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Rapid recovery of desert shrubs is attributed to imbalance of water supply to demand after disturbance in Northwest China

Hai Zhou^{1*†}, Xiangyan Feng^{1,2†}, Zhibin He¹, Qiyue Yang¹, Heng Ren¹ and Wenzhi Zhao^{1*}

Abstract

Background Disturbance is a key driver of changes in terrestrial ecosystems, especially in water limited regions. In the desert ecosystem of Northwest China, shrubs are often foraged by camels and this causes the shrubs lost their aboveground tissues. Although the aboveground tissue could recover after the disturbance, the mechanisms of resprouts' recovery after the disturbance are still poorly understood. We investigated the morphological and physiological characteristics and root water uptake sources of resprouts and non-disturbed seedlings of four desert shrub species that were often foraged by camels.

Results The results showed that the resprouts grew rapidly after the removal of aboveground tissue. The height and aboveground biomass of resprouts reached the level of 5-year-old seedlings following a growing season. Compared to un-disturbed seedlings, higher leaf water potential, leaf hydraulic conductance and photosynthesis rate were observed in resprouts, indicating that resprouts grew rapidly after disturbance. Furthermore, we found that the root water uptake source did not change after disturbance. This indicated that the roots of resprouts kept intact water uptake capacity after disturbance, which could keep supplying sufficient water to the aboveground tissue. Due to the removal of aboveground tissue of the resprouts, the water demand of aboveground tissue decreased, which induced an imbalance of water supply from roots to demand of aboveground tissues of resprouts. This explained the improved physiological performance and rapid recovery of resprouts after disturbance.

Conclusions The imbalance of water supply to demand contributes to the rapid recovery of desert shrubs after disturbance. The findings provide insight into the eco-physiological mechanism for the maintenance of desert ecosystems that are facing disturbance.

Keywords Disturbance, Resprout, Physiological performance, Shrub, Water uptake source

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Introduction

Disturbance is a key driver of the terrestrial ecosystem, which shifts the canopy and understory environmental conditions and ultimately results in biodiversity and species composition alteration (Seidl et al. 2011; Belote et al. 2012). However, disturbance and even the removal of aboveground tissues do not necessarily induce plant mortality (Dietze and Clark 2008; Atwood et al. 2009). New buds sprouted from the stem and/or root stocks grow rapidly to recover the height and biomass at pre-disturbance stage (Bond and Midgley 2003; Clarke et al. 2013). The proposed mechanisms of the rapid growth of resprouts are as follows: (1) due to shoot removal, the established root system of resprouts with relative sufficient water and nutrient supply promotes resprouts growth (Larsen and Johnson 1998; Swaim et al. 2016); (2) the low shoot-to-root ratio of resprouts compared to un-disturbed individuals results in growth competitive advantage (Clemente et al. 2005). Both mechanisms are related to an imbalance in the water and nutrient requirement of shoots versus the resource supply of roots. This possibly results in differences in the physiological properties between resprouts and un-disturbed individuals. However, the knowledge of the physiological properties of the resprouts is still limited.

The growth of plants is determined by a complex network of interdependent physiological processes, wherein a multitude of intricate mechanisms and interactions govern their development, replication, metabolism, and response to external stimuli (Nelissen and Gonzalez 2020; Hilty et al. 2021). Among them, photosynthesis rate, leaf hydraulic conductance, and leaf water status are the key physiological parameters that are associated with plant growth (Brodribb and Holbrook 2003; Ghanoum 2009; Sack et al. 2012). For instance, photosynthesis rate was linearly positively correlated with plant growth rate (Kirschbaum 2011). Leaf hydraulic conductance promotes plant growth through its positive effect on the photosynthesis rate (Scoffoni et al. 2016). Nevertheless, the physiological performance during resprouts growth is poorly understood. Only a few studies investigated the physiological performance during the resprouts regrowth. More work is needed to accurately assess the contribution of improved leaf physiological traits to resprouts growth.

Root water uptake source is critical for plants to meet the canopy transpiration demand and photosynthesis process needs (Grossiord et al. 2017). Past studies proposed that the rapid growth of the plants after the disturbance could be attributed to the sufficient root water supply from the intact root system compared with relative low water demand of new resprouts (Swaim et al. 2016). However, no direct evidence supported this

perspective has been reported yet. As the isotopes of oxygen and hydrogen does not fractionate during root water uptake (Washburn and Smith 1934), the analysis of the stable isotopes of oxygen and hydrogen in water provides a powerful and reliable method to analyze the water sources of plants (Voltas et al. 2015). Using the isotopic method to determine the root water uptake source during the resprouts growth is key to understanding the recovery of plants following the disturbance.

Desert ecosystem, characterized by its arid conditions and scarce availability of water, represents a quintessential example of a fragile ecosystem, often exhibiting a significantly diminished level of biodiversity owing to the harsh and inhospitable nature of its surroundings (Whitford and Duval 2020; Rocha et al. 2021; Warren-Rhodes et al. 2022). Badain Jaran Desert is a typical desert in Northwest China, where several desert plant species and large animals such as camels survived since ancient times (Wang and Zhou 2018; Li et al. 2020; Lu et al. 2023). Shrubs are the main food source of camels, and they are always disturbed by camels in this region. However, the regrowth capacity of desert shrubs and the possible physiological mechanisms behind the disturbance are still unknown. Therefore, investigating the regrowth of the desert shrubs following the disturbance has critical implications for the local ecosystem conservation and management.

In this study, we selected four desert shrub species that are often foraged by camels as the research materials. The aboveground tissue was removed to mimic the camel's feeding processes. The regrowth capacity, physiological performance and root water uptake sources of desert shrubs' resprouts following the disturbance were investigated. We hypothesized that the resprouts of the desert shrubs have evolved rapid growth capacity to acclimate grazing. Due to the physiological processes, such as hydraulic conductance and photosynthesis rate, being closely related to plant growth, we hypothesized that the resprouts exhibit better physiological performance compared with un-disturbed seedlings. Because the disturbance has not damaged the root system, we hypothesized that the water uptake source of the resprouts did not change, which resulted in the relative high root water supply to low canopy demand and thus improved resprouts physiological performance and rapid regrowth following the disturbance.

Materials and methods

Study site and plant materials

The study site was located at Linze Inland River Basin Research Station (100° 8' E, 39° 21' N) in the south-east of Badain Jaran Desert, which belongs to China Flux Observation and Research Network. The study

site is characterized by a typical desert climate with mean annual precipitation of 117 mm, mean annual evaporation of 2390 mm, mean temperature of 7.6 °C, mean wind speed of 3.2 m s⁻¹ and solar radiation of 611,272.8 J cm⁻² a⁻¹ over the past 20 years. The growing season ranges from April to September (Feng et al. 2022b) (<http://lzd.cern.ac.cn>).

Hundreds of camels live in the desert environment in this region and forage shrubs as their main food sources. Here, we selected four mostly foraged shrubs (*Atriplex canescens*, *Caragana korshinskii*, *Hedysarum scoparium* and *Calligonum mongolicum*) as the research materials. The four shrubs are all extremely drought-tolerant species that grow in sand dune and inter-dune lowlands, which are important food sources of desert animals and also are critical sand fixation species surround oases. We measured the growth, physiological traits and root water uptake source of the four desert shrub species and their resprouts to decipher the rapid growth mechanisms after a disturbance.

