



Competition between *Populus euphratica* and *Tamarix ramosissima* seedlings under simulated high groundwater availability

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Abstract: Desert riparian plants experience high variability in water availability due to hydrological fluctuations. How riparian plants can survive with low water availability has been well studied, however, little is known about the effects of high water availability on plant community structuring. We conducted a mesocosm experiment to test whether seedling competition under simulated high groundwater availability can explain the shift of co-dominance of *Populus euphratica* and *Tamarix ramosissima* in early communities to *P. euphratica* dominance in mature ones along the Tarim River in northwestern China. Seedlings of these two plant species were grown in monoculture and mixture pools with high groundwater availability. Results indicated that the above-ground biomass and relative yield of *T. ramosissima* were higher than those of *P. euphratica*. The competitive advantages of *T. ramosissima* included its rapid response in growth to groundwater enrichment and its water spender strategy, as evidenced by the increased leaf biomass proportion and the inert stomatal response to leaf-to-air vapor pressure deficit (VPD). In comparison, *P. euphratica* showed a conservative strategy in water use, with a sensitive response to leaf-to-air VPD. Result of the short-term competition was inconsistent with the long-term competition in fields, suggesting that competition exclusion is not the mechanism structuring the desert riparian plant communities. Thus, our research highlights the importance of mediation by environmental fluctuations (such as lessening competition induced by disturbance) in structuring plant communities along the Tarim riparian zones.

Keywords: community succession; vapor pressure deficit (VPD); stomatal conductance; riparian plant; water use strategy

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Riparian plants are subject to high variability in water availability due to hydrological fluctuations (Naiman and Décamps, 1997; Lytle and Poff, 2004; Stromberg et al., 2007; Stella et al., 2013). Such environmental variability is important for the dynamics of plant populations and community structuring (Hutchinson, 1961; Kotowski et al., 2010). Generally, environmental variability can shape communities through preventing the consistent effect of ecological interactions during harsh periods in which population growth is directly reduced and the intensity of interactions between organisms is lessened (Chesson and Huntly, 1997). Thus, in case of such variable riparian

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environments, while survivability during droughts is important for species success, competitive exclusion is expected to occur more likely during periods with high water availability under which plants are able to achieve rapid growth.

Riparian plant distribution has been shown to be jointly controlled by water availability and competition (Kotowski et al., 2010). Because competition takes place in the context of environmental conditions, competitive advantages need to be considered over a range of conditions (Sher and Marshall, 2003), especially in highly variable riparian habitats (Sabo et al., 2005). In desert riparian environments, for instance, species with the ability to grow rapidly in wet years and tolerate water deficit in drought years may be more competitive (Cleverly et al., 1997). Nevertheless, there have been extensive studies on the effects of flooding (Pollock et al., 1998; Vandersande et al., 2001; Tiegs et al., 2005; Corenblit et al., 2009) and drought (Gasith and Resh, 1999; Rood et al., 2000; Stella and Battales, 2010) on riparian plants, but little attention has been paid on the effects of favorable condition such as when groundwater is highly available.

Riparian plants are often established on newly deposited sediment near river channels after the recession of floods (Scott et al., 1996). As floodplain evolves through channel meandering or narrowing, riparian forests develop even-aged stands, with younger stands nearer to the channel (Stromberg, 1998; Friedman and Lee, 2002), suggesting that plant interactions at early stage play a critical role in the community structuring. In the Tarim Basin of northwestern China, the riparian forests, dominated by *Populus euphratica* Oliv. and sub-dominated by *Tamarix ramosissima* Ledeb. (Zhang et al., 2005), exhibit such a pattern that *P. euphratica* stand ages with distance from the active channel (Han et al., 2007). Commonly, co-dominance of *P. euphratica* and *T. ramosissima* in seedling stands shifts to *P. euphratica* dominance in mature ones (Fig. 1a) (Li et al., 2013). This dominance shift suggests that earlier space occupancy as a result of faster initial development of a species contributes to the species success (Körner et al., 2008). Specifically, *T. ramosissima* as a shrub species needs to suppress *P. euphratica* as a tree species at seedling stage, and vice versa, *P. euphratica* needs to occupy the riparian zones to avoid being suppressed by its co-established competitor at this stage. Seedling stands near channel are more exposed to hydrological fluctuations (Bottollier-Curtet et al., 2013), because the intensity and frequency of hydrological fluctuations decrease along the river-floodplain elevation gradient (Biswas and Mallik, 2010). In the upper reaches of the Tarim River Basin, riparian zones close to the active channel are still prone to naturally hydrological fluctuations that can result in an annual groundwater table variation greater than 2 m (Zhang et al., 2007). The subtle interspecific differences of riparian plants in response to such hydrological fluctuations during early succession may increase over time, and consequently determine the structure of the mature communities (Sher and Marshall, 2003). Therefore, the early competition between *P. euphratica* and *T. ramosissima* is expected to be an important process for structuring the riparian plant communities along the Tarim River.

Recent studies have shown that both *P. euphratica* and *T. ramosissima* are highly dependent on the groundwater availability, evidenced by leaf gas exchanges (Chen et al., 2011), sap flow (Ma et al., 2010), plant-water relations (Fu et al., 2006) and hydraulic conductance (Zhou et al., 2013). These works were conducted on adult plants, indicating that both species show little change in physiology when groundwater is relatively shallow (Chen et al., 2013). Results from another research by Li et al. (2013) indicated that, under shallow groundwater condition, both *P. euphratica* and *T. ramosissima* seedlings exhibited rapid shoot growth, whereas *T. ramosissima* accessed deeper groundwater more rapidly. These works focused on the effects of water availability on riparian plants at an individual level. Studies on the impact of water availability at a community level are entirely lacking. However, in riparian ecosystems in the southwestern USA with great success of *Tamarix* invasion (Glenn and Nagler, 2005), a field work indicated that the dominance of *Tamarix* mostly resulted from reduced competition intensity by native *Populus* and *Salix* due to groundwater decline and/or flood disappearance (Merritt and Poff, 2010). Controlled experiments also showed that these natives are competitive against *Tamarix* under favorable conditions (Sher et al., 2000; Sher and Marshall, 2003; Bhattacharjee et al., 2009). In addition, growth of native seedlings (*Populus* and *Salix*) impervious to *Tamarix* presence and density has

been observed in fields (Sher et al., 2002). These evidences from the *Tamarix* invaded riparian ecosystems imply that *P. euphratica* may outcompete *T. ramosissima* under favorable conditions, a possible mechanism attributed to the success of *P. euphratica* along the Tarim riparian zones.

Our objective was to test whether the seedling competition between *P. euphratica* and *T. ramosissima* under high groundwater availability could explain the shift from *T. ramosissima* and *P. euphratica* co-dominance in early communities to *P. euphratica* dominance in mature ones. We also expected that the stronger competitor had higher water use capacity under high groundwater availability.

1 Materials and methods

1.1 Materials

The studied species, *P. euphratica* and *T. ramosissima*, are phreatophytic woody plants that dominate the riparian zones along the Tarim River in northwestern China. Both species exhibit life history strategies that adapt to riparian environments, such as producing tiny, wind- and water-dispersed seeds, releasing seeds from late summer to early autumn when flood events occur, and germinating on moist sediments after flood recessions. Their establishment niches overlap, leading to mixture seedling communities with similar dominance (Li et al., 2013). This situation means that the interspecific competition between them would be inevitable at seedling stage: the one that develops dense stands to occupy the riparian space earlier would be in a competitive advantage. Therefore, we used 3-year-old seedlings, the age when the canopy has not closed and neither species has developed dense stands in fields (Li et al., 2013).

Seeds of both species were collected in August 2011 from natural populations and then sown in a common garden at the Aksu Water Balance Station, Chinese Academy of Sciences (40°27'N, 80°45'E, hereafter Aksu Station), where the experiment was carried out. Then in March 2013, seedlings with heights ranging from 35 to 42 cm were transplanted into outdoor concrete pools designed for simulating different groundwater conditions.

1.2 Experimental design

The experimental pools were 2.8 m×1.8 m in area and 1.5 m in depth, with sealed bottoms and drainage valves at different depths. There was a coarse-sand layer (20-cm in thickness) at the bottom of each pool, above which loosely structured, loamy (sand:silt:clay averaged 25:70:5) soil that was collected from a riparian site was filled. In each pool a plastic pipe was vertically inserted for groundwater observation. There were total 10 pools gridded by concrete walls, seven for mixture to examine the competitive effects, two for *P. euphratica* monoculture and one for *T. ramosissima* monoculture as the reference for intraspecific effects. Seedlings were planted at the same density for all pools, with an inter- and between-row space of 0.4 m, thus yielding 28 seedlings per pool. This density was similar to that of the mixture seedling communities at the same stage in fields. Species were alternated in space for mixture pools.

After transplantation, the bottom drainage valves were kept open, and weekly flood irrigations were carried out until the groundwater treatment initiation (on 1 July). In this way, soils in pools were kept moist while soil inundation was avoided, which promoted seedling establishment in the pools. From 1 July to 15 September (end of the experiment), drainage valves were closed and the groundwater was kept at 0.4–0.6 m below soil surface through flood irrigation. Groundwater depth in each pool was observed daily. Once the groundwater was close to 0.6 m in depth, water was added by flood irrigation. After each irrigation, if the groundwater was shallower than 0.4 m, a drainage valve at this depth was opened to drain the excess water. Thus during the treatment period, the groundwater in each pool fluctuated with a small range. Here we only focused on the shallow groundwater condition because the work by Li et al. (2013), who compared the eco-physiology of the two species under a range of groundwater conditions, indicates that *P.*

euphratica can likely compete against *T. ramosissima* at seedling stage only when groundwater is highly available. In addition, we have conducted a primary competition experiment (initiated in 2012), confirming that *P. euphratica* was excluded under the condition without groundwater availability (Fig. 1b).



Fig. 1 Photographs showing plant communities in a riparian zone of the Tarim River (a) and a primary competition experiment conducted in a pool without groundwater availability (b). (a) *Tamarix ramosissima* (brown leaves) juveniles have been suppressed by those of *Populus euphratica* (yellow or green leaves) in the foreground in which there is similar abundance between the two species, and *P. euphratica* becomes dominant in the adult stand. (b) *P. euphratica* has been excluded from a pool without groundwater availability in the next year.

1.3 Data collections

As plant height is an important measure for competition effects, we numbered all seedlings in all pools and documented the changes in height for each seedling during the experiment. The initial heights were measured before the groundwater treatment. We had planned to measure the height monthly, but we observed that the seedlings grew rapidly under the experimental condition. Then from 22 July, the measurement was adjusted to be carried out weekly. At the end of the experiment, the above-ground biomass of each seedling was harvested and fresh biomass was immediately weighed. Then we randomly sampled 5 seedlings of each species from each mixture pool, 10 seedlings from each monoculture pool, of which leaves and branches were separated, and then weighed after being oven-dried to constant weight at 70°C. We used the dry/fresh biomass ratio of each species in each pool to calculate dry above-ground biomass of each seedling in corresponding pools.

We determined plant water status by measuring pre-dawn (ψ_{pd}) and midday (ψ_{md}) xylem water potential with a PMS Model 1000 (PMS Instrument Co., Albany, USA) pressure chamber. Plant water status was measured twice, one on 14 August and the other on 12 September. Measurements were carried out between 05:30 and 06:30 for ψ_{pd} , local time, and between 15:30 and 16:30 for ψ_{md} . For each time, plant water status was determined on 2 or 3 randomly selected seedlings in each monoculture pool, and 1 or 2 of each species in each mixture pool.

Gas exchange was measured by a portable photosynthesis system equipped with a CO₂ injector (Li6400, Li-Cor, Lincoln, USA), with a standard chamber used for determining the stomatal responses to leaf-to-air vapor pressure deficit (VPD). Measurements were conducted on the youngest mature leaves in full exposure to sunlight. We carried out all of the leaf-gas exchange measurements between 10:30 and 13:30, local time, on clear days in August and early September, before which the seedlings' root systems had undergone enough time to acclimate to the water environment in pools. