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Whole-Plant Water Use and Hydraulics of *Populus euphratica* and *Tamarix ramosissima* Seedlings in Adaption to Groundwater Variation

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Abstract: Riparian phreatophytes in hyperarid areas face selection pressure from limiting groundwater availability and high transpiration demand. We examined whole-plant water use and hydraulic traits in *Populus euphratica* and *Tamarix ramosissima* seedlings to understand how they adapt to groundwater variations. These species coexist in the Tarim River floodplain of western China. Measurements were performed on 3-year-old seedlings grown in lysimeters simulating various groundwater depths. *P. euphratica* had relatively greater leaf area-specific water use due to its comparatively higher sapwood area to leaf area ratio (H_v). A high H_v indicates that its sapwood has a limited capacity to support its leaf area. *P. euphratica* also showed significantly higher leaf-specific conductivity (k_{sl}) than *T. ramosissima* but both had similar sapwood-specific conductivities (k_{ss}). Therefore, it was H_v rather than k_{ss} which accounted for the interspecific difference in k_{sl}. When groundwater was not directly available, k_{sl} and H_v in *P. euphratica* were increased. This response favors water loss control, but limits plant growth. In contrast, *T. ramosissima* is more capable of using deep groundwater. Stomatal sensitivity to increasing leaf-to-area vapor pressure deficit was also higher in *P. euphratica*. Overall, *P. euphratica* is less effective than *T. ramosissima* at compensating for transpirational water loss at a whole-plant level. For this reason, *P. euphratica* is restricted to riverbanks, whereas *T. ramosissima* occurs over a wide range of groundwater depths.

Keywords: desert riparian habitat; hydraulic architecture; hydraulic conductance; phreatophyte; stomatal sensitivity

1. Introduction

Riparian phreatophytic plants in arid regions face two major water-related challenges. One is groundwater access which is determined by root growth rate and changes in groundwater depth. The other is the fact that the canopy water supply must contend with high transpirational demand caused by a high leaf-to-air vapor pressure deficit (*LVPD*), even when the plants have groundwater access [1]. High *LVPD* prevails in desert riparian zones inhabited by phreatophytes. However, the groundwater depth there is highly variable [2] because there are substantial groundwater flow variations in arid regions. Moreover, human activity has introduced widespread hydrological alterations [3]. These perturbations significantly affect the establishment, survival, growth, and community structure of riparian plants [4,5]. In the riparian ecosystems of the southwestern U.S., the native *Populus* and *Salix* species were replaced by the invasive *Tamarix* species. Flow regime alterations, including subsequent groundwater decline, were the major factors responsible for this species substitution [6,7]. *Tamarix* expansion has reduced river runoff due to its high demand for water. Nevertheless, it has also diminished the availability of water resources

for human consumption [8]. This scenario highlights the importance of understanding water use and riparian plant hydraulics to elucidate ecological processes and to improve and sustain riparian ecosystem management.

Knowing plant responses to changes in water availability helps to predict plant adaptions to environmental variations and determine trends in vegetation dynamics as a result of a changing climate [9,10]. In application, this is also helpful for developing eco-friendly solutions in managing riverine ecosystems [11] and improving regional evapotranspiration monitoring [12,13]. However, our understanding of plant responses to water availability is very limited, particularly in arid ecosystems [14]. Certain desert riparian ecosystems are characterized by highly variable water availability. Learning the differential responses of coexisting plant species to varying water availability is necessary to understand plant water relations in these ecosystems [15]. In general, plant species which grow rapidly during high water availability and tolerate drought are relatively more competitive in riparian communities [16]. When groundwater descends below the root zones, plants must rely on precipitation. This response induces plant species composition changes [17]. The composition changes which followed the *Tamarix* invasion of the southwestern U.S. were the result of alterations in plant water use in response to groundwater variations. The predominant *Tamarix* stands had very high evapotranspiration rates, even as groundwater levels dropped [18].

There are species-specific differences in ecophysiological response to water availability. These provide some insight into plant adaptions [19]. Plants growing in extremely variable conditions have powerful regulatory mechanisms which modulate water transport according to water availability. These compensations help maintain plant physiological functions [20]. The stomata control water flux and loss during drought. The hydraulic transport system [21] also regulates water relations. The greatest hydraulic conductivity losses occur in the xylem during drought [22]. The sapwood-specific hydraulic conductivity (k_{ss}) characterizes xylem hydraulic efficiency. The leaf-specific hydraulic conductivity (k_{sl}) defines the sapwood hydraulic capacity to meet the transpirational demand of a given leaf area [23]. A higher k_{sl} may be driven by the xylem hydraulic capacity, the sapwood/leaf area ratio, or both. Plants in water-limited ecosystems may alter their biomass allocation according to water availability to optimize their survival and/or productivity [24]. Therefore, in order to understand water use strategies in response to water availability changes, it is necessary to address plant–water relations at the whole-plant scale [25–27] and across a wide range of water availabilities. Plant hydraulics and stomatal behavior are closely correlated with carbon gain [28,29]. Consequently, a comparative study of the hydraulic traits of different plant species may account for species distributions at varying water availabilities and explain the divergence of plant adaptions.

The vast inland Tarim Basin of central Eurasia has a hyperarid climate characterized by high evaporative demand and extremely low precipitation (annual mean ~50 mm). Desert riparian vegetation grows along the 1321 km length of the Tarim River and is predominated by *Populus euphratica* and *Tamarix ramosissima* [30]. These phreatophytes are highly dependent on groundwater that declines with increasing distance from the active channel [31]. As the Tarim river is mainly recharged by glacier melt from surrounding mountains [32], great hydrological fluctuations can result in an annual groundwater variation greater than 2 m, even in riparian zones close to the active channel [33]. Increased agricultural water use over the past 50 years has declined groundwater in the whole basin, leading to the intensive degeneration of the desert riparian forest, especially in the lower reaches of the river [34]. This triggered an ecological engineer in 2000 to artificially delivered water to rise groundwater levels in the lower reaches of the river, thus conserving the desert riparian vegetation [34]. However, the rise in groundwater only occurred hundreds of meters near the riverbank [35]. Groundwater availability is still a key problem for desert riparian plants in the Tarim Basin.

P. euphratica and *T. ramosissima* share the same establishment niche because they are both established in newly deposited sediments after flood recessions and form co-

dominant seedling stands near the active channel [36]. Their dominances change with increasing distance from the channel due to alterations in groundwater level [31]. This can be related to their water uses and the underlying hydraulics, as inequalities in hydraulic response to water conditions cause niche differentiation among plant species within the same habitat [37]. Currently, comparative studies on water relations between these co-occurring species include stomatal response to *LVPD* [38], xylem resistance to embolism [39], leaf-level water use [40], sap flow and water resources [41], and so on. These works basically focus on hydraulics at an organ level, but studies on the whole-plant level water use, as well as in relation to plant hydraulics, are entirely lacking. However, hydraulic traits are coordinated [42] and their relationships depend on water availability [43].

Our objective was to compare the water use and hydraulics of the phreatophytes *P. euphratica* and *T. ramosissima* in adaption to the groundwater variations they encounter in their coexisting habitats along the Tarim River riparian zones. We used lysimeters to simulate varying groundwater depths and compare water use and underlying hydraulic traits at a whole-plant level. Measurements included daily whole-plant water use, plant water status, hydraulic functional traits (k_{ss}, k_{sl}, and stomatal sensitivity to *LVPD*), and structural traits (H_v and wood density).

2. Materials and Methods

2.1. Plant Materials and Experiment Design

The experiment was carried out at the Aksu Water Balance Station, Chinese Academy of Sciences (40°27′ N, 80°45′ E; hereafter, Aksu Station) in 2009. Three-year-old *Populus euphratica* and *Tamarix ramosissima* seedlings were grown in homemade lysimeters 1.2 m in height and 0.3 m in inner diameter, as shown in Figure 1. Transplanted seedlings were ~50 cm tall. At this stage, neither species had yet established dense stands. There was one seedling per lysimeter. The seedlings were established then subjected to the equivalent of 20 cm, 60 cm, and 100 cm distance from the groundwater between early July and mid-September. Each treatment included five replicates per species. Therefore, there were 2 species × 3 treatments × 5 replicates = 30 lysimeters in total for the experiment. For experimental procedure details, see the work by Li et al. [36]. An automatic weather station (M520, Vaisala Co. Ltd., Vantaa, Finland) was set ~50 m from the experimental site to measure and record meteorological data including rainfall, temperature, pressure, wind direction and velocity, relative humidity, solar radiation, etc.

(a)　　　　　　　　　　　　　　　　　　　　　　　　**(b)**

Figure 1. *Populus euphratica* (**a**) and *Tamarix ramosissima* (**b**) growing in lysimeters.

2.2. Measurements

Daily evapotranspiration (*ET*) rates were obtained for each lysimeter in August, one month after the seedlings were subjected to the groundwater treatments. The volume of water added to maintain the corresponding groundwater depth in each lysimeter was

recorded daily. Plant water status was determined on 31 August by measuring predawn (ψ_{pd}) and midday (ψ_{md}) xylem water potentials (ψ) with a PMS Model 1000 pressure chamber (PMS Instrument Co., Albany, OR, USA). ψ_{pd} and ψ_{md} were measured ~30 min before sunrise and at solar noon, respectively. On 31 August, gravimetric soil water content was measured for three lysimeters per species per treatment. These plants were also selected for rooting depth observation and biomass harvest. Soil water content was determined by sampling at 10 cm increments from the soil surface to the corresponding groundwater depth then drying and weighing the samples.

Stomatal response to *LVPD* was evaluated with a portable photosynthesis system (Li6400, LI-COR Biosciences, Lincoln, NE, USA) consisting of a standard chamber fitted with a light source (6400-02B, LI-COR Biosciences, Lincoln, NE, USA). Measurements were conducted on clear days in August between 10h30 and 13h30, local time. To assess sensitivity to increasing *LVPD*, the relative humidity (*RH*) within the cuvette was first set to 60% then progressively decreased to the lowest possible level by absorbing all water vapor from the air entering the LI-COR system (*HR* = 0% in the reference chamber). The *LVPD* response assay was repeated on three individuals per species per treatment. The cuvette CO_2 concentration was maintained at 400 ppm and the photosynthetic photon flux density (*PPFD*) was held at the light saturation points previously determined by light response measurements [36]. These were 2400 μmol m^{-2} s^{-1} for *P. euphratica* and 1800 μmol m^{-2} s^{-1} for *T. ramosissima.* Leaves within the cuvette were cut immediately after each measurement and their leaf areas were measured. Thence, the gas exchange parameters were recalculated in the LI-COR system.

At the end of the experiment, three randomly selected seedlings per species per treatment were harvested to measure specific leaf area (*SLA*) and total leaf area (*TLA*). On each sampled seedling, fresh leaves from three randomly selected branches were gently extended onto a white board, and then photographed for area calculation using Image Pro Plus software (Media Cybernetics Inc., Rockville, MD, USA). The average *SLA* of each sampled seedling was obtained from the ratio of leaf area to dry biomass. Therefore, the *TLA* of each sampled seedling was estimated as average *SLA* × total harvested leaf biomass. Because leaves of *T. ramosissima* are cylindrical, we calculated the actual leaf surface area as the photographic projected area $\times \pi/2$, as described by Li et al. [36]. To estimate the sapwood-specific conductivity at the whole-plant scale, the sapwood area was evaluated by measuring the cross-sectional areas of the main stem at the soil surface. Heartwood was excluded from the calculations and differentiated from the sapwood by its distinct color. Wood density was measured on a debarked ~10-cm-long stem segment excised from each seedling sample. Fresh volume was measured by water displacement at a constant 20 °C. Sample mass was measured after 48 h drying. Wood density was reported as dry mass per unit fresh volume.

2.3. Data Processing and Statistics

Potential evapotranspiration (*PET*) was estimated from daily weather data by the FAO Penman–Monteith method [44]. To partition soil evaporation (*E*) from evapotranspiration (*ET*), *E* was estimated by calculating the soil water flux (*K(S)*) in unsaturated soil using a combination of Van Genuchten's equation [45] and Mualem's model [46] to predict unsaturated hydraulic conductivity:

$$K(S) = K_s \frac{\left\{1 - (\alpha S)^{n-1}\left[1 + (\alpha S)^n\right]^{-m}\right\}^2}{\left[1 + (\alpha S)^n\right]^{m/2}} \tag{1}$$

where K_s is the saturated hydraulic conductivity (cm d^{-1}) and α, *m*, and *n* are empirical parameters shaping the retention curve.

For the soils used in this experiment, K_s = 3.67 cm d^{-1} was determined by the constant head method [47]. In addition, α = 0.0081, *n* = 1.3481, and *m* = 0.2582 were derived from the soil water retention curve plotted by the pressure chamber method. Whole-plant water

use was estimated from the difference between the *ET* and the soil evaporation on August 30 at the same time that soil water content, plant water potential, and *TLA* were evaluated.

The Huber value (H_v, cm^2 m^{-2}) was calculated as the ratio of sapwood area to *TLA*. Whole-plant hydraulic conductance (K_{plant}, g d^{-1} MPa^{-1}) was calculated as $K_{plant} = (ET - E)/[(\psi_{pd} - \psi_{md})]$ [26,48]. Leaf area-specific whole-plant hydraulic conductance (k_{sl}, g d^{-1} m^{-2} MPa^{-1}) was calculated by dividing K_{plant} by *TLA*. Sapwood-specific whole-plant hydraulic conductance (k_{ss}, g d^{-1} cm^{-2} MPa^{-1}) was calculated by dividing K_{plant} by sapwood area. Stomatal sensitivity was calculated by $\Delta g_s / \Delta LVPD$ where Δg_s and $\Delta LVPD$ are the differences in stomatal conductance and *LVPD*, respectively, when *RH* is decreased. Differences in hydraulic traits among species and treatments were tested by two-way *ANOVA*. Statistical analyses were run in SPSS v.11.0 (IBM Corp., Armonk, NY, USA).

3. Results

Daily *PET* fluctuated and trended to decrease with time in August, while daily water uses per individual, with the exception *P. euphratica* grown at 100 cm groundwater depth, trended to increase with time (Figure 2), indicating plant water use increasing with plant growth during the experiment. Here, the daily water use per individual included transpiration and soil evaporation, but the soil evaporation only occupied a slight portion of the total (<5% even under shallow groundwater condition), as estimated on the hydraulic conductivity in unsaturated soils sampled on 30 August. Thus, the daily water use per lysimeter could reflect the changes in whole-plant water use during the observation period.
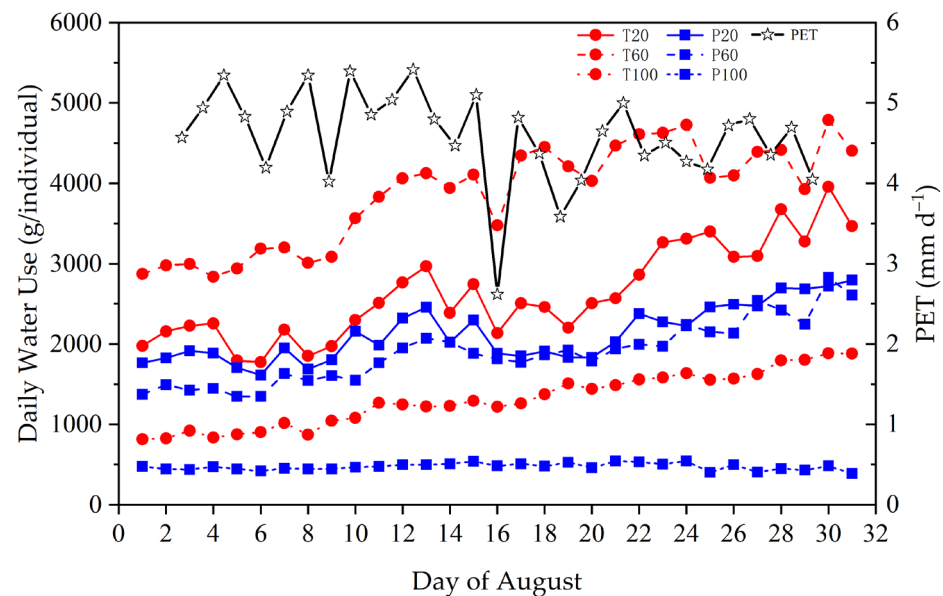
Figure 2. Daily *PET* (mm d^{-1}) and water use (g d^{-1}) per lysimeter with *Populus euphratica* and *Tamarix ramosissima* seedlings grown 20 cm, 60 cm, and 100 cm from the groundwater level.

As shown in Figure 2, the whole-plant water use differed between species and among treatments. For *P. euphratica*, seedlings grown 20 cm and 100 cm groundwater depths had similar daily water use, both >5 times higher than those at 100 cm groundwater depth at the end of the experiment. Differently, *T. ramosissima* seedlings grown at 60 cm groundwater depth had the highest water use, followed by those at 20 cm and 100 cm groundwater depth, respectively. *T. ramosissima* seedlings at both 20 cm and 60 cm groundwater depths had greater water use than *P. euphratica* ones. In comparison to the unchanged water use of *P. euphratica* seedlings grown at 100 cm groundwater depth, water use of *T. ramosissima* under the same condition underwent a clear increase, resulting in a greater difference in water use between species in the late stage of the experiment.

PET-normalized whole-plant daily water use increased linearly with *TLA* in *P. euphratica* ($p < 0.001$; Figure 3). However, the correlation between these two variables was weak in *T. ramosissima* ($p = 0.06$; Figure 3). The slope of the regression was greater for *P. euphratica* than *T. ramosissima*. Therefore, the water use per leaf area at each *PET* was higher in *P. euphratica* than *T. ramosissima*.
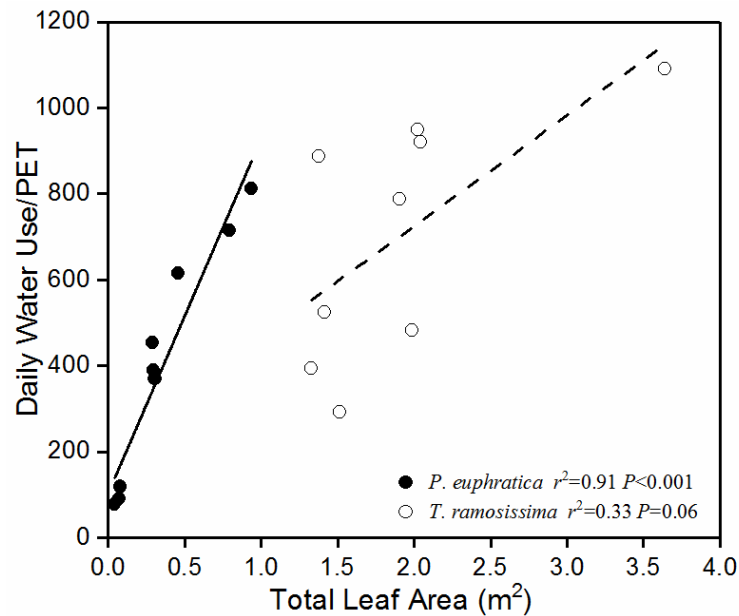