Experimental design

Four desert shrub species (*A. canescens*, *C. korshinskii*, *H. scoparium* and *C. mongolicum*) were planted in the field in 2018. To mimic the animal feeding process, six individuals of each species were reaped at about 20 mm above the ground in the spring of 2022 (March). The resprouts were growing rapidly during the growing season. At the end of the growing season (September), the resprouts that went through a growing season were one-year-old resprouts and the seedlings that have not reaped were five-year-old seedlings. To explore the rapid recovery mechanisms of the resprouts, we compared the differences in morphological traits, physiological traits and water sources between one-year-old resprouts and five-year-old seedlings of four desert shrub species.

Resprouts growth

The resprouts growth performance was reflected by the shrubs' height and biomass. At the end of the growing season of 2022, we measured the height and biomass of five-year-old shrubs and one-year-old resprouts to evaluate the regrowth of the four desert shrub species after disturbance. For one-year-old resprouts and five-year-old seedlings, the plant height and biomass were measured in six individuals for replication. The shrub's height was measured by a commercial tape (deli l.147-1498203, Deli group, Ningbo, China) by measuring the distance from the ground level to the top of the highest leaf at the shoot. The aboveground tissues were harvested and the biomass of the shrubs was measured by the oven-dry method. The reaped shrubs were put into the oven (DHG-9075, Ganyi LLC, Shanghai, China) at 80 °C for 72 h to get dried. Then

the biomass of the shrubs was measured using a balance (ME204E, Mettler Toledo, Zurich, Switzerland).

Leaf water potential

Leaf water potential in predawn (Ψ_{pre}) and midday (Ψ_{mid}) of five-year-old shrubs and one-year-old resprouts were measured by the Scholander-type pressure chamber (Model 1515D; PMS Instrument Company, Corvallis, OR, USA). Ψ_{pre} is the leaf water potential in predawn, representing the maximum leaf water potential; Ψ_{mid} is the leaf water potential in the midday, representing the lowest leaf water potential that plants experienced over the day. For each species, six leaves were randomly sampled from six individuals in the predawn and midday. The sampled leaves were put into a black plastic bag to prevent solar radiation. Then we blew air into the bag and sealed the bag to stop leaf water loss. The sampled leaflet in the bag was equilibrated for 20 min before the leaf water potential measurement. The petiole of the equilibrated leaflet was wrapped by parafilm and the end of the petiole was cut by a blade. Then the leaflet was put into the chamber and pressurized nitrogen by 0.2 kPa per second. The water potential was recorded when water was pressured out from the leaflet.

Hydraulic conductance measurements

This study utilized a high-pressure flow meter (HPFM-Gen3; Dynamax Inc, Houston, TX, USA) to measure the leaf hydraulic conductance of the four desert shrub species. The mature shoots with leaves were sampled at predawn and put into a bucket filled with ultrapure water in September of 2022. The end of the shoots was recut underwater to prevent artificial embolism. Then the leaf petiole was cut under the ultrapure water, and the leaf petiole was connected to the high-pressure flow meter via compression fittings. The high-pressure flow meter tank was pressurized with nitrogen to 0.4–0.5 MPa, and the deionized water, free from air bubbles, was pumped out from the silicone tubing system (Upchurch Scientific, Oak Harbor, WA, USA). Leaf hydraulic conductance was determined by connecting a pressure transducer (Omega PX-180; Omega Engineering, Stamford, CT, USA) at the upper end of the eight-port valve and calculating the pressure-flow rate curve. Finally, the results were standardized to 25 °C to correct for the viscosity of water passing through the silicone tubing. For each species, the hydraulic conductance of six leaves from three individuals was measured.

Gas exchange measurements

The gas exchange characteristics of the four desert shrub species were measured using the Li-6400XT (Li-COR Biosciences, Lincoln, NB, USA). This study focused on

the photosynthetic rate, stomatal conductance, and transpiration rate of five-year-old shrubs and one-year-old resprouts. Measurements were conducted on fully expanded mature leaves between approximately 9:00 and 10:00 on clear days in September of 2022. To assess the gas exchange capacity of desert plants in the field, a transparent leaf chamber was used to keep leaf temperature, air humidity, and CO₂ concentration consistent with the surrounding environment. Light-saturated photosynthesis was measured when photosynthetically active radiation reached 1600 μmol m⁻² s⁻¹. The leaf temperature ranged 25–30 °C, the CO₂ partial pressure was at about 400 ppm and a relative humidity ranged from 10 to 30%. The data was recorded after the leaf photosynthesis reached its steady-state, which took about 10–20 min. Water use efficiency was calculated as photosynthesis divided by stomatal conductance. For the shrubs with needle-shaped leaves, such as *H. scoparium* and *C. mongolicum*, a needle leaf chamber was used to measure their gas exchange characteristics. After measurements, the leaf area was scanned and the leaf surface area inside the chamber was used to calibrate gas exchange values. At least six leaves from three individuals of each desert shrub were selected as replicates.

Isotopic analyses

To explore whether the root water uptake source changed after the disturbance, we measured the stable isotopes of oxygen and hydrogen in the xylem and soil water. The soil samples were sampled from 0 to 300 cm soil depth (0, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 120, 140, 160, 180, 200, 220, 240, 260, 280, 300 cm, respectively) by auger boring method. About 0.5 dm³ soil were sampled from each soil profile. The soil samples were put into a sealed glass bottle and stored in the refrigerator at 2 °C before isotopic analysis. A cryogenic vacuum distillation system was used to extract water from the xylem and soil samples (Ehleringer et al. 1999). The glass arm was attached with a Pyrex collection tube at one end, and an ignition tube containing xylem or soil samples at the other end. Then, the ignition tube containing samples was heated at 100 °C for 1 h to make the water evaporate to the collection tubes. The collection tubes were submerged in liquid nitrogen to let the evaporated water condense. The extraction stopped when no further water evaporated from the samples. The hydrogen- and oxygen-isotopic composition was measured by an Isotope Ratio Infrared Spectroscopy (IRIS) system, the liquid water isotope analyzer (912-0008-1001, Los Gatos Research Inc., Mountain View, CA, USA) with the precision of 0.1‰ for δ¹⁸O, and 0.3‰ for δD, respectively (Yang et al. 2015). The stable hydrogen and oxygen isotope values (δD, δ¹⁸O) are

reported in per mil (‰) relative to the Vienna Standard Mean Ocean Water (VSMOW), which was calculated as:

$$\delta D/^{18}O = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000\text{‰},$$

where R_{sample} and R_{standard} are the hydrogen and oxygen stable isotopic compositions (¹⁸O/¹⁶O, D/¹H) of VSMOW, respectively.

Statistics

The differences in growth, physiological traits and root water uptake source between five-year-old shrubs and their one-year-old resprouts were evaluated by one-way ANOVAs (Duncan). The water sources of the shrubs were evaluated by the IsoSource mixing model (Phillips et al. 2005). Due to the groundwater table is about 300 cm in the study site, we divided the soil water sources as shallow soil water (0–50 cm), middle soil water (50–150 cm), deep soil water (150–300 cm) and groundwater following a previous literature (Zhou et al. 2016). All statistical analysis and plotting were performed by R programming (R Core Team 2023).

Results

The regrowth capacity of the resprouts following the disturbance

For the four desert shrub species, the buds of resprouts all sprouted in the retained stems (Fig. 1). The resprouts grew rapidly in the growing season of the current year. The height of the four five-year-old desert shrubs ranged from 100 to 150 cm (Fig. 2a). After one growing season, the height of the one-year-old resprouts recovered to the same level as the five-year-old shrubs (Fig. 2a). The biomass of five-year-old *C. korshinskii*, *H. scoparium* and *C. mongolicum* was higher than that of *A. canescens*. Similar to the rapid regrowth of shrubs' height, the biomass of one-year-old resprouts of the four species also showed no significant differences compared with five-year-old seedlings (Fig. 2b), indicating a strong regrowth capacity of desert shrubs following disturbance.

The physiological performance of 5-year-old shrubs and their resprouts

Four 1-year-old resprouts species showed better physiological performance compared with five-year-old shrubs. The four five-year-old desert shrubs showed leaf water potential in predawn ranging from – 1.2 to – 0.8 MPa (Fig. 3). The leaf water potential in midday was distinct ranging from – 2.2 to – 1.5 MPa. The leaf water potentials of one-year-old resprouts were higher than that of five-year-old shrubs. The differences between predawn and midday leaf water potential ($\Psi_{\text{pre}} - \Psi_{\text{mid}}$) were lower

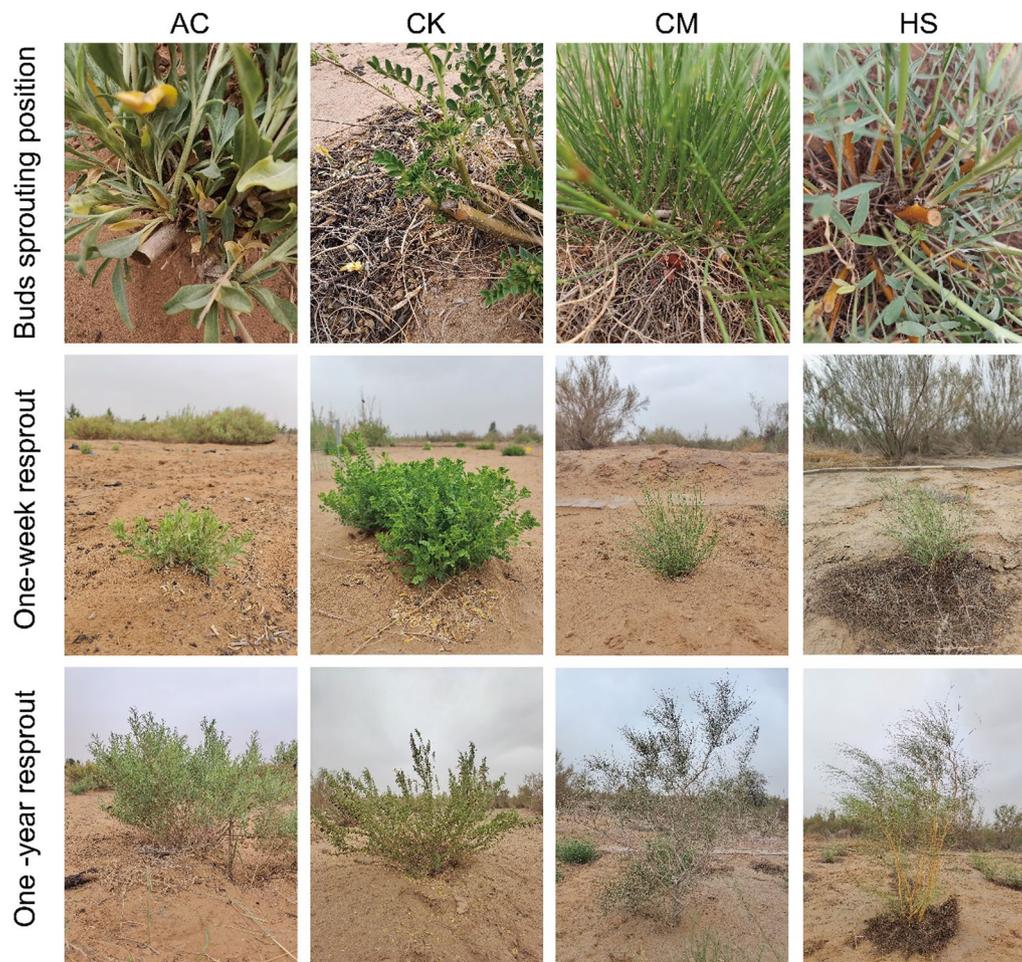


Fig. 1 Morphologies of the resprouts of four desert shrub species following a disturbance. The images showed the buds sprouting position, one-week-old resprouts and one-year-old resprouts of four desert shrub species. AC *A. canescens*, CK *C. korshinskii*, CM *C. mongolicum*, HS *H. scoparium*

in one-year-old resprouts compared with five-year-old shrubs (Fig. 3).

Higher leaf hydraulic conductance was observed in one-year-old resprouts than in five-year-old shrubs. Leaf hydraulic conductance was about two times higher in *A. canescens* and *C. korshinskii* than in *C. mongolicum* and *H. scoparium* (Fig. 4).

The photosynthesis rate, stomatal conductance and transpiration rate of the four desert shrub species ranged from 10 to 13 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, 0.12 to 0.18 $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ and 3.5 to 5.0 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$. The photosynthesis rate and stomatal conductance of one-year-old resprouts were significantly higher than those of five-year-old shrubs (Fig. 5a, b). The transpiration of one-year-old *A. canescens* and *C. korshinskii* resprouts were higher than that of their five-year-old seedlings. No significant differences between one-year-old resprouts and five-year-old seedlings in *C. mongolicum* or *H. scoparium*

were found (Fig. 5c). Additionally, the water use efficiency showed no significant differences between one-year-old resprouts and five-year-old seedlings in any of the four species (Fig. 5d).

Root water uptake during the resprouts rapid growth

Based on the stable isotope method, we found that the δD and $\delta^{18}\text{O}$ in the xylem water of different species exhibited significant differences ($P < 0.05$) (Fig. 6). Most xylem water and soil water samples were distributed to the lower right side of the LMWL (local meteoric water line) with low slopes of 3.21. However, the xylem water isotopic compositions of the same species among the control and resprouts had no pronounced difference. The isotopic signatures in the xylem water of all the shrubs were within the range of isotopic ratios in soil water from the deep soil layers that were larger than 150 cm.

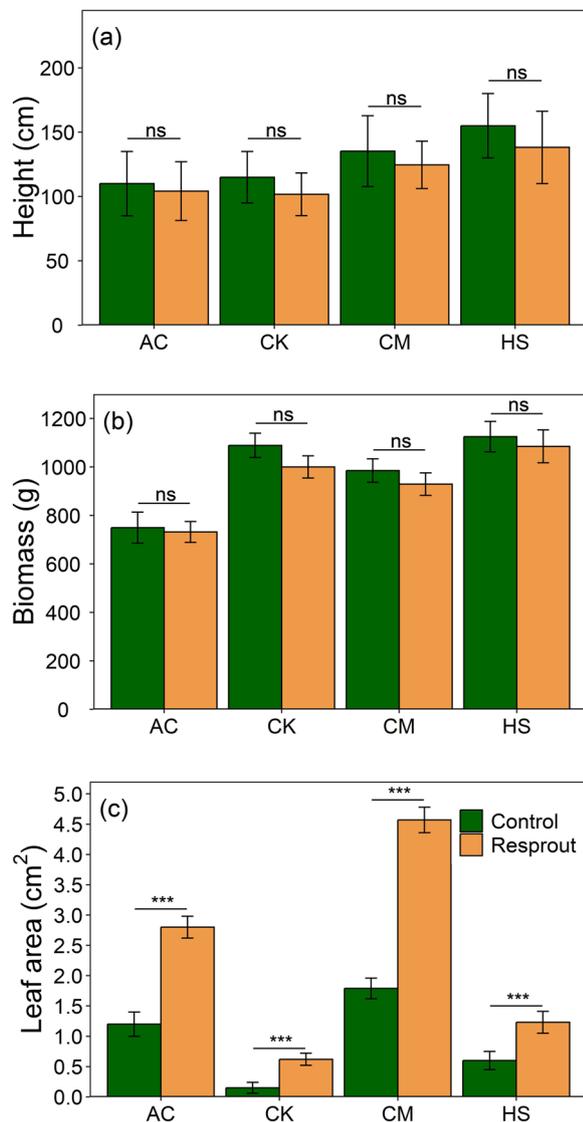


Fig. 2 Height, biomass and leaf area of one-year-old resprouts and five-year-old seedlings. Darkgreen labeled control represents 5-year-old seedlings; tan labeled resprout represents 1-year-old resprouts; AC *A. canescens*, CK *C. korshinskii*, CM *C. mongolicum*, HS *H. scoparium*; ns indicates non-significant differences detected; standard error bar was showed above each column (one-way ANOVAs)

Four five-year-old desert shrubs showed similar root water uptake patterns, which were majorly dependent on deep soil and groundwater. Specifically, *A. canescens* absorbed about 10% water from the shallow soil, 20% from the middle soil, 30% from the deep soil, 40% water from groundwater; *C. korshinskii* absorbed about 10% water from the shallow soil, 15% from the middle soil, 30% from the deep soil, 45% water from groundwater; *C. mongolicum* absorbed about 10% water from the shallow soil, 20% from the middle soil, 25% from

the deep soil, 45% water from groundwater; *H. scoparium* absorbed about 15% water from the shallow soil, 15% from the middle soil, 25% from the deep soil, 45% water from groundwater (Fig. 7). The root water uptake source of one-year-old resprouts was similar to that of the five-year-old shrubs. No significant differences in root water sources were found between one-year-old resprouts and five-year-old shrubs, indicating sufficient water supplement following the disturbance (Fig. 7).

Discussion

Improved physiological performance promotes rapid resprouts growth following the disturbance

The sprouting site of the buds in resprouts after the disturbance was often observed in the rootstock (Bellingham and Sparrow 2000; Bond and Midgley 2003). Different from the resprouts sprout from the basal (Clarke et al. 2013), we found the four desert shrub species' buds all sprouted from the reserved stem (Fig. 1). This indicates that the desert shrubs could keep the stem surviving after the aboveground shoot removal (Meier et al. 2012). The possible mechanism behind this is that the removal of the aboveground shoot has caused the conduits embolized and occluded by gums or tyloses, which could effectively stop the stem water loss and keep the reserved stem alive (De Micco et al. 2016). Thus, the alive stems with protected meristematic tissue sprout new shoots from the reserved stems (Bond and Midgley 2001; Zeppel et al. 2015). This may promote the rapid regrowth capacity of the desert shrubs following the disturbance. In addition, due to about 20 mm stems being kept, the reserved stem that stored carbohydrates possibly promoted the rapid recovery of resprouts.

Consistent with a previous literature that reported the resprouts grow rapidly after the disturbance (Swaim et al. 2016), we also observed that the resprouts of the four desert shrub species grew rapidly after the shoot removal. The resprouts grew only one year to reach five-year-old seedlings' height and biomass (Fig. 2). This suggests that young seedling resprouts may recover faster than adult plant resprouts. Rapid plant growth was thought to be closely related to plant physiological processes (Kraft et al. 2015). It has been reported that the physiological properties such as leaf water status, hydraulic conductance and photosynthesis rate were closely related to plant growth (Tardieu and Simonneau 1998; Flexas et al. 2006). Our results showed strong evidence supporting this perspective. We found that leaf water potential was higher no matter at predawn or midday in one-year-old resprouts than that in five-year-old seedlings (Fig. 3). The higher leaf water potential indicates better leaf water status of resprouts and this would ultimately promote cell expansion and leaf development, especially

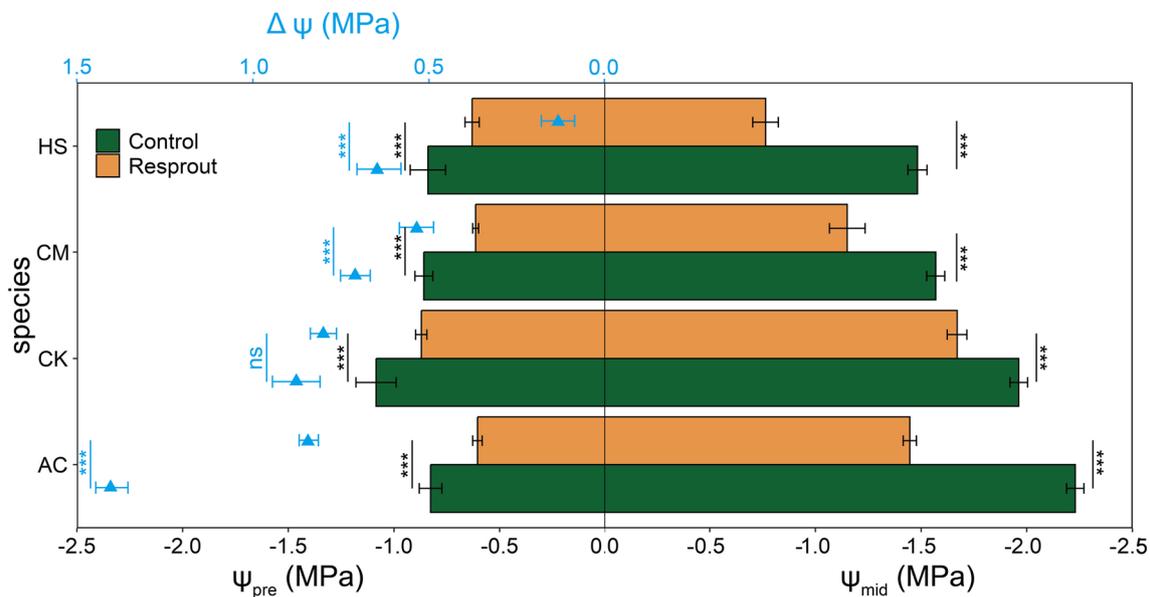


Fig. 3 Leaf water potential of one-year-old resprouts and five-year-old seedlings. Predawn and midday leaf water potential of one-year-old resprouts and five-year-old seedlings. Darkgreen labeled control represents five-year-old seedlings; tan labeled resprout represents one-year-old resprouts; Δ indicates the differences between leaf water potential in midday and predawn; ψ_{pre} represents leaf water potential at predawn; ψ_{mid} represents leaf water potential at midday; *** ($P < 0.001$) indicates significant differences between one-year-old resprouts and five-year-old seedlings; ns indicates non-significant differences detected; AC *A. canescens*, CK *C. korshinskii*, CM *C. mongolicum*, HS *H. scoparium*; standard error bar was showed above each column (one-way ANOVAs)

in water-limited regions (Pantin et al. 2012). Furthermore, we found increased leaf hydraulic conductance in resprouts (Fig. 7). As the leaves of one-year-old resprouts were about 2–4 times larger than that of the five-year-old seedlings (Fig. 2c), the one-year-old resprouts with higher leaf hydraulic conductance possibly had wider or denser conduits compared to the five-year-old seedlings (Domec et al. 2012; Schreiber et al. 2016). High leaf hydraulic conductance is the basis for photosynthetic productivity as it reflects sufficient water supply to the leaf (Scoffoni et al. 2016). Accordingly, higher photosynthesis rate and stomatal conductivity were also observed in the resprouts (Fig. 4). However, the difference of the transpiration rate between one-year-old resprout and five-year-old seedlings in *C. mongolicum* and *H. scoparium* was not significant. This could be attributed to the differences in stomatal structures (Xu and Zhou 2008; Bertolino et al. 2019). The effect of a high leaf hydraulic conductance on transpiration, on the other hand, could be negated by a minor soil-leaf water potential difference, which appears to be the case here, as leaf water potential was less negative in the resprouts. In summary, a consistent

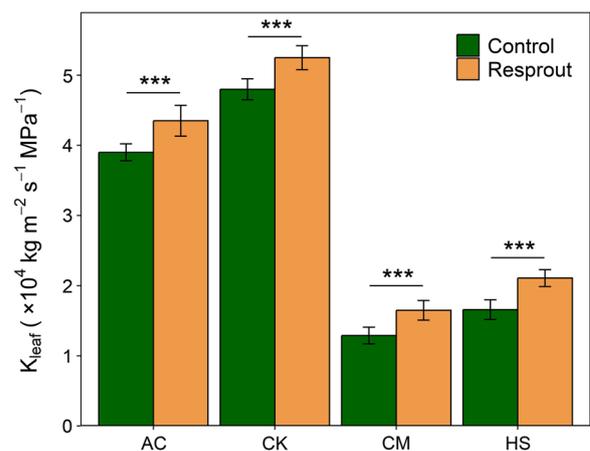


Fig. 4 Leaf hydraulic conductance of one-year-old resprouts and five-year-old seedlings. Darkgreen labeled control represents five-year-old seedlings; tan labeled resprout represents one-year-old resprouts; *** ($P < 0.001$) indicates significant differences between one-year-old resprouts and five-year-old seedlings; AC *A. canescens*, CK *C. korshinskii*, CM *C. mongolicum*, HS *H. scoparium*; standard error bar was showed above each column (one-way ANOVAs)

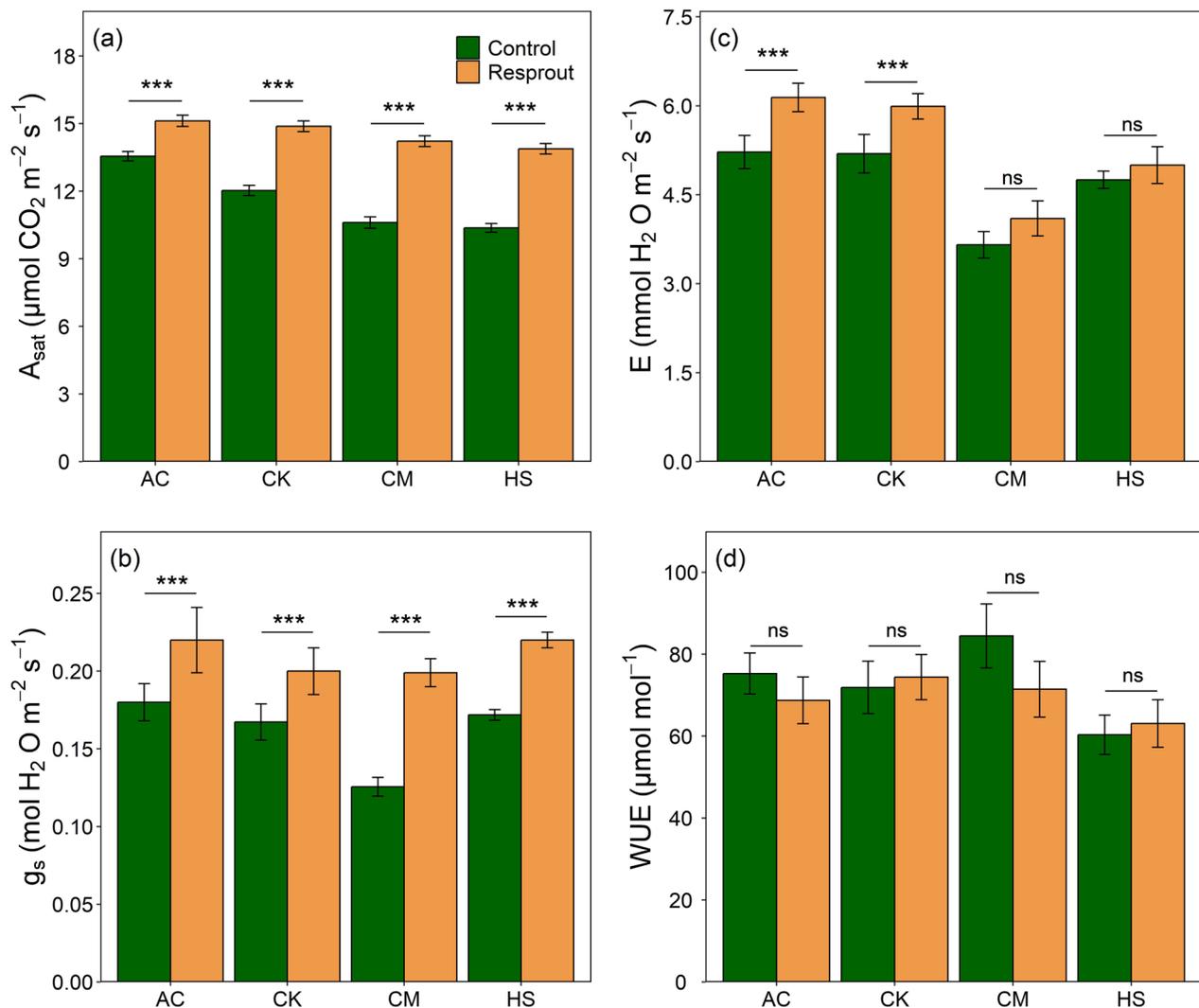


Fig. 5 Gas change characteristics of five-year-old seedlings and one-year-old resprouts. **a** Photosynthesis rate (A_{sat}), **b** stomatal conductance (g_s), **(c)** transpiration rate (E) and **(d)** water use efficiency (WUE) of one-year-old resprouts and five-year-old seedlings. Darkgreen labeled control represents five-year-old seedlings; tan labeled resprout represents one-year-old resprouts; *** ($P < 0.001$) indicates significant differences between one-year-old resprouts and five-year-old seedlings; ns indicates non-significant differences detected; AC *A. canescens*, CK *C. korshinskii*, CM *C. mongolicum*, HS *H. scoparium*; standard error bar was showed above each column (one-way ANOVAs)

physiological mechanism was observed in the resprouts of desert shrubs following the disturbance. This indicates that desert shrubs have evolved the capacity of rapid recovery after the disturbance, which assures sustainable interactions between desert plants and herbivorous animals. Besides the physiological performance, the rapid growth of the resprouts may also be associated with a shift in the allocation pattern of current-year assimilates. The possible mechanism is that carbohydrates stored in roots could be remobilized to support the growth of resprouts, which needs to be explored in future studies.

Intact root water uptake source of resprouts induced the imbalance between water supply and demand and thus improved physiological performance

The low shoot-to-root ratio of resprouts induced the rapid height and biomass recovery in young resprouts (Andrews et al. 1999; Clemente et al. 2005). However, no evidence of intact root water uptake source of resprouts was reported in these studies. By using the isotopic tool, our study demonstrated for the first time that the root water source of resprouts did not change (Fig. 6). This indicates that the root system of the resprouts at different

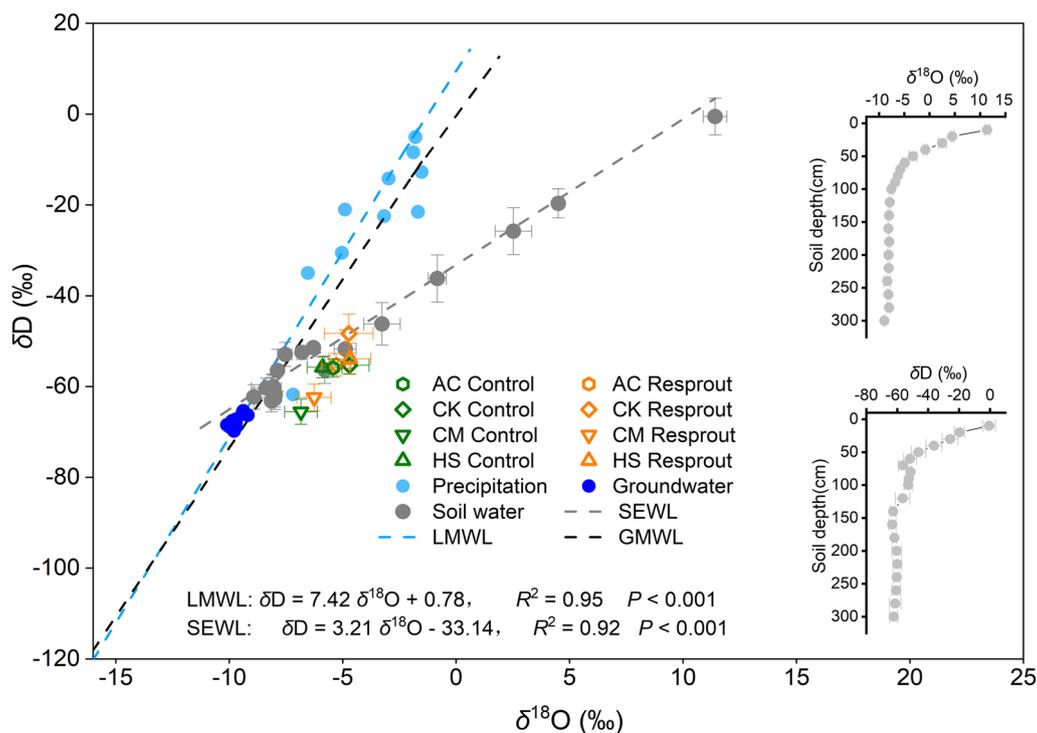


Fig. 6 Relationships between δD and $\delta^{18}O$ signatures in precipitation, soil water, groundwater and xylem water of the different shrub species. *GMWL* the global meteoric water line, *LMWL* the local meteoric water line, *SEWL* soil water evaporation line which is fitted based on the isotopic values of soil water, *AC* *A. canescens*, *CK* *C. korshinskii*, *CM* *C. mongolicum*, *HS* *H. scoparium*

depths kept water uptake ability after the aboveground tissue removal. Therefore, the relatively higher water supply from the root system but low water demand from the small resprouts cause a water supply and demand imbalance in resprouts (Fig. 8). The relatively higher water supply to demand explained the higher leaf water potential and leaf hydraulic conductance in resprouts. As a consequence, the increased leaf water potential and hydraulic conductance induced the high stomatal conductance, photosynthesis capacity, and growth rate of the resprouts (Liu et al. 2015; Feng et al. 2022a; Fig. 8). Additionally, because the nutrients could also be transported to leaves through the vascular system, the excess water transportation would transport excess nutrients to the leaves (Lucas 2010; White and Ding 2023). This might be a possible mechanism of the high photosynthetic rate in resprouts as well.

Implications of rapid resprouts growth of desert shrubs to desert ecosystem management

The rapid growth of the resprouts could offset the vegetation loss caused by the disturbance. Over the past decades, the application of eco-environmental protection has caused a boom in camels all over the world (Faye 2020). Shrubs are one of the main food sources for camels in the

desert. In addition, camels are large animals that require lots of food source to support their large body metabolism (Chuluunbat et al. 2014). Rapid shrub regrowth after the disturbance would guarantee sufficient food sources for this large animal and make the desert ecosystem sustainable. Therefore, adopting appropriate management policy in the desert area would be possible to feed the increased camel number. Specifically, (1) silvicultural management of desert shrubs according to local carrying capacity of water; (2) improving conservation of the camels' habitat by establishing protected area; (3) clipping desert shrubs as feed storage for camels based on their rapid recovery ability. As previously reported, silvicultural management is widely used as a measure to stop sand expansion and protect the oasis from wind and sand violation (O'Hara 2015; Ameray et al. 2021), and it is becoming a popular measure to maintain the biodiversity and ecosystem function (Vild et al. 2013; Strubelt et al. 2019). According to the rapid recovery potential of desert shrubs, clipping management would simultaneously increase the ecosystem function and guarantee the large animal's food source. Raising proper management policy according to the characteristics of rapid resprouts growth of desert shrubs would thus help achieve healthy and sustainable development in the desert region.

