幅提高,水分亏缺状况得到缓解,而不具吸水能力的植物种持续受到干旱胁迫影响(Munné-Bosch & Alegre, 1999)。在云雾林中的观测发现,利用氢氧同位素示踪计算得到的凝结水对欧洲云杉(*Picea abies*)水分来源的贡献率可达31%(Berry *et al.*, 2014),吸收凝结水产生的茎流逆流占旱季蒸腾量的9% (Gotsch *et al.*, 2014)。长期凝结水添加可显著提高供试植物的株高、生物量(庄艳丽和赵文智, 2010; Zhuang & Ratchiffe, 2012; Liu *et al.*, 2020)。已有研究发现,荒漠区植物普遍具有叶片吸水潜力(郑新军等, 2011; 王飞等, 2020; 杨利贞等,

2020),巴丹吉林沙漠、腾格里沙漠、库布齐沙漠的部分沙生植物叶片具有吸水功能,并通过吸收大气凝结水,改善自身水分状况,维持生理生态功能(庄艳丽和赵文智, 2010; Yan *et al.*, 2015; Gong *et al.*, 2019)。然而,目前并不清楚毛乌素沙地两种典型的沙生灌木黑沙蒿(又名油蒿)(*Artemisia ordosica*)和北沙柳(*Salix psammophila*)是否具有此种功能。

植物叶片具有多种吸水结构,露水可通过叶毛(Eller *et al.*, 2016)、角质层(Goldsmith *et al.*, 2013; Eller *et al.*, 2016)、气孔(Kim & Lee, 2011)、水孔(叶片尖端或边缘的排水结构)(Martin & von Willert, 2000)等结构进入叶片,并经过叶肉组织向维管束运移(Kim & Lee, 2011; Eller *et al.*, 2016)。由于气孔的水力导度远大于其他结构,一般认为气孔是主要的吸水通道;而当夜间气孔关闭时,叶片吸水可能主要通过角质层(Eller *et al.*, 2016)。沙生植物的叶片通常具有特殊的耐旱特征,如下陷的气孔和致密的角质层,但目前并不清楚这些叶片特性如何影响吸水。此外,一些沙生灌木如红砂(*Reaumuria soongarica*),具有特定的吸水结构(Wang *et al.*, 2016a),但其他沙生植物能否通过特殊结构吸收水分并不清楚。

黑沙蒿和北沙柳作为毛乌素沙地的典型固沙灌木,在生长季频繁遭受严重的土壤干旱,干旱期月蒸腾量可下降约50%(杨强, 2016)。通过同位素示踪方法研究发现,黑沙蒿和北沙柳的吸水深度主要集中在0–40 cm (Cheng *et al.*, 2006; 朱雅娟等, 2010),但并未将露水纳入这两种植物的水分来源分析。毛乌素沙地年凝结水量相当于年降水量的10% (郭晓

楠, 2017), 已有研究通过叶片浸水实验表明黑沙蒿具有较强的叶片吸水潜力(杨利贞等, 2020), 露水可能是该地区植物的重要额外水源。本研究以毛乌素沙地典型沙生灌木黑沙蒿和北沙柳作为研究对象, 通过同位素标记模拟凝结水浸润实验和荧光标记模拟凝结水浸润实验, 分别探究两种灌木叶片吸收凝结水的功能与途径, 旨在从沙生灌木叶片吸水的角度, 了解沙生植物的水分利用策略和干旱适应机制。

## 1 材料和方法

### 1.1 研究区概况

本研究在毛乌素沙漠西南边缘的宁夏盐池毛乌素沙地生态系统国家定位观测研究站(37.07°–38.17° N, 106.50°–107.68° E, 海拔1 530 m)开展。研究区属半干旱大陆性季风气候, 年平均气温为8.1 °C, 冬夏温差为28 °C, 昼夜温差为20 °C。年降水量为292 mm, 雨季为6–9月, 降水量约占全年的80% (Jia *et al.*, 2018)。凝结水年发生天数占全年的78%, 日凝结水量为(0.15 ± 0.08) mm (郭晓楠, 2017)。研究区植被主要由黑沙蒿、北沙柳、蒙古山竹子(*Corethro-dendron fruticosum* var. *mongolicum*)、柠条锦鸡儿(*Caragana korshinskii*)等灌木, 以及赖草(*Leymus secalinus*)、沙蓬(*Agriophyllum squarrosum*)等草本植物组成(Bai *et al.*, 2018; Jia *et al.*, 2018)。

### 1.2 实验材料准备

2019年4月, 在装满风沙土的栽植盆(11.34 L)中扦插北沙柳枝条。5月, 将固定沙地上正常生长的黑沙蒿植株移栽到与北沙柳相同规格的栽植盆中。定期用地下水(氢稳定同位素比值( $\delta D$ )  $\approx$  -50‰)浇灌黑沙蒿和北沙柳植株, 保持植物组织氘同位素丰度稳定。

### 1.3 同位素标记模拟凝结水浸润

2019年8月, 分别进行黑沙蒿和北沙柳离体枝条的模拟凝结水浸润实验。实验前, 在固定沙丘选择长势良好的黑沙蒿和北沙柳植株各10株, 连续3天于9:00使用地下水浇水, 每株3–5 L。第4天6:00开始, 连续在野外进行5次取样, 平均间隔15 min。每次选取植物向阳面长势良好的小枝, 采集植株顶端长25–30 cm的枝条装入冷藏箱并带回实验室。

将离体枝条分为两组, 其中1组(5个枝条)放置30 min自然失水, 另1组(5个枝条)不进行失水处理。将未失水枝条与失水枝条分别置入离心管, 用封口膜密封, 在-40 °C冰箱中储存, 用于测量凝结水浸

润前的叶片水、茎水同位素。另取5条未失水枝条与失水枝条, 进行模拟凝结水浸润试验。试验前对受试枝条称质量, 然后对枝条切口进行密封隔水, 将其悬挂在通风橱内。通风橱内安装超声波加湿器, 加湿所用的水为氘同位素标记水( $\delta D \approx 495.4\text{‰}$ ), 加湿速率为600 mL·h<sup>-1</sup>, 保持通风橱内空气相对湿度维持在98%左右。模拟凝结水浸润4 h后, 取出枝条擦干表面水分并再次称质量。随后, 将受试枝条上分离的叶片和茎干装入离心管并密封, 置于-40 °C冰箱用于测量浸润后叶片和茎干水分的氘丰度。试验当天连续进行5次取样及模拟凝结水浸润处理, 每次取样及浸润处理过程中的枝条质量、叶片水氘丰度和茎水氘丰度为1个重复, 共5个重复。

### 1.4 荧光标记模拟凝结水浸润

为了探究黑沙蒿和北沙柳两种沙生灌木叶片吸水的途径, 采用荧光标记的水进行模拟凝结水浸润处理。使用塑料袋和防水隔热黏土封住北沙柳和黑沙蒿植株的栽植盆, 将其置入PVC板材制成的黑箱中, 使用超声波加湿器加湿, 保持黑箱内空气相对湿度维持在98%左右。加湿水为0.1%荧光增白剂溶液, 此种荧光剂对植物无毒害作用, 只能通过质外体途径运输, 能够很好地示踪叶片水分吸收和运移途径。受试植株模拟凝结水浸润4 h后取出, 摘取叶片及小枝并用蒸馏水清洗, 用滤纸擦干后使用植物切片机(MTH-1, NK Systems, Osaka, Japan)横切叶片和小枝, 得到荧光剂水溶液模拟凝结水浸润后的植物组织切片。将浸润前和浸润后的叶片及小枝切片固定在90%甘油磷酸缓冲液中, 使用荧光显微镜(BM-19AY, 上海彼爱姆光学仪器制造有限公司, 上海)在350 nm激发光下观察并拍照, 并利用激光共聚焦荧光显微镜(TCS SP8 STED 3X, Leica, Wetzlar, Germany)在405 nm激发光下观察并拍照。此外, 取黑沙蒿和北沙柳的叶片在烘箱内45 °C烘干48 h, 喷金处理后使用扫描电子显微镜(S4800, Hitachi, Tokyo, Japan)观察叶片表面形态与气孔构造。

### 1.5 同位素分析

使用低温真空蒸馏法(Dawson & Ehleringer, 1993)从叶片和茎干中提取水。在真空蒸馏前去除茎干表皮以得到木质部水。并使用液态水同位素分析仪(DLT-100, ABB, Quebec, Canada)测定叶片水和茎水的氢氧同位素组成。水中氢稳定同位素比值采用标准 $\delta$ 表示法( $\delta$ ), 如下所示:

$$\delta D (\text{‰}) = (R_{\text{sample}} - R_{\text{standard}}) / R_{\text{sample}} \times 1000 \quad (1)$$

式中,  $R_{\text{sample}}$ 和 $R_{\text{standard}}$ 分别表示植物组织水和标准水(标准平均海水, SMOW)的同位素比值。 $\delta D$ 的测量精度为 $\pm 0.3\text{‰}$ 。鉴于样品中残留的有机污染物会干扰同位素分析(Schultz *et al.*, 2011), 使用基于同位素比值红外光谱法的LWIA光谱污染识别软件来校正 $\delta D$  (West *et al.*, 2011)。

使用两箱线性模型(Schreel *et al.*, 2019a)计算凝结水对叶片水和茎水的相对贡献:

$$f_{\text{dew}} = \frac{\delta D_{\text{post-immersion}} - \delta D_{\text{pre-immersion}}}{\delta D_{\text{dew}} - \delta D_{\text{pre-immersion}}} \times 100 \quad (2)$$

式中,  $\delta D_{\text{post-immersion}}$ 为浸润后每个植物样品的氘同位素丰度,  $\delta D_{\text{pre-immersion}}$ 为浸润前植物样品的平均氘同位素丰度,  $\delta D_{\text{dew}}$ 为凝结水的氘同位素丰度。

## 1.6 统计分析

利用SPSS 23.0进行独立样本 $t$ 检验, 分析枝条质量、叶片水 $\delta D$ 和茎水 $\delta D$ 在浸润前后的差异, 以及凝结水对叶片水和茎水的相对贡献率在失水枝条和未失水枝条之间的差异。显著性水平统一设置为 $\alpha = 0.05$ , 当 $p < \alpha$ 时, 即为处理有显著效果。

## 2 结果

### 2.1 凝结水浸润前后枝条质量变化

结果显示, 黑沙蒿与北沙柳未失水枝条质量在

浸润前后无显著差异( $p > 0.05$ ), 黑沙蒿失水枝条质量在浸润后显著提高了2.04% ( $p < 0.01$ ), 北沙柳失水枝条质量在浸润后提高了6.74% ( $p < 0.01$ )(图1)。

### 2.2 叶片水同位素和茎水同位素变化

两种植物离体枝条经过4 h模拟凝结水浸润后, 叶水 $\delta D$ 相比浸润前显著增加( $p < 0.01$ ; 图2)。浸润前的黑沙蒿及北沙柳叶水 $\delta D$ 在 $-50\text{‰}$ – $0$ 之间; 浸润后, 黑沙蒿失水及未失水枝条叶水 $\delta D$ 和北沙柳未失水

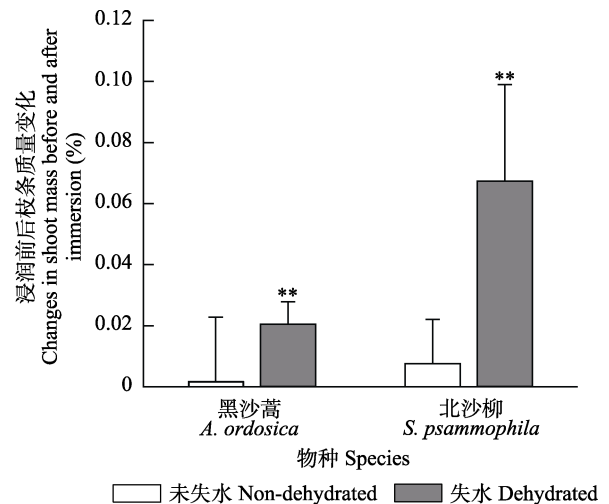


图1 黑沙蒿和北沙柳离体枝条浸润前后的质量变化(平均值 $\pm$ 标准差)。\*\*,  $p < 0.01$ 。

Fig. 1 Changes in shoot mass of *Artemisia ordosica* and *Salix psammophila* before and after immersion (mean  $\pm$  SD). \*\*,  $p < 0.01$ .

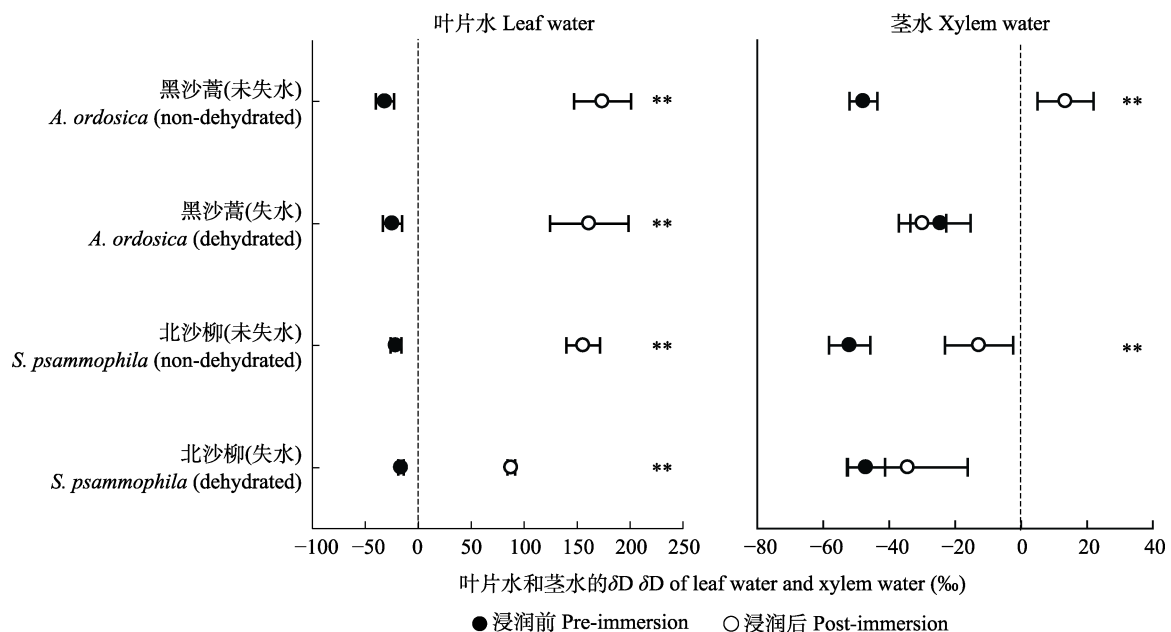


图2 黑沙蒿和北沙柳在浸润前后的叶片水与茎水氢稳定同位素比值( $\delta D$ )变化(平均值 $\pm$ 标准差)。\*\*,  $p < 0.01$ 。

Fig. 2 Changes in hydrogen stable isotope ratio ( $\delta D$ ) for leaf water and xylem water of *Artemisia ordosica* and *Salix psammophila* before and after immersion (mean  $\pm$  SD). \*\*,  $p < 0.01$ .



枝条叶水 $\delta D$ 在100‰–200‰之间, 北沙柳失水枝条叶水 $\delta D$ 较低(87.74‰)。浸润前黑沙蒿及北沙柳枝条的茎水 $\delta D$ 在–60‰–0之间; 浸润后, 黑沙蒿和北沙柳未失水枝条茎水 $\delta D$ 显著增加( $p < 0.01$ ), 黑沙蒿和北沙柳失水枝条茎水变化不显著( $p > 0.05$ )。

实验结果显示, 凝结水对两种植物叶片水的贡献率达到20%–40%, 对茎水的贡献率小于20% (图3)。凝结水对未失水枝条的叶片水、茎水贡献率都高于失水枝条。其中, 凝结水对北沙柳未失水枝条叶水的贡献率显著高于失水枝条( $p < 0.01$ ), 对黑沙蒿及北沙柳未失水枝条茎水的贡献率显著高于失水

枝条( $p < 0.05$ )。

### 2.3 凝结水浸润前后叶片及小枝荧光示踪

图4显示, 黑沙蒿叶片表面较为光滑, 北沙柳叶片背面较为光滑, 腹面密布毛簇且零散分布丝状叶毛。黑沙蒿和北沙柳的气孔均下陷。

浸润前的黑沙蒿叶片无自发荧光, 浸润后的黑沙蒿叶片角质层、厚角组织、海绵组织、维管束均观察到荧光(图5B), 其中厚角组织和维管束中有大量示踪剂富集。浸润前北沙柳叶片有较强的自发荧光, 存在于表皮、叶肉和维管束中(图5E)。对比浸润前后的北沙柳叶片荧光示踪, 仅能看出质外体示

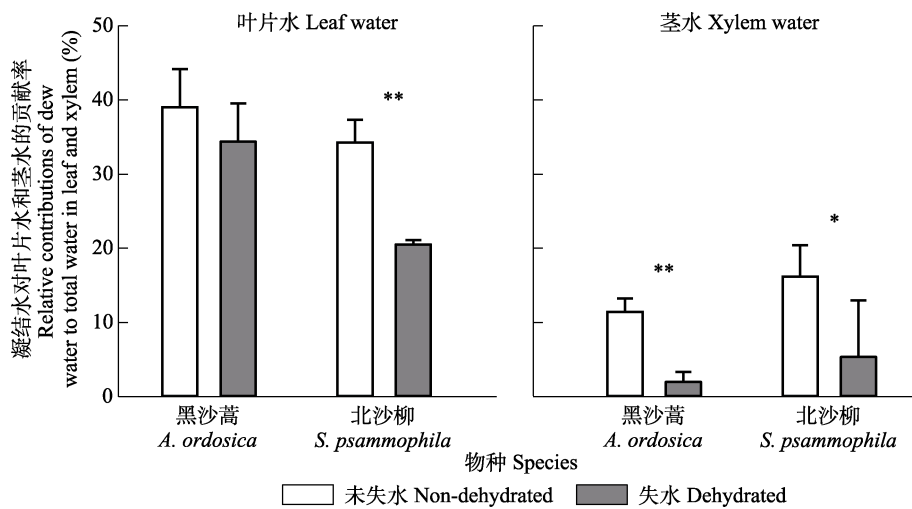


图3 凝结水对黑沙蒿和北沙柳叶片水与茎水的相对贡献率(平均值±标准差)。\*,  $p < 0.05$ ; \*\*,  $p < 0.01$ 。

Fig. 3 Relative contributions of condensate to total water in leaf and xylem of *Artemisia ordosica* and *Salix psammophila* (mean  $\pm$  SD). \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ .

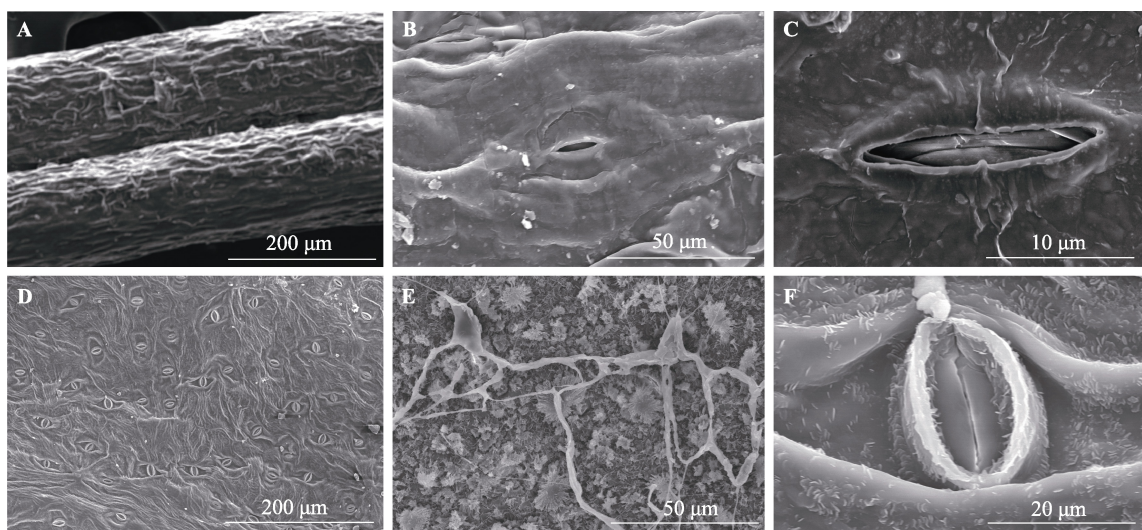


图4 黑沙蒿和北沙柳叶面及气孔形态。A, 黑沙蒿叶表。B, C, 黑沙蒿气孔。D, 北沙柳叶片背面。E, 北沙柳叶片腹面。F, 北沙柳叶片气孔。

Fig. 4 Leaf surface and stomata of *Artemisia ordosica* and *Salix psammophila*. A, Leaf surface of *A. ordosica*. B, C, Stomata of *A. ordosica*. D, Abaxial side of leaf of *S. psammophila*. E, Adaxial side of leaf of *S. psammophila*. F, Stomata of *S. psammophila*.

踪剂附着在叶片背面的表皮细胞,无法判定质外体荧光示踪剂是否进入叶肉和维管束(图5F)。浸润前的黑沙蒿和北沙柳小枝韧皮部、木质部均有自发光,浸润后黑沙蒿和北沙柳小枝中表皮、韧皮部、木质部和髓处的荧光亮度显著增强,表明质外体示踪剂分布在黑沙蒿和北沙柳小枝的表皮、韧皮部、木质部和髓中(图5D、5H)。

黑沙蒿和北沙柳叶片横切面均观察到了荧光,荧光剂分布在黑沙蒿叶片的角质层、气孔、厚角组织、海绵组织和维管束中(图6B)。黑沙蒿叶片横截面凹槽处的荧光强烈,大量荧光剂富集在厚角组织和维管束中(图6C)。荧光剂分布在北沙柳叶片的角质层、气孔、海绵组织、栅栏组织、维管束中(图6E),其中,维管束有大量荧光剂富集。北沙柳叶片背面比腹面的荧光强烈(图6F)。

### 3 讨论

模拟凝结水浸润后,黑沙蒿和北沙柳的失水离体枝条质量显著增加,叶片水和茎水氢同位素值显著改变(图1,图2),表明在水分亏缺条件下,黑沙蒿和北沙柳存在叶片吸水过程,而未失水的离体枝条质量无显著变化,说明叶片并未吸水,或叶片吸水约等于同时段蒸腾耗水。叶片内外水势差是叶片吸水的动力,当植物叶片发生水分亏缺时,更低的叶片水势提高了叶片内外水势梯度,从而提高叶片吸水速率(Cassana *et al.*, 2016);另外,由于水分从叶片运移至小枝的阻力大于水分在叶片内扩散的阻力,叶片吸收的水分会首先补充叶片,提高膨压,再向枝条运输(Berry *et al.*, 2019)。因此,叶片水分饱和和亏缺可能决定了叶片吸水的潜力,缺水叶片的水分饱和和亏缺更大,吸水潜力更大。

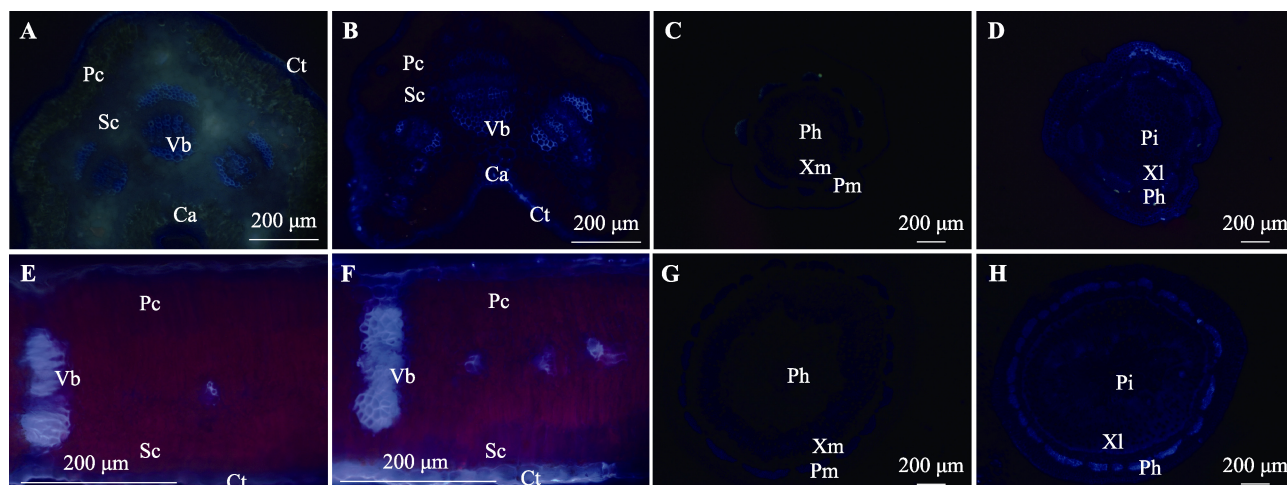
模拟凝结水浸润后,相比黑沙蒿,北沙柳离体枝条质量增加率更高,表明北沙柳叶片可能具有更强的吸水能力。以往的研究发现,北沙柳比黑沙蒿有更低的叶水势(尹立河等, 2016)。叶水势越低,叶片大气间水势差越大,叶片吸水能力越强(Cavallaro *et al.*, 2020; 潘志立等, 2021)。相比黑沙蒿,北沙柳的气孔小而密(任昱等, 2021)。气孔密度的增加,可显著提高叶片与外界环境的水汽交换能力(贺金生等, 1994)。黑沙蒿与北沙柳叶片质地差异也可能影响吸水能力,黑沙蒿叶片半肉质、退化成线形,北沙柳叶片草质。尽管叶片浸水实验发现,肉质、退化

类叶片具有更高的吸水潜力(郑新军等, 2011),但吸水潜力强的叶片吸水速率较慢,在自然露水浸润事件中吸水量低(Gotsch *et al.*, 2015; Berry *et al.*, 2019)。此外,干旱半干旱区植物叶片可能存在促进吸水与降低耗水的平衡(郑新军等, 2011; Schreel & Steppe, 2020)。半肉质、退化成线形的黑沙蒿的黑沙蒿叶片在降低水分向外扩散的同时,可能也降低了水分向内通过的能力。

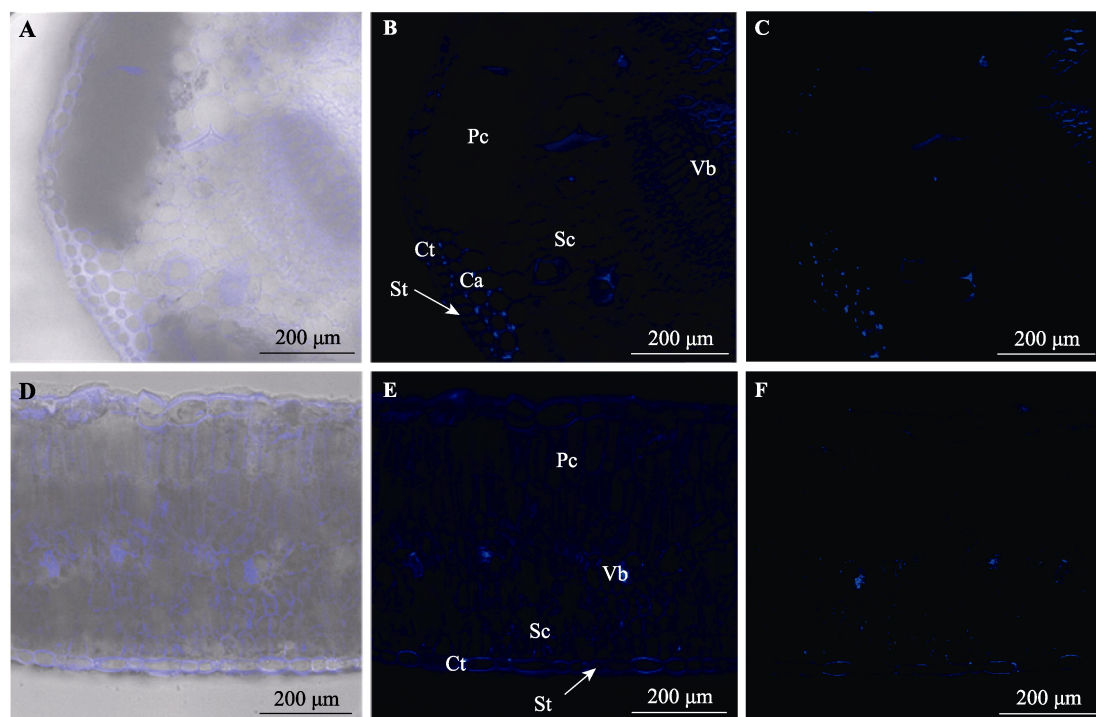
模拟凝结水浸润后,黑沙蒿和北沙柳离体枝条叶片水同位素组成均发生了显著改变。根据叶片水同位素组成改变计算出的凝结水对叶片水和茎水的贡献率远大于枝条质量增加率(图1),表明叶片在凝结水浸润中,发生了与凝结水之间水汽净通量为0的双向交换。双向交换过程中,凝结水置换叶水,并改变了叶片水同位素组成(Goldsmith *et al.*, 2017)。在离体枝条浸润实验中,凝结水对失水枝条的叶水和茎水相对贡献率小于未失水枝条,这是由于双向交换强度主要受大气湿度和气孔导度影响(Dongmann *et al.*, 1974),缺水叶片的气孔部分关闭降低了水汽交换速率(Schreel *et al.*, 2019b),但并未改变失水叶片通过水势梯度吸收凝结水。

