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Review

Research Advances in Plant Physiology and Ecology of Desert Riparian Forests under Drought Stress

Yaning Chen [1,*], Yapeng Chen [1], Honghua Zhou [1], Xingming Hao [1,2], Chenggang Zhu [1], Aihong Fu [1], Yuhai Yang [1] and Weihong Li [1]

[1] State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China; chenyp@ms.xjb.ac.cn (Y.C.); zhouhh@ms.xjb.ac.cn (H.Z.); haoxm@ms.xjb.ac.cn (X.H.); zhuchg@ms.xjb.ac.cn (C.Z.); fuah@ms.xjb.ac.cn (A.F.); yangyh@ms.xjb.ac.cn (Y.Y.); liwh@ms.xjb.ac.cn (W.L.)

[2] Akesu National Station of Observation and Research for Oasis Agro-Ecosystem, Akesu 843017, China

* Correspondence: chenyn@ms.xjb.ac.cn

Abstract: Under drought stress, desert riparian forest plants are highly self-regulating and have their own unique water use and regulation strategies, which can respond positively in several aspects such as physiology, ecology, and individual phenotypes when coping and adapting to the stresses brought by external environmental changes. In addition, as an important component of arid zone ecosystems, desert riparian forest plants maintain the cycling process of energy and material in desert areas. Therefore, it is of great ecological value to study the role played by desert riparian forest plants in desertification control and biodiversity conservation in arid zones. The purpose of this study is to provide basic data and scientific basis for the conservation, and restoration of desert riparian forests in the inland river basin of arid zone. In this paper, the physiological and ecological responses of desert riparian plants under drought stress were analyzed by reviewing the literature and focusing on the key scientific issues such as drought avoidance mechanisms, water use, and water redistribution, and the relationship between interspecific water competition and resource sharing of desert riparian plants. The results showed that: (1) In the inland river basin of arid zone, desert riparian plants show a mutual coordination of increasing soluble sugars, proline, malondialdehyde (MDA), and decreasing peroxidase (POD), to form a unique drought avoidance mechanism, and improve their drought tolerance by changing leaf stomatal conductance resulted from regulating abscisic acid (ABA) and cytokinin (CTK) content. (2) Desert riparian forest plants have their own unique water use and regulation strategies. When the degree of drought stress increased, *Populus euphratica* enhanced the water flow of dominant branches by actively sacrificing the inferior branches to ensure and improve the overall survival chances of the plant, while *Tamarix ramosissima* weaken hydraulic conductance, and increase subsurface material inputs by reducing plant height to cope with drought stress. (3) The root systems of desert riparian plants have hydraulic uplift and water redistribution functions, and, in the hydraulic uplift process of *P. euphratica* and *T. ramosissima* root systems, there is a possibility of assisting with other species in water utilization and the existence of a resource sharing mechanism.

Keywords: drought stress; desert riparian forests; plant physiology; damage avoidance mechanism; water use; water competition

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1. Introduction

Drought stress alters gene expression and causes cellular damage in plants [1]. Desert riparian forest plants are the main producers of inland river basin ecosystems in arid zones. These plants maintain the cyclic process of energy and material in desert areas, and constitute the core building blocks of desert ecosystems. As an important part of arid ecosystems, desert riparian forest plants are the product of long-term adaptation to arid environments and have developed unique water use and survival strategies that have important ecological value in the control of desertification and biodiversity conservation [2]. Thus, the physiological ecology of desert riparian forest plants under drought stress is emerging as a hot research topic [3,4].

In dryland inland river basins, hydrological processes control ecological processes, so water conditions have a direct impact on the stability of watershed ecosystems [5,6]. As a critical part of arid zone ecosystems, desert riparian forests, especially the non-zonal plants in these forests, depend mainly on groundwater (soil water) and surface water [7]. In some inland river basins without surface water recharge, groundwater is the main water source for sustaining the survival and growth of the plants. Variations in groundwater level and soil water heterogeneity control the composition and pattern of desert riparian forests, and are closely related to plant community health and ecosystem stability [8–10].

Under drought stress, desert riparian forest plants have strong self-regulatory functions and respond positively to multiple aspects, including physiology and biochemistry indices (such as stomatal conductance, soluble sugars, proline, MDA, POD, abscisic acid (ABA), and cytokinin (CTK), and so on) to adapt to or avoid the damages from stresses [11–14]. Riparian plants mainly use soil moisture in the early growth stage and tend to use groundwater in the later growth stage [15]. Xia et al. found that in the freshwater habitat of the Yellow River Delta, the depth of groundwater burial had a significant effect on the physiological activity of *Tamarix ramosissima* in the Yellow River Delta, and the variation in the depth of groundwater burial significantly changed the relative soil water content, which affected the photosynthetic efficiency of *Tamarix ramosissima* [16].