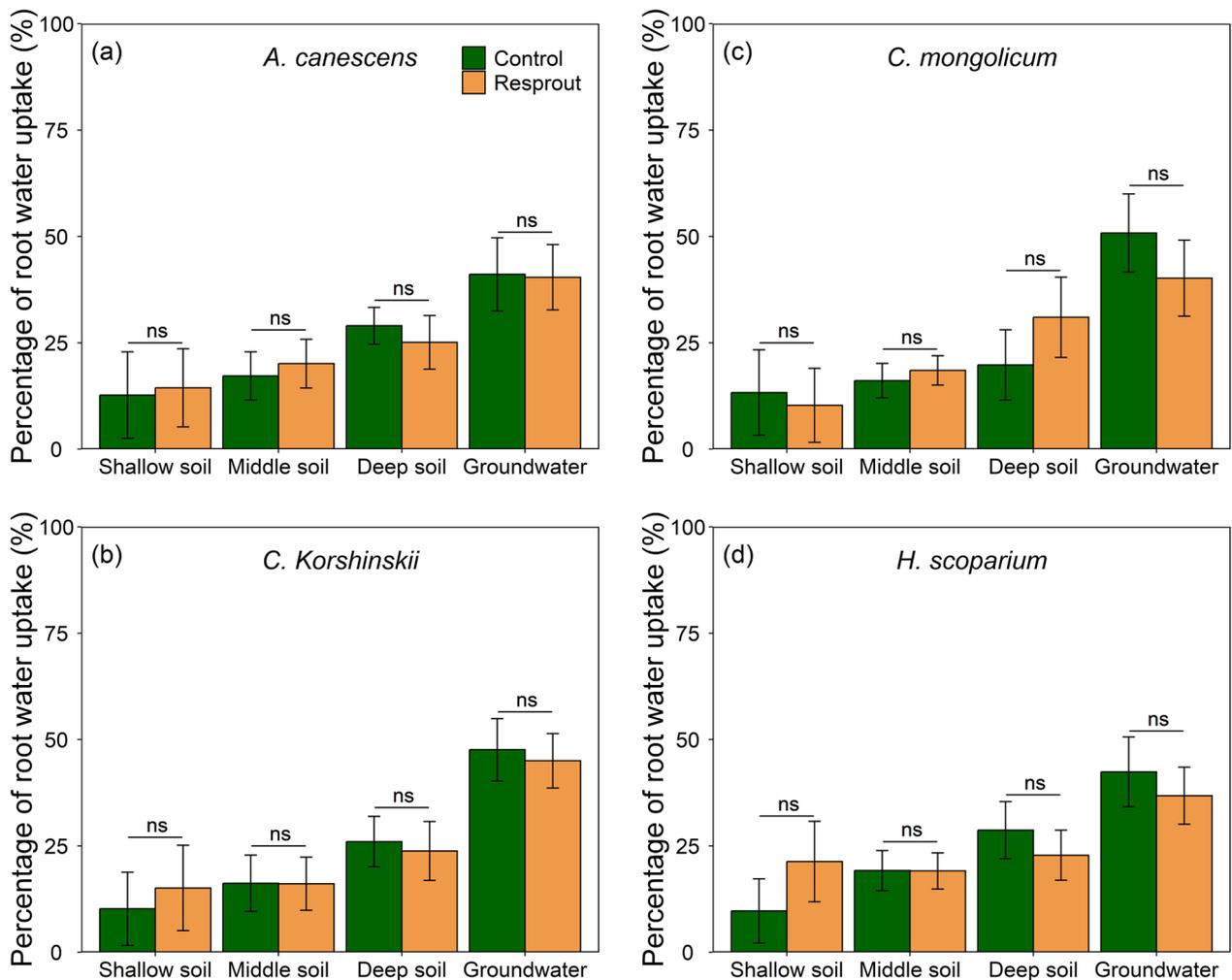


Fig. 7 Percentage of root water uptake of four five-year-old desert shrubs and one-year-old resprouts. Percentage of root water uptake from shallow soil, middle soil, deep soil and groundwater of (a) *A. canescens*; (b) *C. korshinskii*; (c) *C. mongolicum*; (d) *H. scoparium*. Darkgreen labeled control represents five-year-old seedlings; tan labeled resprout represents one-year-old resprouts; ns indicates non-significant differences between one-year-old resprouts and five-year-old seedlings; standard error bar was shown above each column (one-way ANOVAs)

Conclusions

Our findings revealed that the rapid recovery of the resprouts of desert shrubs was related to the improved physiological performance following the disturbance. The intact root water uptake ability of the resprouts after the aboveground tissue removal induced a relatively higher

water supply and low demand and thereby resulted in improved physiological performance and rapid resprouts growth. The findings provided insight that controlling an appropriate scale of shrubs in the desert is possibly an efficient ecosystem management measure in the face of the increasing camel population and blown sand threat.

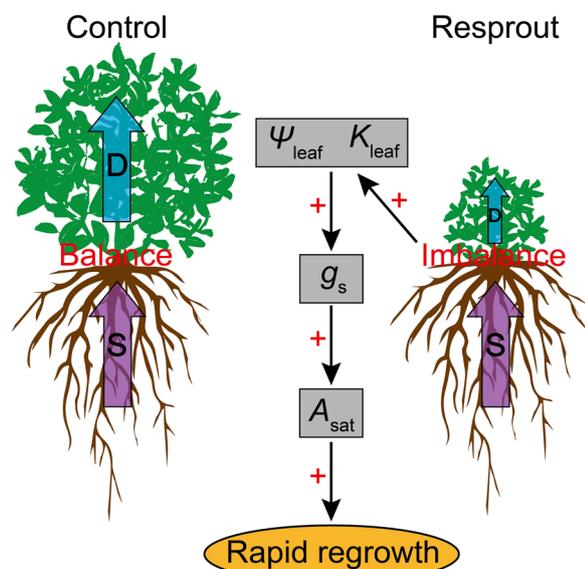


Fig. 8 Conceptual framework of resprouts rapid regrowth of desert shrubs. Under the control condition, the root water supply (S) equals canopy water demand (D). Disturbance caused the decreased canopy water demand, thus causing the imbalance between water supply and demand. Higher root water supply relative to low canopy water demand induced higher leaf water potential (ψ_{leaf}) and hydraulic conductance (K_{leaf}), which supports higher stomatal conductance (g_s) and ultimately contributes to higher photosynthesis rate (A_{sat}) and rapid resprouts growth

Abbreviations

AC	<i>Atriplex canescens</i>
CK	<i>Caragana korshinskii</i>
CM	<i>Hedysarum scoparium</i>
HS	<i>Calligonum mongolicum</i>
GMWL	Global meteoric water line
LMWL	Local meteoric water line
SEWL	Soil water evaporation line

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Author contributions

Hai Zhou: Conceptualization, Formal analysis, Writing—original draft, Funding acquisition. Xiangyan Feng: Conceptualization, Methodology, Software, Writing—original draft, Funding acquisition. Zhibin He: Formal analysis, Methodology. Qiyue Yang: Methodology, Software. Heng Ren: Formal analysis, Software. Wenzhi Zhao: Conceptualization, Writing—review and editing, Funding acquisition.

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Availability of data and materials

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors approved the manuscript for publication in ecological processes.

Competing interests

No competing interest exists in this manuscript.

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References

- Ameray A, Bergeron Y, Valeria O, Montoro Girona M, Cavard X (2021) Forest carbon management: a review of silvicultural practices and management strategies across boreal, temperate and tropical forests. *Curr For Rep* 7:245–266
- Andrews M, Sprent JI, Raven JA, Eady PE (1999) Relationships between shoot to root ratio, growth and leaf soluble protein concentration of *Pisum sativum*, *Phaseolus vulgaris* and *Triticum aestivum* under different nutrient deficiencies. *Plant Cell Environ* 22:949–958
- Atwood CJ, Fox TR, Loftis DL (2009) Effects of alternative silviculture on stump sprouting in the southern Appalachians. *Forest Ecol Manag* 257:1305–1313
- Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. *Oikos* 89:409–416
- Belote RT, Jones RH, Wieboldt TF (2012) Compositional stability and diversity of vascular plant communities following logging disturbance in Appalachian forests. *Ecol Appl* 22:502–516
- Bertolino LT, Caine RS, Gray JE (2019) Impact of stomatal density and morphology on water-use efficiency in a changing world. *Front Plant Sci* 10:427588
- Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol Evol* 16:45–51
- Bond WJ, Midgley JJ (2003) The evolutionary ecology of sprouting in woody plants. *Int J Plant Sci* 164:S103–S114
- Brodrribb TJ, Holbrook NM (2003) Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. *Plant Physiol* 132:2166–2173
- Chuluunbat B, Charruau P, Silbermayr K, Khorloojav T, Burger PA (2014) Genetic diversity and population structure of Mongolian domestic Bactrian camels (*Camelus bactrianus*). *Anim Genet* 45:550–558
- Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE et al (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytol* 197:19–35
- Clemente AS, Rego FC, Correia OA (2005) Growth, water relations and photosynthesis of seedlings and resprouts after fire. *Acta Oecol* 27:233–243
- De Micco V, Balzano A, Wheeler EA, Baas P (2016) Tyloses and gums: a review of structure, function and occurrence of vessel occlusions. *IAWA J* 37:186–205
- Dietze MC, Clark JS (2008) Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. *Ecol Monogr* 78:331–347
- Domec J-C, Lachenbruch B, Pruyn ML, Spicer R (2012) Effects of age-related increases in sapwood area, leaf area, and xylem conductivity on height-related hydraulic costs in two contrasting coniferous species. *Ann Forest Sci* 69:17–27
- Ehleringer JR, Schwinning S, Gebauer R (1999) Water use in arid land ecosystems. Blackwell Science, Oxford
- Faye B (2020) How many large camelids in the world? a synthetic analysis of the world camel demographic changes. *Pastoralism* 10:25

- Feng XY, Zhong LF, Tian QY, Zhao WZ (2022) Leaf water potential-dependent leaflet closure contributes to legume leaves cool down and drought avoidance under diurnal drought stress. *Tree Physiol* 42:2239–2251
- Feng XY, Lin PF, Zhao WZ (2022) The physiological constraints of alpine treeline in Qilian Mountains. *Forest Ecol Manag* 503:119761
- Flexas J, Bota J, Galmes J, Medrano H, Ribas-Carbo M (2006) Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. *Physiol Plantarum* 127:343–352
- Ghannoum O (2009) C₄ photosynthesis and water stress. *Ann Bot* 103:635–644
- Grossiord C, Sevanto S, Dawson TE, Adams HD, Collins AD, Dickman LT et al (2017) Warming combined with more extreme precipitation regimes modifies the water sources used by trees. *New Phytol* 213:584–596
- Hilty J, Muller B, Pantin F, Leuzinger S (2021) Plant growth: the what, the how, and the why. *New Phytol* 232:25–41
- Kirschbaum MUF (2011) Does enhanced photosynthesis enhance growth? Lessons learned from CO₂ enrichment studies. *Plant Physiol* 155:117–124
- Kraft NJB, Godoy O, Levine JM (2015) Plant functional traits and the multidimensional nature of species coexistence. *P Natl Acad Sci USA* 112:797–802
- Larsen DR, Johnson PS (1998) Linking the ecology of natural oak regeneration to silviculture. *Forest Ecol Manag* 106:1–7
- Li Y, Zhao H, Hu L, Leppanen JJ (2020) Cladoceran communities in soda lakes of the Badain Jaran desert, NW China. *J Arid Environ* 177:101433
- Liu H, Xu QY, He PC, Santiago LS, Yang KM, Ye Q (2015) Strong phylogenetic signals and phylogenetic niche conservatism in ecophysiological traits across divergent lineages of Magnoliaceae. *Sci Rep* 5:12246
- Lu C, Wang NA, Zhang L, Li ZL, Zhao WW, Li M et al (2023) Palaeoenvironmental evolution of the Badain Jaran Desert hinterland during the Early to Middle Holocene: a multi-proxy reconstruction on Taerlegetu paleolake, northwest China. *Palaeogeogr Palaeoclimatol* 611:111359
- Lucas WJ (2010) Plant vascular biology and agriculture. *J Integr Plant Biol* 52:4–7
- Meier AR, Saunders MR, Michler CH (2012) Epicormic buds in trees: a review of bud establishment, development and dormancy release. *Tree Physiol* 32:565–584
- Nelissen H, Gonzalez N (2020) Understanding plant organ growth: a multidisciplinary field. *J Exp Bot* 71:7–10
- O'Hara KL (2015) What is close-to-nature silviculture in a changing world? *Forestry* 89:1–6
- Pantin F, Simonneau T, Muller B (2012) Coming of leaf age: control of growth by hydraulics and metabolics during leaf ontogeny. *New Phytol* 196:349–366
- Phillips DL, Newsome SD, Gregg JW (2005) Combining sources in stable isotope mixing models: alternative methods. *Oecologia* 144:520–527
- R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria
- Rocha JL, Godinho R, Brito JC, Nielsen R (2021) Life in deserts: the genetic basis of mammalian desert adaptation. *Trends Ecol Evol* 36:637–650
- Sack L, Scoffoni C, McKown AD, Frole K, Rawls M, Havran JC et al (2012) Developmentally based scaling of leaf venation architecture explains global ecological patterns. *Nat Commun* 3:837
- Schreiber SG, Hacke UG, Chamberland S, Lowe CW, Kamelchuk D, Bräutigam K et al (2016) Leaf size serves as a proxy for xylem vulnerability to cavitation in plantation trees. *Plant Cell Environ* 39:272–281
- Scoffoni C, Chatelet DS, Pasquet-kok J, Rawls M, Donoghue MJ, Edwards EJ et al (2016) Hydraulic basis for the evolution of photosynthetic productivity. *Nat Plants* 2:16072
- Seidl R, Schelhaas MJ, Lexer MJ (2011) Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Global Change Biol* 17:2842–2852
- Strubelt I, Diekmann M, Griesse D, Zacharias D (2019) Inter-annual variation in species composition and richness after coppicing in a restored coppice-with-standards forest. *Forest Ecol Manag* 432:132–139
- Swaim JT, Dey DC, Saunders MR, Weigel DR, Thornton CD, Kabrick JM et al (2016) Predicting the height growth of oak species (*Quercus*) reproduction over a 23-year period following clearcutting. *Forest Ecol Manag* 364:101–112
- Tardieu F, Simonneau T (1998) Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *J Exp Bot* 49:419–432
- Vild O, Rolecek J, Hedl R, Kopecky M, Utinek D (2013) Experimental restoration of coppice-with-standards: response of understorey vegetation from the conservation perspective. *Forest Ecol Manag* 310:234–241
- Voltas J, Lucabaugh D, Chambel MR, Ferrio JP (2015) Intraspecific variation in the use of water sources by the circum-Mediterranean conifer *Pinus halepensis*. *New Phytol* 208:1031–1041
- Wang XS, Zhou YY (2018) Investigating the mysteries of groundwater in the Badain Jaran Desert, China. *Hydrogeol J* 26:1639–1655
- Warren-Rhodes K, Phillips M, Davila A, McKay CP (2022) Insights of extreme desert ecology to the habitats and habitability of Mars. In: Ramond J-B, Cowan DA (eds) *Microbiology of hot deserts*. Springer International Publishing, Cham, pp 235–291
- Washburn EW, Smith ER (1934) The isotopic fractionation of water by physiological processes. *Science* 79:188–189
- White PJ, Ding G (2023) Long-distance transport in the xylem and phloem. Marschner's mineral nutrition of plants. Elsevier, Amsterdam, pp 73–104
- Whitford WG, Duval BD (2020) Chapter 3—characterization of desert climates. In: Whitford WG, Duval BD (eds) *Ecology of desert systems*, 2nd edn. Academic Press, San Diego, pp 47–72
- Xu Z, Zhou G (2008) Responses of leaf stomatal density to water status and its relationship with photosynthesis in a grass. *J Exp Bot* 59:3317–3325
- Yang YS, Bu CF, Mu XM, Zhang KK (2015) Effects of differing coverage of moss-dominated soil crusts on hydrological processes and implications for disturbance in the Mu Us Sandland, China. *Hydro Process* 29:3112–3123
- Zeppel MJB, Harrison SP, Adams HD, Kelley DI, Li G, Tissue DT et al (2015) Drought and resprouting plants. *New Phytol* 206:583–589
- Zhou H, Zhao WZ, Zhang GF (2016) Varying water utilization of *Haloxyylon ammodendron* plantations in a desert-oasis ecotone. *Hydro Process* 31:825–835

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