模拟凝结水浸润后,未失水的黑沙蒿和北沙柳枝条茎水氢同位素显著富集(图2),这可能是叶片吸收的水分运移至茎干,改变了茎水同位素组成。叶片吸水运移在很多植物种均有发现,当叶片水势高于茎干和根系,叶片吸收的水分可以向下运移至茎、根乃至根际土壤(Laur & Hacke, 2014; Eller *et al.*, 2016)。沙生植物频繁经受水分胁迫,叶片吸水向下运移可以缓解植物栓塞,减少植物在干旱期的死亡率(McCulloh *et al.*, 2011; Mayr *et al.*, 2014)。此外,一些研究发现,同化枝及未栓化的枝条也具有吸水能力(Sparks *et al.*, 2001; Mayr *et al.*, 2014),而且枝条吸收的水分可以通过渗透势向内运输,直接补充木质部以缓解栓塞(Mayr *et al.*, 2014)。在本研究中,凝结水对北沙柳茎水的相对贡献率较高,很可能是北沙柳枝条直接吸水的结果。

荧光标记凝结水浸润后,黑沙蒿和北沙柳叶片的气孔和角质层均有示踪剂聚集(图5,图6)。叶片的气孔吸水现象已在番茄(*Solanum lycopersicum*)、梭梭(*Haloxylon ammodendron*)等植物中发现(Burkhardt *et al.*, 2012; Wang *et al.*, 2016b)。当气孔被水分浸润时,凝结水中的盐离子、气溶胶会降低水面张力,促



**图5** 浸润前后黑沙蒿和北沙柳叶片横切面荧光示踪。**A, E**, 浸润前黑沙蒿和北沙柳叶片横切面荧光示踪。**B, F**, 浸润后黑沙蒿和北沙柳叶片横切面荧光示踪。**C, G**, 浸润前黑沙蒿和北沙柳小枝横切面荧光示踪。**D, H**, 浸润后黑沙蒿和北沙柳小枝横切面荧光示踪。Ca, 厚角组织; Ct, 角质层; Pc, 栅栏组织; Ph, 韧皮部; Pi, 髓; Sc, 海绵组织; Vb, 维管束; Xl, 木质部。  
**Fig. 5** Cross-sections of leaf and twig of *Artemisia ordosica* and *Salix psammophila* in fluorescent tracing before and after immersion. **A, E**, Cross-sections of the leaf of *A. ordosica* and *S. psammophila* before immersion. **B, F**, Cross-sections of the leaf of *A. ordosica* and *S. psammophila* after immersion. **C, G**, Cross-sections of the twig of *A. ordosica* and *S. psammophila* before immersion. **D, H**, Cross-sections of the twig of *A. ordosica* and *S. psammophila* after immersion. Ca, collenchyma; Ct, cuticles; Pc, palisade cells; Ph, phloem; Pi, pith; Sc, spongy mesophyll; Vb, vascular bundle; Xl, xylem.



**图6** 黑沙蒿和北沙柳叶片横切面荧光示踪(激光共聚焦)。**A, D**, 黑沙蒿和北沙柳叶片横切面明场+荧光。**B, E**, 黑沙蒿和北沙柳叶片横切面荧光示踪。**C, F**, 黑沙蒿和北沙柳叶片横切面荧光明亮部位。Ca, 厚角组织; Ct, 角质层; Pc, 栅栏组织; Sc, 海绵组织; St, 气孔; Vb, 维管束。  
**Fig. 6** Cross-sections of leaf of *Artemisia ordosica* and *Salix psammophila* in fluorescent tracing (confocal laser scanning). **A, D**, Cross-sections of the leaf of *A. ordosica* and *S. psammophila* under fluorescence and bright light. **B, E**, Cross-sections of the leaf of *A. ordosica* and *S. psammophila* under fluorescence. **C, F**, Fluorescent bright spot in cross-sections of the leaf of *A. ordosica* and *S. psammophila* under fluorescence. Ca, collenchyma; Ct, cuticles; Pc, palisade cells; Sc, spongy mesophyll; St, stomata; Vb, vascular bundle.