In their recent study, Chen et al. combined an analysis of the physiological and ecological characteristics of plants at different groundwater depths in the lower reaches of the Tarim River, which is the largest inland river in China. The researchers proposed different groundwater table levels that would result either in the survival or degradation of *Populous euphratica* and *Tamarix ramosissima*, the major species of building plants of desert riparian forests [17,18]. Desert riparian forest plants respond positively to and adapt to drought stress in a variety of ways, including physiology, ecology, and individual phenotypes [11–13]. Evenari's study suggests that desert plants have many physiological adaptations to extreme drought, but that most of the adaptations belong to the homeohydric plant. These plants have numerous mechanisms that enable them to survive drought [19]. Forage grass *Medicago sativa* leaf, stem, and root biomass in arid and semi-arid regions decreases with water stress and proline concentration increases with decreasing soil water content [20]. Water stress can increase the content of betaine, amino acids, proline, phenols, flavonoids, soluble proteins, and soluble sugars as well as the activities of catalase and peroxidase in maize [21]. Other scholars have also discussed the water use and water transport characteristics of desert riparian forest plants in terms of water acquisition methods, water physiological and ecological characteristics (e.g., sap flow, water potential, xylem hydraulic conductivity, etc.), and root water redistribution [22–26]. As well, they have analyzed the unique physiological responses and ecological characteristics of desert riparian forest plants under long-term drought conditions. In the context of emergent global drought trends and increasing human exploitation of water resources [27,28], the physiology and ecology of desert riparian forest plants, as an important component of arid zone ecosystems, are being more intensively studied in recent years.

In the present paper, the physiological and ecological responses of desert riparian plants under drought stress levels were analyzed by reviewing the relevant literature, focusing on key scientific issues such as drought avoidance mechanisms, interspecific water use characteristics, water redistribution, and root hydraulic lift processes, with a view to providing basic data and scientific basis for the conservation and restoration of desert riparian forests in inland river basins in arid zones.

2. Preventing Damage Mechanisms for Desert Plants under Drought Stress

The Tarim River basin is located in the arid zone of northwest China. In this area, the physiological indicators of desert riparian plants are highly sensitive to changes in groundwater level. In some broken streams downstream of inland rivers, groundwater (soil water) is the main water source for desert riparian plants, and the groundwater table depth reflects the degree of drought stress on plants [10,29,30]. At different groundwater table depths, desert riparian plants exhibit different intrinsic regulatory processes and external phenological characteristics, and some kind of mutual coordination occurs between the two, thus forming a unique drought avoidance mechanism. This individual and/or collective response process to drought stress and harm avoidance by the plants also provides an important reference for us to determine critical groundwater levels for the survival of desert riparian forests.

2.1. Plant Physiological Metabolic Processes under Drought Stress

Desert riparian forest plants actively adapt to drought stress. Under extreme drought conditions, water stress is the most direct and major factor limiting plant growth and development [31,32]. When the groundwater depth is deeper and under water stress, desert riparian plants can actively respond to drought stress caused by groundwater depth by regulating the content of osmoregulatory substances and the activity of protective enzymes in their bodies, while various physiological metabolic processes will act synergistically to enhance their drought resistance and self-adaptation [33].

Results from monitoring and analyzing the lower reaches of the Tarim River, which is the largest inland river in China, showed that under drought stress, desert plant leaves exhibited a particular response. Specifically, they enhanced their cellular osmotic potential through the accumulation of osmoregulatory substances such as soluble sugars and proline to actively adapt to external stress [13,19]. This physiological metabolic process to increase cellular protoplasm concentration and enhance plant stress resistance is a physiological response that enables plants to resist drought and maintain their normal life activities, effectively mitigating the effects of drought stress.

However, it is worth pointing out that there are also mechanisms for the mutual coordination of various physiological metabolisms in plants. Under drought stress, soluble sugars, proline, malondialdehyde (MDA) content, and superoxide dismutase (SOD) activity of plant leaves all increase. At the same time, peroxidase (POD) activity tends to decrease significantly and there is a compensatory relationship between them (Table 1). This cooperative characteristic of desert plants effectively enhances their ability to cope both individually and collectively with drought stress [6]. The results showed that the groundwater level was closely related to chlorophyll, soluble sugar, and proline of *Tamarix ramosissima* [34–36].

Table 1. Correlation coefficient between groundwater depth and physiological indexes of *Populus euphratica*, *Tamarix ramosissima*, and *Phragmites australis*.

Plant Species	Chlorophyll	Soluble Sugar	PRO	MDA	SOD	POD
Populus euphratica	−0.67 **	0.33	0.49 *	0.84 **	0.73 **	−0.80 **
Tamarix ramosissima	−0.77 **	0.44	0.50 *	0.66 **	0.74**	−0.81 **
Phragmites australis	−0.71	0.32	0.84 *	0.82 *	0.87 *	−0.62

Note: * and ** represent significant at 0.5 and 0.01 levels, respectively. PRO: proline; MDA: malondialdehyde; SOD: superoxide dismutase; POD: Peroxidase.

2.2. Plant Damage-Avoidance Mechanisms under Drought Stress

Riparian forest ecosystems in arid deserts consist of three layers: trees, shrubs, and grasses. The trees are mainly *Populous euphratica*, the shrubs are mainly *Tamarix ramosissima,* and the herbs are *Apocynum venetum* L., *Karelinia caspia* Less., *Hexinia polydichotoma*, and *Phragmites australis* [37]. Under drought stress, trees and shrubs in desert riparian forests, mainly *P. euphratica* and *T. ramosissima*, are characterized by their well-developed root systems [38,39], strong heterogeneous leaves, and root tillers [12,40]. These features combine various intrinsic regulatory processes and external phenological characteristics to build up avoidance mechanisms that help the plants adapt and cope with drought stress [41]. Adult

P. euphratica and *T. ramosissima* have deep root systems and can thrive in groundwater table depths of 4–6 m. However, when the groundwater depth is further increased and drought stress is aggravated, the osmotic potential of plant tissues of these desert riparian plants is reduced through the accumulation of soluble sugars and free proline (Figure 1). This results in a rise in cellular protoplasm concentration that serves to enhance the stress-resistance of plants [42,43].

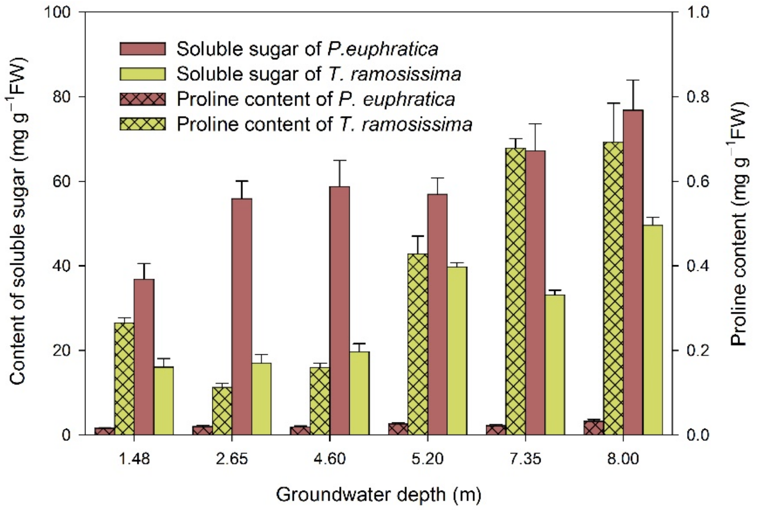

Figure 1. The change of soluble sugar and proline content of *Populus euphratica* and *Tamarix ramosissima* grown at different groundwater depths.

In some study results, constructive species of desert riparian forests in the lower Tarim River, such as *P. euphratica* and *T. ramosissima*, along with herbaceous plants such as *Apocynum venetum* L. and *Phragmites australis*, established their own adaptive regulatory mechanisms to avoid damage. They did this by reducing the osmotic potential through the accumulation of soluble sugars in leaves. However, the plant avoidance mechanisms differed among the plants, with *P. euphratica* mainly being regulated by soluble sugars and *T. ramosissima* mainly being regulated by proline [44]. When *Populus euphratica* is subjected to drought stress, a large number of superoxide dismutase (SOD) will be produced in the body to remove reactive oxygen species, control lipid oxides in cells, resist the damage of reactive oxygen species, reduce the damage of membrane system, and maintain the balance of osmotic regulation [45].

2.3. Drought-Resistance Mechanism of Plants under Drought Stress

Under a long-term drought environment, desert riparian plants have gradually formed their own drought-resistance structures and characteristics. They have also adapted to this special environment with their own unique ways of survival based on common drought resistance. Different physiological indicators of desert riparian forest plants show different sensitivities in the level of plant drought resistance, which is mainly determined by their own physiological resistance, structural characteristics, and their rhythm of growth and development processes. When subjected to drought stress, the common response of desert riparian plants to maintain their water status is to close stomata to minimize tissue water dissipation [46,47].

Plants can influence leaf stomatal conductance by regulating abscisic acid (ABA) and cytokinin (CTK) content to improve their drought tolerance [48,49]. The results of a recent study showed that with increasing groundwater depth, the ABA content of the leaves of *P. euphratica* (the only natural tree among the desert riparian plants in the lower reaches of the Tarim River) gradually increased, while the CTK content continuously decreased (Figure 2A). This synergistic effect of ABA and CTK served to close stomata and reduce transpiration [13,50]. In contrast, for shrubs and herbs such as *T. ramosissima* and *A. venetum*, the changes in ABA and CTK contents differed according to the degree of drought stress: under mild drought stress, the ABA and CTK contents of *T. ramosissima* and *A. venetum* leaves exhibited positive increases (Figure 2B,C), with the increased CTK content attenuating the increased ABA signaling effect. This mechanism allowed the leaves to continuously maintain a certain degree of stomatal activity, thus improving the plant's drought resistance. However, when drought stress increased, ABA and CTK were negatively increased (Figure 2B,C), and the down-regulation of CTK content inhibited the plant growth rate and reduced transpiration demand [50]. This response comprises an active plant adaptation to drought stress.

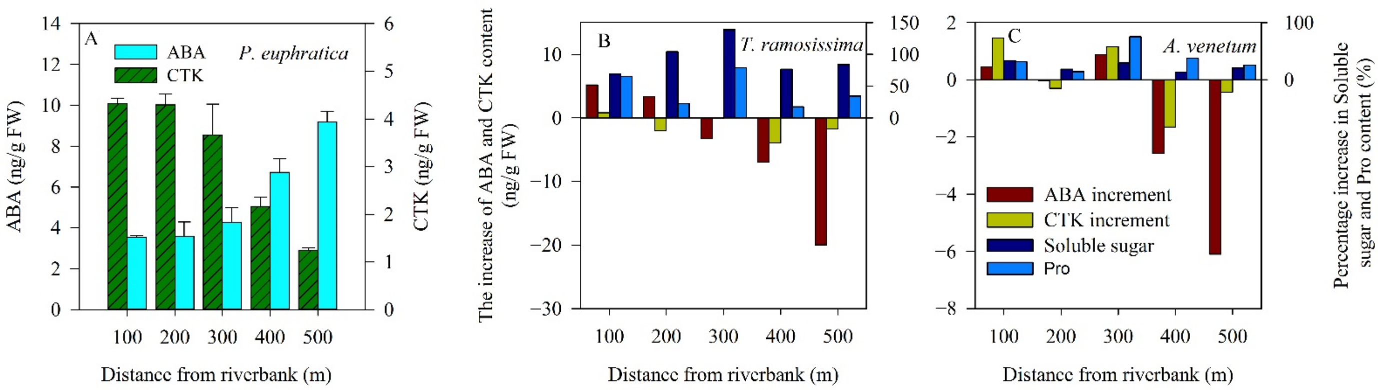

Figure 2. The change of abscisic acid (ABA), cytokinin (CTK) content of *Populus euphratica* (**A**), and the increase of ABA, CTK, proline (PRO), and soluble sugar of *Tamarix ramosissima* (**B**) and of *Apocynum venetum* (**C**) grown at different distance from riverbanks.

Additionally, the sensitivity of soluble sugars and proline to ABA response also differed between *T. ramosissima* and *A. venetum*. When expressed as a functional substance for increasing amounts of ABA concentration, the increase of ABA in *A. venetum* leaves mainly induced the accumulation of proline (Figure 2D). On the other hand, the increase of ABA in *T. ramosissima* mainly induced the accumulation of soluble sugars (Figure 2C) to improve its drought tolerance.

Desert riparian plants are a critical part of an arid zone ecosystem [51]. Studying the physiological adaptation and exploring the survival strategies of desert riparian plants to drought stress is important to ecological conservation in arid zones [14]. The present researches on plant–drought relationship in the Tarim River basin showed that the desert riparian plants displayed a variety of active adaptations to cope with drought stresses. Moreover, these adaptive strategies interacted in desert riparian plants (Table 2).

Table 2. Active adaptation strategies for the main desert riparian plants under drought stress based on physiological metabolic process in the Tarim River Basin.

Adaptive Strategies	*Populus euphratica*	*Tamarix ramosissima*
Mutual coordination of various physiological metabolisms	Increasing soluble sugars, PRO, MDA, and SOD while decreasing activity of POD	Increasing soluble sugars, PRO, MDA and SOD while decreasing activity of POD
Damage-avoidance mechanisms	Mainly regulated by soluble sugars	Mainly regulated by PRO
Drought-resistance mechanism	Increasing ABA while decreasing CTK	Increasing both ABA and CTK in mild drought; decreasing both ABA and CTK in stronger drought

3. Water Use and Regulation Strategies of Desert Riparian Plants

Analyzing the water use and regulation strategies of desert riparian plants is important for revealing the adaptation mechanisms of these plants to drought stress. Under drought stress, desert riparian plants reveal unique survival strategies. The water use and regulation strategies of the studied plants under drought stress were systematically analyzed using three different scales: individual, population, and community. The analysis was accomplished by monitoring water transport in the lower reaches of the Tarim River basin, by investigating upward extrapolation from individual plant transpiration to population transpiration water consumption, and from community to ecosystem transpiration water consumption.

3.1. Individual-Scale Water Use Strategies

Under drought stress, different types of desert riparian plants exhibit different response mechanisms and adaptation strategies [52]. These manifest not only in the differences of individual physiological and ecological responses under a range of drought stress gradients, but also in variations in water transfer and regulation strategies [53–56]. In a recent study of the water use strategies of different types of individual plants under drought-stressed environments in the lower reaches of the Tarim River basin, it was found that *P. euphratica* was subjected to mild drought stress in groundwater depths of 4–6 m. The study showed that at this depth, *P. euphratica* mainly adapted to water stress through limiting branch xylem hydraulic conductivity and coordinating the uniform growth of plants. However, when the groundwater depth exceeded 6 m, the degree of drought stress increased and the water transfer mechanism of *P. euphratica* changed. Namely, the branch xylem was no longer the main resistance site for water transfer in the plant, but was replaced by the root xylem as the primary resistance site for limiting water flow. Further, the *P. euphratica* under study enhanced the water flow of dominant branches by actively sacrificing the inferior branches (Figure 3A,B) to ensure and improve the overall survival chances of the plant as a whole [25]. This is consistent with the research results that the buried depth of groundwater decreases and the height of *P. euphratica* increases significantly, which is in line with the habitat adaptation law of desert riparian forest plants [57].

Interestingly, in this process, the *P. euphratica* plant's leaf shape also underwent changes. These alterations occurred to enhance the plant's photosynthetic performance by improving leaf surface energy balance to improve water use efficiency. The plant *T. ramosissima* likewise showed a fascinating coping mechanism in response to perceived drought. According to different habitats, *T. ramosissima* will adopt different adaptation mechanisms and water use strategies, and change its absorption mode in the process of obtaining more stable water [58]. As the most important shrub of the desert riparian plants, *T. ramosissima* copes with drought stress by reducing its height (Figure 3C,D). By doing so, it enhances osmoregulation, weakens hydraulic conductance, and increases subsurface material inputs, among other major strategies.

3.2. Population-Scale Water Use Strategies

At the population scale, the water use strategies of desert riparian forest plants were systematically analyzed by taking desert riparian forest community building species as the research objects. It was found that water use strategies differed across *P. euphratica* plants of different ages. Stands of primarily young and mature *P. euphratica* trees focused on growth and adopting an aggressive water use strategy. Water use in these trees can be described as "profligate", displaying high water consumption as an adaption to environmental stresses. However, over-mature *P. euphratica* forests tended to be resistant and adopt a conservative survival strategy. In so doing, they employed a "conservative" water use strategy, in which less water was used to obtain more CO_2 assimilation in order to maintain optimal plant life [59].

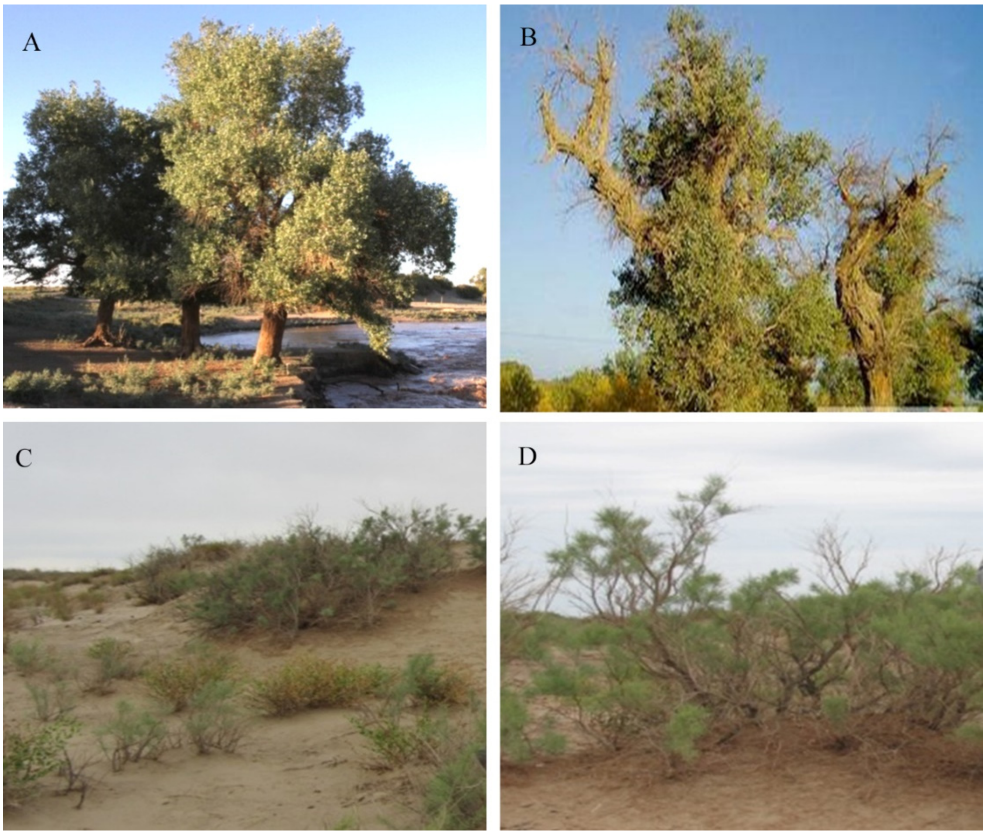

Figure 3. Growth state of *Populus euphratica* and *Tamarix ramosissima* at different groundwater depths: (**A**) *Populus euphratica* grown at shallow groundwater depth; (**B**) *Populus euphratica* grown at deeper groundwater depth; (**C**) *Populus euphratica* grown at shallow groundwater depth; (**D**) *Tamarix ramosissima* grown at deeper groundwater depth.

During the study of the individual water storage function of *P. euphratica*, it was found that the plant maintained a considerable amount of sap flow for replenishing water deficit in xylem and leaves, even during leaf stomatal closure at night [60,61]. This indicates that the calculation of water storage in *P. euphratica* based on nighttime sap flow alone will underestimate the amount of water stored in the plant, and that it may be more accurate to use the extreme value time of *P. euphratica* stem diameter as the calculation node for sap flow to replenish water deficit in trees. Accordingly, the proportion of internal water storage to daily transpiration was calculated by combining sap flow and meteorological factors, i.e., 24% for young *P. euphratica*, 29% for mature *P. euphratica*, and 8% for over-mature *P. euphratica*. This proportion of water storage reflects that young and mature *P. euphratica* have a stronger ability to self-regulate water, while over-mature *P. euphratica* have a weaker ability to do so. Moreover, young *P. euphratica* trees are the first to exhaust water storage and the first to "die of thirst", while over-mature forests are the last.

3.3. Transpiration Water Consumption Characteristics of Desert Riparian Forest Plants

The results of sap flow monitoring showed that during the peak growing season (July and August), the water consumption of young *P. euphratica* trees (DBH (diameter at breast height) = 6 cm) was 8.38 ± 1.23 L, while that of mature trees (DBH = 17 cm) was 27.06 ± 3.15 L, and that of over-mature trees (DBH = 46 cm) was 25.52 ± 2.67 L (Figure 4). The method of upward extrapolation from individual plant transpiration to population transpiration, and from community to ecosystem transpiration was investigated by analyzing the transpiration water consumption of different scales of desert riparian forests. The daily transpiration water consumption in the experimental area was 3.1 ± 0.3 mm/d for young stands, 2.8±0.4 mm/d for mature stands, and 2.2 ± 0.2 mm/d for over-mature stands during July and August (Figure 4), based on a stand-scale transpiration water consumption model. The model used the relationship between the DBH and sapwood area, and the DBH and sap flux density.

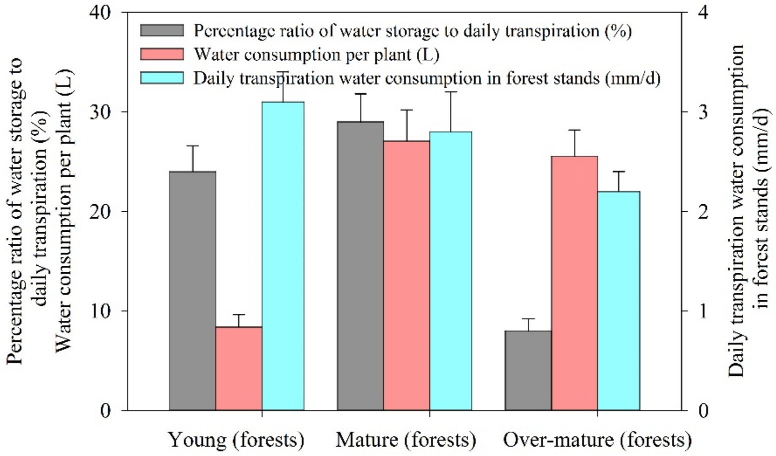

Figure 4. Percentage ratio of water storage to daily transpiration, and water consumption in different ages of *Populus euphratica* trees or forest stands.

In applying the same water consumption model, a total amount of 382.37 mm from June to October in the *P. euphratica* stands of the experimental area was deduced on a single *P. euphratica* scale [62,63]. The differences in transpiration water consumption was mainly due to variations in density and leaf area index across the *P. euphratica* stands. The transpiration water consumption differences were also linked to the type of strategies adopted by the plants at different ages.

4. Interspecific Water Competition and Sharing Mechanisms of Desert Riparian Forest Plants

Desert riparian plants have developed their unique morphology and characteristics under long-term arid environments. These characteristics have enabled them to adapt to desert habitats. Chief among their drought-response features is a well-developed root system, as groundwater (soil water) is an important water source for sustaining the survival of desert riparian plants [64]. The well-developed root system of these plants can increase the water absorption surface and improve water uptake efficiency, enabling them to maintain a greater water uptake ability under drought conditions and thereby mitigate any damage caused by drought stress. At the same time, the various species exhibit water competition relationships and resource sharing mechanisms in the process of using their root systems to obtain groundwater.

4.1. Water Competition among Plant Species

In areas of arid zones with scarce precipitation, a plant's root system is a key component of its ability to obtain groundwater and thereby sustain its survival [65]. *P. euphratica* and *T. ramosissima*, as the main building blocks of desert riparian forests, have well-developed and deep root systems with large root/crown comparisons, allowing them to survive even at significant groundwater depths [66].

By combining plant oxygen isotopes and PSI (proportional similarity index), the water uptake layer level of plants in the lower reaches of the Tarim River were analyzed, and it was found that changes in groundwater depths altered the water use relationships of *P. euphratica* and *T. ramosissima*. Moreover, it was found that there is a certain type of water competition between desert riparian plant species in the process of root access to groundwater. At groundwater depths of 1.8 m and 3.8 m, there was no significant difference between the $\delta^{18}O$ values of xylem water in *P. euphratica* and *T. ramosissima*. When the PSI reached 0.94, indicating shallow groundwater depths, the water uptake areas of

P. euphratica and *T. ramosissima* mostly overlapped with each other (Figure 5). This means that *P. euphratica* and *T. ramosissima* may utilize the same water sources, and that they are engaged in an obvious water competition relationship [64]. Studies have shown that the aboveground biomass and relative yield of *T. ramosissima* are higher than that of *P. euphratica* under the condition of available groundwater in highland [67]. The competitive advantages of *T. ramosissima* include the rapid response of growth period to groundwater enrichment and water consumption strategy; *P. euphratica* showed a more conservative strategy in water use and was sensitive to VPD. The study further shows that when *P. euphratica* is disturbed by flood, the strategy of "sitting and waiting" is conducive to its growth and survival, so as to avoid being excluded by competition in the early succession [68].

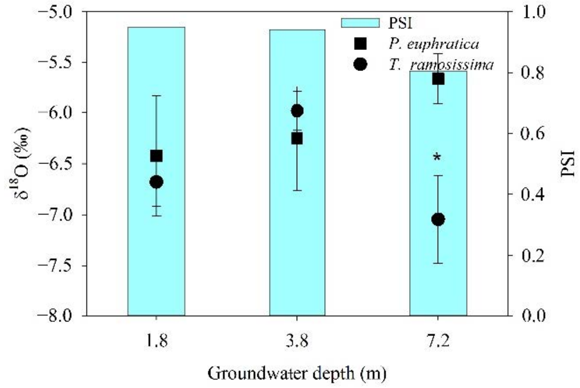

Figure 5. The $\delta^{18}O$ value of plant xylem water and the proportional similarity index (PSI) of the proportional water uptake between *Populus euphratica* and *Tamarix ramosissima* grown at different groundwater depths. * indicate a significant difference ($P < 0.05$) between the $\delta^{18}O$ values of xylem water in *P. euphratica* and *T. ramosissima* grown at the same groundwater depth.

However, with increases in groundwater depth, the PSI of *P. euphratica* and *T. ramosissima* decreased significantly, and the water competition between the species appeared to weaken. The results of the plant sample survey showed that the tops of the *T. ramosissima* plants did not die at deeper groundwater depths, whereas top-dieback was clearly evident in *P. euphratica*. These findings suggest that *P. euphratica* plants are highly dependent on groundwater and are likely less able to adapt to changes in groundwater depth than *T. ramosissima* plants. More specifically, *P. euphratica* adapts to changes by reducing aboveground biomass, whereas *T. ramosissima* adapts by further developing its underground root system.

In the lower reaches of the Heihe River, where the groundwater depth is shallow (3–5 m), the stable isotope compositions (δD, $\delta^{18}O$) of xylem water of different desert riparian plants and their potential water sources at various depths were characterized. In so doing, it was found that *P. euphratica* mainly used groundwater from 200 to 320 cm, *T. ramosissima* mainly absorbed soil water at 200–300 cm, *Hippophae neurocarpa* at 0–20 cm, *Karelinia caspia* at 50–100 cm, and *Peganum harmala* at 0–20 cm [69]. Based on the results of the above tests and analyses of water uptake depths of different trees, shrubs, and herbaceous plant species, the following main conclusions were drawn: there may be water competition between *H. neurocarpa* and *P. harmala*, and between *P. euphratica* and *T. ramosissima* in the process of groundwater acquisition, but there was no significant water competition among other plant species, such as *T. ramosissima*, *H. neurocarpa*, and *K. caspia*, which have different water absorption layer levels. These results provide important scientific and technological support for species selection as well as optimal species combination and assembly in the restoration process of damaged ecosystems in the lower reaches of inland rivers in arid zones.

4.2. Hydraulic Uplift and Water Redistribution of Plant Root System

The root system of desert riparian plants has the function of hydraulic uplift and water redistribution. The distribution position of fine roots of *P. euphratica* and *T. ramosissima* is mainly at 0-120 cm on the surface of the soil. Drought will lead to serious shortage of surface soil moisture and damage the function of fine roots. In order to resist drought, the roots of *P. euphratica* and *T. ramosissima* both transport soil water and groundwater from deep layer to surface layer through hydraulic redistribution [9,62]. This mechanism improves the water use efficiency. Therefore, water redistribution is a physiological mechanism to resist drought. The research shows that the contribution rates of root water redistribution to transpiration in growing season are 38.75% and 19.44% respectively [11,62].

In the hydraulic uplift process of the *P. euphratica* and *T. ramosissima* root systems, there is the possibility that they assist with other species in water utilization, as well as engage in a resource-sharing process. Our observational study revealed that when the difference between plant leaf temperature and air saturation water vapor pressure reached a certain threshold, the root system sap flow rate appeared to be negative, resulting in the occurrence of hydraulic uplift. During the comparative analysis of lateral root sap flow rates of *P. euphratica* in the lower reaches of the Tarim River and the lower reaches of the Heihe River, it was found that the mean daily variation, minimum, and nighttime negative sap flow of these plants were 0.30 cm/h, −2.65 cm/h and −2.34 cm/h, and 3.82 cm/h, −1.05 cm/h, and −0.80 cm/h, respectively (Figure 6). These measurements indicate that at the single root level, the water uplift and water redistribution effects of *P. euphratica* in the lower reaches of the Tarim River, where the groundwater depth is deeper, were significantly greater than in the lower reaches of the Heihe River, where the groundwater depth is shallower. At the same time, the soil layer level where hydraulic uplift occurred was deeper than in the lower reaches of the Heihe River [62].

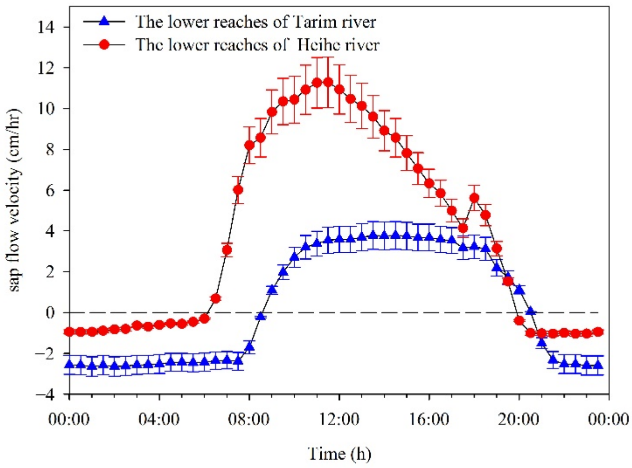

Figure 6. Diurnal variation of lateral root flow rate of *Populus euphratica* in the lower reaches of Tarim River and Heihe River.

Furthermore, a comparative analysis of the ecological effects of root hydraulic uplift and water redistribution at different groundwater depths revealed that the deeper the root distribution, the more significant the hydraulic uplift and water redistribution of plant roots. Deeper root distribution was also more likely to induce water redistribution in deeper soils, as well as to lower the proportion of the contribution of water redistribution to transpiration [24,70,71]. The degree of improvement of soil water conditions in the lower reaches of the Tarim River by hydraulic uplift of *P. euphratica* roots (32% of water consumption by uplift) was significantly greater than that in the lower reaches of the Heihe River (10% of water consumption by uplift) [62]. It appears that the hydraulic uplift function of deep-rooted plants such as *P. euphratica* and *T. ramosissima* improves shallow soil water conditions and facilitates the survival of shallow-rooted plants grown at deeper groundwater depth [24,72]. This important feature resolves the question of why shallow-rooted herbaceous plants exist in areas with deeper groundwater depths.

4.3. Plant Habitat Range and Plant Life Form Relationship

Different tolerances of plants to environmental determine their habitat range [73]. Plant life form is a specific expression of plant adaptation to the environment, and its formation is the result of convergent adaptation of different plants to the same environmental conditions [74,75]. The same life form reflects that plants have the same or similar requirements or adaptability to the environment [76]. The width of the suitable range of desert riparian forests is closely related to the plant life form. The results of our study show that among the desert riparian forest plants, *P. euphratica*, *T. ramosissima*, *K. caspia*, and *Alhagi sparsifolia Shap.*, all share certain traits, namely a low degree of xylem embolism, high hydraulic conductivity (Figure 7), strong adaptability to drought stress, a wide ecological niche, and suitable range [25]. These plants are the major constructive species of desert riparian forests. Even so, there are specific life form relationships among the plants in different communities under different moisture conditions. During the monitoring and analysis of desert riparian forest plant communities in the lower reaches of the Heihe River, it was found that when groundwater was sufficient, the communities composed of over-mature *P. euphratica*, young *P. euphratica*, *T. ramosissima*, and *Sophora alopecuroides* L. tended to promote the rapid growth of young *P. euphratica* and *T. ramosissima*, while the growth of over-mature *P. euphratica* and *S. alopecuroides* slowed down. Communities composed of *T. ramosissima* and *k. caspia* tended to promote the rapid growth of *T. ramosissima*, while the growth of *k. caspia* was slowed. However, when enduring water-stressed environments, a single *T. ramosissima* or *Reaumuria soongorica* tended to grow rapidly, and herbaceous plants such as *S. alopecuroides* and *K. caspia* coexisted with deep-rooted plants such as over-mature *P. euphratica* and *T. ramosissima* [52]. These relationships between suitable range and life form of desert riparian plants also provide an important scientific and technical reference for the determination of preferred species and assemblages of optimal species during the restoration of damaged ecosystems in the lower reaches of inland rivers in arid zones.

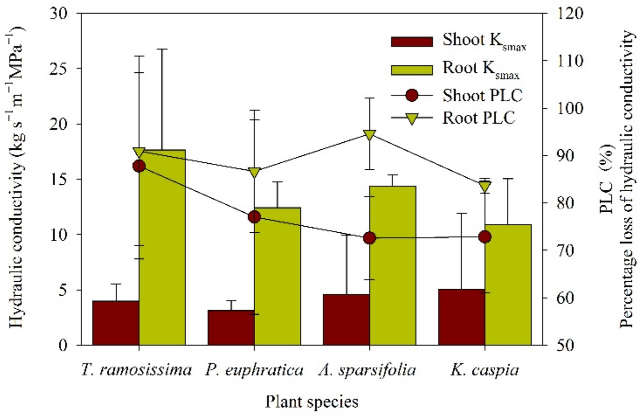

Figure 7. Shoot and root hydraulic conductivity and its percentage loss (PLC) of desert riparian plants.

5. Conclusions

Desert riparian plants form the core of the desert ecosystem, and maintain the energy and material cycling process in desert areas. Therefore, studying the physiological responses of this vegetation to environmental stress in the Tarim River basin while also exploring its adaptation strategies to environmental changes is important to ecological conservation research, particularly in relation to desert riparian forests in arid zones. In studying the drought-stress environment of the Tarim River basin, the present research showed that desert riparian plants displayed active adaptation, and that plant physiological ecology can analyze plant–environment relationships, including material metabolism and energy transfer patterns. As well, plant physiological ecology can analyze plant response processes and adaptation mechanisms to different environmental conditions in terms of physiological mechanisms. In fact, because plant ecology can provide physiological explanations for many current and anticipated ecological and environmental problems, it is gaining an increase in research attention.

Under long-term drought environment, desert riparian forests in arid zones have formed a series of unique adaptation strategies. These plants can actively enhance their adaptation to drought through the accumulation of osmoregulatory substances such as soluble sugars and proline, which resulted in a damage-avoidance mechanism to drought stress for plants. Meanwhile, these plants can enhance their drought resistance by a mutual coordination of increasing soluble sugar, PRO, MDA, SOD, and decreasing POD in plants. Additionally, they can improve their drought tolerance by regulating ABA and CTK content.

Desert riparian plants also display a series of water use strategies to cope with drought stress. For individual *P. euphratica*, it mainly adapts to mild drought stress through limiting branch xylem hydraulic conductivity, but it resists severe drought stress by limiting root xylem hydraulic conductivity. For population, young and mature *P. euphratica* trees display a high-water consumption to drought stresses, while over-mature trees usually show a "conservative" water use strategy. For stands, *P. euphratica* stands of different ages also show different transpiration water consumption characteristics to drought stress, and their transpiration water consumption became small with the increasing ages. There are a series of water competition and sharing mechanisms among the desert riparian plants under drought stress. The trees and shrubs with deep roots may exist with water competition, for example, both *P. euphratica* and *T. ramosissima* use mainly groundwater. However, there is also water sharing between trees or shrubs with deep root and herbs with shallow root plants.

By investigating the physiological and ecological problems of desert riparian plants under drought stress, the reasonable (2–4 m), stressed (4–6 m), and critical groundwater table (below 9 m) levels were determined by analyzing changes in the physiological metabolic indexes of desert riparian plants at different groundwater table depths. Based on observations of the adaptability, ecological niche, and suitable range of different plants under drought stress, *P. euphratica*, *T. ramosissima*, *A. sparsifolia*, *S. alopecuroides*, and *K. caspia* were proposed as the preferred species and the best species combination for the restoration of damaged ecosystems in the lower reaches of inland rivers in arid zones. Overall, good results were obtained from our experimental demonstration of damaged ecosystem restoration in the Tarim River basin. These results could potentially be applied to similar arid zones elsewhere in China and around the world.

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