Figure 3. Relationships between *PET* (mm d^{-1}) normalized daily water use (g d^{-1}) and whole-plant leaf area in *Populus euphratica* and *Tamarix ramosissima* grown at a groundwater level gradient.

The relationship between *TLA* and basal stem diameter followed a power function model for both species (Figure 4). Within the observed diameter range, the *TLA* of *T. ramosissima* increased at a faster rate with diameter than that of *P. euphratica*. For each diameter, the *TLA* of *T. ramosissima* was several orders of magnitude higher than that of *P. euphratica*. Therefore, the stems of *T. ramosissima* supported higher leaf area than those of *P. euphratica*.
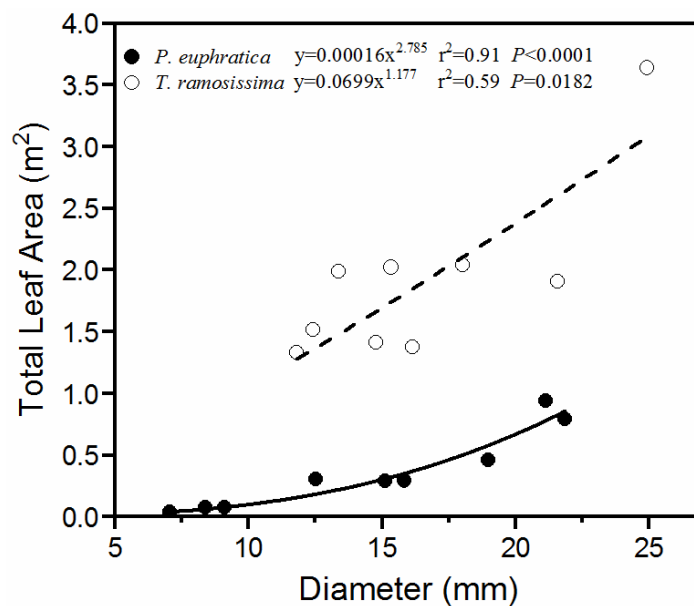

Figure 4. Relationship between leaf area and basal stem diameter in *Populus euphratica* and *Tamarix ramosissima* individuals.

At the end of experiment, we found that both species, under 20 cm groundwater depth, had a shallow rooting depth less than 50 cm (Table 1), with abundant absorbing roots distributed surrounding the groundwater level [34]. *P. euphratica* root reached groundwater level under 60 cm groundwater depth, but not under 100 cm groundwater depth. In comparison, *T. ramosissima* roots under both 60 cm and 100 cm groundwater depths reached the bottom of lysimeters (Table 1), with abundant absorbing roots distributed in the cobble layer in the lysimeters (observations), which indicates *T. ramosissima* had a greater root growth rate to acclimate to groundwater alterations.

Table 1. Rooting depths (cm) of *P. euphratica* and *T. ramosissima* grown at 20 cm, 60 cm, and 100 cm groundwater depths (DGW). Values are means $\pm$ SE ($n = 3$).

Treatment	20 DGW	60 DGW	100 DGW
P. euphratica	48.2 ± 1.3	87.8 ± 7.8	73.9 ± 9.4
T. ramosissima	47.7 ± 4.6	bottom reached	bottom reached

There were significant species effects on wood density, H_v, k_{sl}, and stomatal sensitivity to *LVPD* (Table 2). *P. euphratica* had higher k_{sl} and H_v and lower wood density than *T. ramosissima* (Figure 5). The treatment effect was significant only for wood density. There was a significant species $\times$ treatment interaction for H_v and k_{sl}. This observation indicated different hydraulic architecture and functional responses of the species to groundwater variations.

Table 2. Probabilities determined by ANOVA for species, treatment, and species $\times$ treatment effects on wood density, Huber value (H_v), whole-plant leaf area-specific hydraulic conductance (k_{sl}), whole-plant sapwood-specific hydraulic conductance (k_{ss}), and stomatal sensitivity to *LVPD* ($\Delta g_s / \Delta LVPD$).

Factor	Species	Treatment	Species $\times$ Treatment
wood density	<0.001	0.017	0.395
H_v	<0.001	0.173	0.007
k_{sl}	<0.001	0.43	0.045
k_{ss}	0.104	0.847	0.684
$\Delta g_s / \Delta LVPD$	<0.001	0.238	0.101

The variables had different change patterns between treatments for each species. The k_{sl} was highest at 100 cm groundwater depth for *P. euphratica* but was still significantly ($p < 0.05$) lower than that that for *T. ramosissima* in shallow groundwater (Figure 5A). For each species, there were no significant differences among treatments in terms of k_{ss} (Figure 5B). There were similar patterns between treatments in both species with regard to wood density. It was significantly ($p < 0.05$) higher at 100 cm groundwater depth than it was for the shallower groundwater treatments (Figure 5C). The pattern of H_v was similar to that for k_{sl}. *P. euphratica* seedlings at 100 cm groundwater depth had higher k_{sl} than other treatments but the opposite was true for *T. ramosissima* (Figure 5D). At 20 cm groundwater depth, $\Delta g_s / \Delta LVPD$ for *P. euphratica* was significantly ($p < 0.05$) greater than it was for the deeper groundwater treatments. In contrast, the highest $\Delta g_s / \Delta LVPD$ for *T. ramosissima* was measured in the 60 cm groundwater depth treatment (Figure 6).
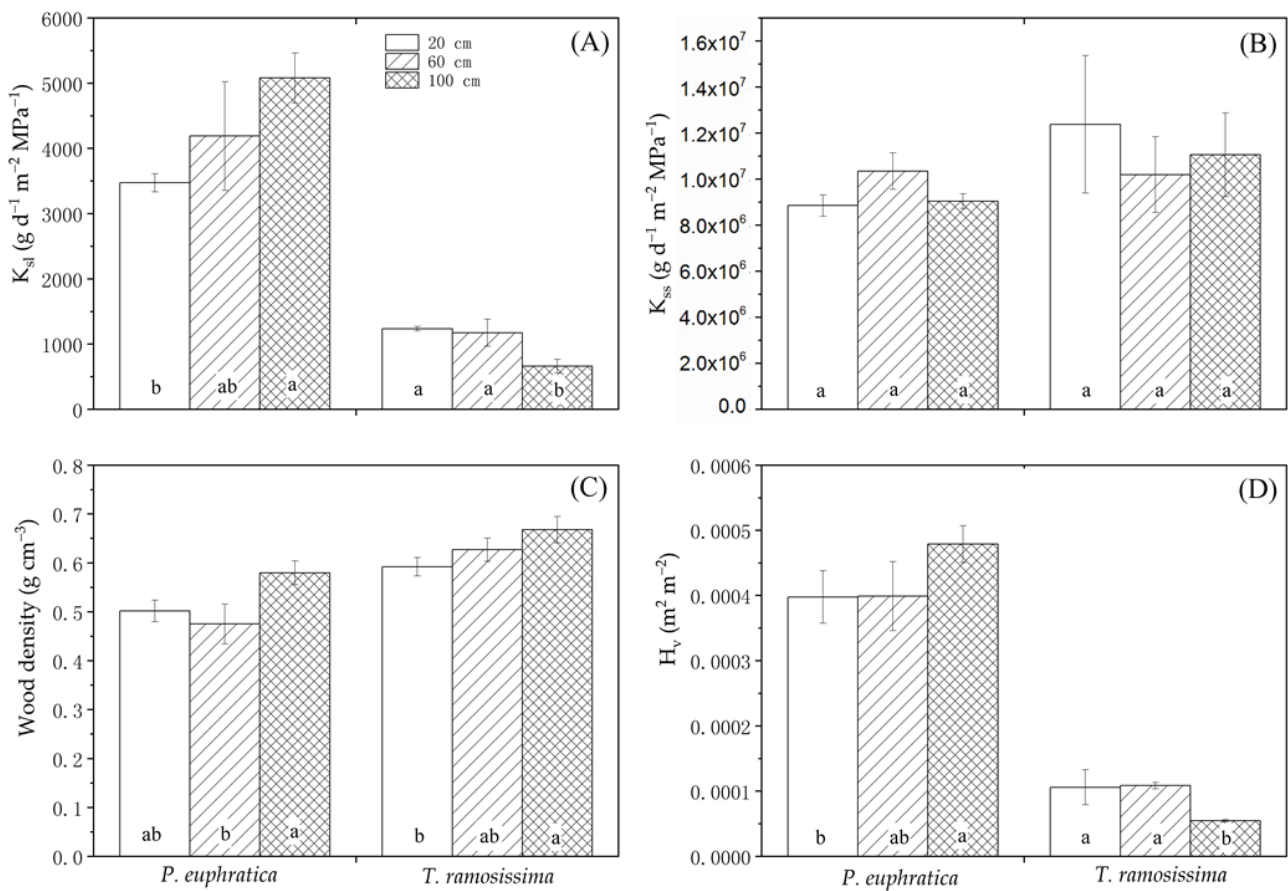
Figure 5. Whole-plant leaf area-specific hydraulic conductance (**A**), sapwood-area hydraulic conductance (**B**), wood densities (**C**), and Huber values (**D**) for *Populus euphratica* and *Tamarix ramosissima* seedlings grown 20 cm, 60 cm, and 100 cm from the groundwater level. Values are mean ± SE. Letters indicate significant differences among treatments for each species as determined by ANOVA ($p < 0.05$).
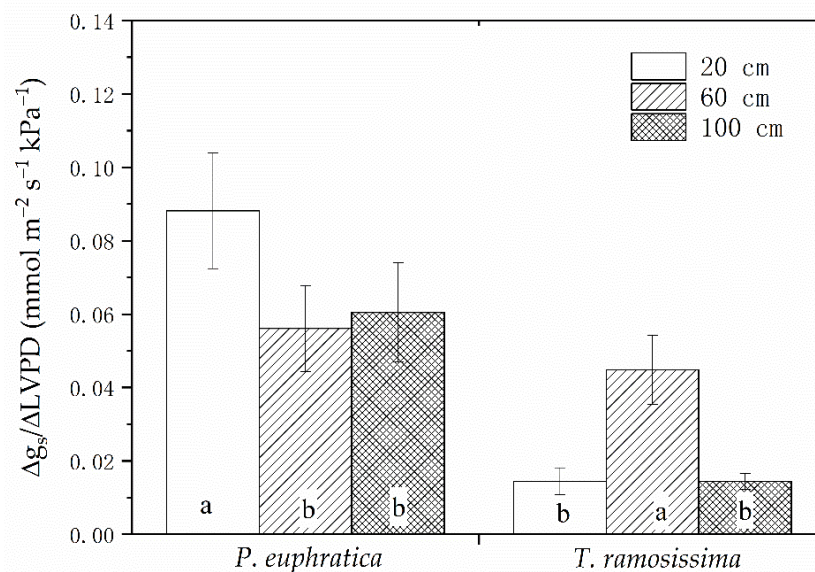
Figure 6. Stomatal conductance in response to increases in leaf-to-air vapor pressure deficit (*LVPD*) expressed as the ratio of Δg_s to $\Delta LVPD$. Values are mean ± SE. Letters indicate significant differences among treatments for each species as determined by ANOVA ($p < 0.05$).