进液态水通过气孔(Burkhardt *et al.*, 2001, 2012)。由于气孔导度占叶面导度的95%以上, 一般认为白天

气孔未关闭时, 气孔是叶片吸水的主要通道(Riederer & Schreiber, 2001; Berry *et al.*, 2019)。本项研究模拟



了夜间露水浸润,发现叶片吸水仍存在明显的气孔途径。近些年来研究发现,尽管气孔在夜晚部分关闭,但仍能保持15%的气孔导度(Caird *et al.*, 2007),一些荒漠植物甚至可达30% (Snyder *et al.*, 2003),黑沙蒿也存在夜间气孔开放的现象(陈栋等, 2015)。夜间气孔开放可以帮助植物补充养分和缓解栓塞(Caird *et al.*, 2007),也间接促进了叶片吸水。

角质层也被认为是叶片吸水的主要途径(Yates & Hutley, 1995; Goldsmith *et al.*, 2013)。角质层由带有羟基和羧基的长碳链脂肪酸聚合物组成,其中的分子间隙及分子上的羟基、羧基亲水基团可使水渗透进入叶内。在本研究中,荧光剂分布于黑沙蒿表面和北沙柳叶片两面。此外,荧光示踪显示,北沙柳叶片背面的角质层比腹面富集了更多的荧光剂(图6F),这可能是腹面的叶毛簇具有一定的斥水性。尽管一些植物的叶毛具有亲水性,能够促进叶面浸润乃至直接吸收水分(Schönherr, 2006; Wang *et al.*, 2010),但叶毛的性质和密度会影响叶面的润湿性,当叶毛密度大于25 Ind.·mm<sup>-2</sup>时,叶面具有很强的斥水性(Brewer *et al.*, 1991)。北沙柳腹面密布的叶毛具有遮蔽气孔、阻止蒸发的功能,但也降低了叶面润湿性和气孔导度,从而降低了腹面的吸水能力。

荧光示踪结果显示,黑沙蒿和北沙柳叶片吸收的水分经气孔、角质层吸收后运移至叶肉、维管束(图5, 图6),其中黑沙蒿的厚角组织聚集了大量荧光剂(图6B、6C)。由于厚角组织的细胞壁含有大量亲水纤维素和果胶,所以富含厚角组织的黑沙蒿叶片凹槽处吸水能力最强,并形成角质层、厚角组织、海绵组织、到维管束的吸水通路。此外,黑沙蒿与北沙柳叶片维管束比海绵组织、栅栏组织的荧光信号更加强烈(图6E、6F),表明叶片吸收的水分部分留存在维管束。模拟凝结水浸润后,黑沙蒿和北沙柳小枝表皮、韧皮部、木质部、髓均发现荧光剂,说明叶片吸收的水分可能运移至小枝。由于小枝的荧光在各个结构上有相似的强度,我们推测小枝表皮细胞可能同样具有吸收凝结水的能力,并通过管胞向木质部、韧皮部、髓运移。

在模拟凝结水浸润实验中,水分亏缺的黑沙蒿和北沙柳具有更强的叶片吸水能力。荒漠地区土壤干旱事件频发,但土壤干旱期不乏小降水事件,以及小降水事件后的凝结水事件(Guo *et al.*, 2016)。缺水植物的叶片吸水能够显著改善植物的水分生理状

况(Cassana *et al.*, 2016; Schreel & Steppe, 2020),叶片吸收凝结水可能是沙生植物适应沙地频繁土壤干旱的重要抗旱策略。

尽管本研究确认了毛乌素沙地典型灌木黑沙蒿与北沙柳具有叶片吸水的功能,但叶片吸水对沙生灌木生理生态的影响并不清楚。诸如沙生灌木水分生理对叶片吸水的响应,叶片吸水通量相对蒸腾的比率,长期叶片吸收凝结水对沙生灌木功能性状的影响等问题尚待进一步研究。未来的研究可通过野外原位监测植物生理生长指标对凝结水事件的响应,更为深入地认识沙生植物叶片吸水的功能及其生理生态作用。

## 4 结论

本研究通过同位素标记模拟凝结水浸润实验和荧光标记模拟凝结水浸润实验,确认了毛乌素沙地两种典型灌木黑沙蒿和北沙柳均有叶片吸水的能力,并发现水分亏缺的叶片吸水能力更强。黑沙蒿和北沙柳均可以通过叶毛和气孔吸收凝结水,黑沙蒿叶片凹槽处和北沙柳叶片背面的吸水能力较强。黑沙蒿叶片吸收的水分经厚角组织、海绵组织运移至维管束。北沙柳叶片吸收的水分经栅栏组织、海绵组织运移至维管束。黑沙蒿和北沙柳叶片吸收的凝结水部分贮存在维管束并向下运移至小枝。

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