4. Discussion

Our study compared whole-plant water use and relevant hydraulic traits for *Populus euphratica* and *Tamarix ramosissima* at simulated groundwater depth conditions. *T. ramosissima* was found to have greater whole-plant water use than *P. euphratica*, even under ample groundwater conditions supply (Figure 2). A linear correlation between *PET*-normalized daily water use and *TLA* shows that the water use of both phreatophytes was highly dependent on *TLA*. Nevertheless, the total leaf area of *T. ramosissima* was only weakly correlated with *PET*-normalized water use (Figure 3). This species had a comparatively higher leaf-area maintenance per unit sapwood area (Figure 4), which could be promoted by its faster root growth to access declined groundwater (Table 1). Therefore, leaf area-based water use is relatively less constrained by the total leaf area at the individual level. This finding is consistent with the observation that *T. ramosissima* has a very high water demand due to its high leaf area index [8]. The whole-plant k_{ss} of *P. euphratica* was comparable to that of *T. ramosissima* but its k_{sl} was relatively larger (Figure 5). For this reason, the difference in leaf area-based water use between species was explained by the inequalities in their leaf-specific and not sapwood-specific hydraulic efficiencies. The relatively higher H_v in *P. euphratica* (Figure 5D) suggests that comparatively less leaf area was maintained by each sapwood area. The higher H_v favored a higher k_{sl} in *P. euphratica* (Figure 5A). The interspecific variations in k_{sl} were driven by shoot leaf-sapwood allocation rather than by xylem hydraulic efficiency (k_{ss}) in both *P. euphratica* and *T. ramosissima*.

P. euphratica and *T. ramosissima* must efficiently transport water from the groundwater to the leaves despite the high transpirational demand of their hyperarid environment [49]. Rooting depth differed between species and treatments in this study (Table 1). Therefore, groundwater treatments substantially influence water transport resistance at the soil–root interface, where the most resistance occurs along the whole SPAC system [50]. Differences in plant height (0.9–1.5 m for *P. euphratica* and 1.1–1.4 m for *T. ramosissima* [36]) are comparatively minor sources of water transport resistance. The soil-to-leaf path length contributes little to the differences in hydraulic behavior because it has only a slight impact on the gravitational potential of water (0.01 MPa m^{-1}) in plants. Moreover, vascular structure is not able to change much in a short growing season. Thus, our observations reflected the adaptions in hydraulic architecture (leaf area-sapwood area) and water transportation (stomatal and xylem conductance) in response to variations in groundwater availability.

In general, most of the observed parameters indicated a divergence in hydraulic behavior between coexisting species. Lower k_{sl} was associated with lower H_v in *T. ramosissima*. This observation is consistent with the strong correlation between these two variables [51]. Since k_{ss} is unable to compensate for a lower k_{sl} driven by H_v, *T. ramosissima* would present with relatively steeper xylem pressure gradients at each transpiration rate, supported by the observation that *T. ramosissima* has greater resistance to embolism than *P. euphratica* [39]. In fact, *T. ramosissima* reduced xylem water potential to more negative levels than *P. euphratica* [38]. In contrast, *P. euphratica* is extremely vulnerable to cavitation, as are certain other poplar species. It has a small hydraulic safety margin [52] and is therefore prone to a functional loss of xylem conductivity under high transpirational demand, even when the groundwater is shallow [53]. *P. euphratica* mitigates the risk of embolism by maintaining high k_{sl} via elevated H_v. In this way, it reduces the water potential gradient generated by transpiration, whereas *T. ramosissima* avoids embolism by developing a safer xylem.

Stomatal behavior may have evolved from the coordination of stomatal control and soil-to-leaf water transport capacity [54]. *P. euphratica* stomata were relatively more sensitive to increases in *LVPD* than those of *T. ramosissima* (Figure 6). This observation was consistent with the fact that g_s declines sharply with increasing *LVPD* [38]. In contrast, the stomata of *T. ramosissima* were relatively indifferent to increasing *LVPD*. Consequently, *T. ramosissima* maintains a comparatively higher g_s under high transpirational demand than *P. euphratica*. Even with ample groundwater, *P. euphratica* cannot compensate for water loss under high transpirational demand as effectively as *T. ramosissima* because stomatal response to *LVPD* depends upon foliar water loss [55]. Stomatal regulation and other hydraulic

traits influence carbon and water balances in plants [56] and interact with environmental water availability, ultimately influencing the distribution of plant species [57]. Though the sensitive stomatal response to *LVPD* in *P. euphratica* may control water loss, in the case of *P. euphratica* stands with groundwater hardly recharged by runoff, the consequent stomatal closure would ultimately lead to plant dieback due to carbon starvation. This can help us to understand the decline in *P. euphratica* stands far away from channel [58]. Correspondingly, the relatively greater hydraulic safety in *T. ramosissima* may account for its occurrence in a wide range of groundwater depths [39].

Within species, all factors except k_{ss} varied among treatments (Figure 5). Therefore, hydraulic plasticity is vital for adaption to fluctuations in groundwater depth. High wood density in trees growing where the groundwater is deep may ensure hydraulic safety when water availability is low. A negative correlation between wood density and xylem hydraulic efficiency has often been reported [59]. With increasing groundwater depth, *P. euphratica* maintains high k_{sl} by increasing H_v. This response is consistent with observed increases in H_v to compensate for declining water availability [60]. In contrast, *T. ramosissima* decreased k_{sl} in areas where the groundwater was deep. This response must have been the result of a decrease in H_v since k_{ss} did not change (Figure 5B). *Tamarix* invests in foliage growth [61], which disproportionately increases leaf area relative to sapwood area. This mechanism may explain the decreases in k_{sl} and H_v in *T. ramosissima* growing where the groundwater was deep. It is unknown why *P. euphratica* has relatively higher stomatal sensitivity to *LVPD* when it grows over shallow groundwater, whereas stomatal sensitivity to *LVPD* is comparatively high for *T. ramosissima* growing at moderate groundwater depth. This discrepancy may be elucidated by a thorough understanding of the diurnal changes which occur in the balance between leaf water supply and transpiration [62].

5. Conclusions

In the present study, we investigated whole-plant water use and hydraulic traits in two phreatophytes on the Tarim River floodplain adapting to groundwater variations. *T. ramosissima* was found to have greater whole-plant water use regardless of groundwater conditions, which can be attributed to several hydraulic traits such as fast root growth, higher leaf area maintenance per sapwood area, indifferent stomatal response to *LVPD*, and greater hydraulic safety margin. While k_{ss} is similar between species, H_v is greatly lower in *T. ramosissima*, indicating that the significantly lower k_{sl} was driven by H_v. Increased k_{sl} and H_v in *P. euphratica* grown in deep groundwater favor water loss control, but limit plant growth, indicating *P. euphratica* is not as capable as *T. ramosissima* to use deep groundwater. Our findings provide an understanding of the expansion of *T. ramosissima* in areas with groundwater decline in the Tarim River Basin.

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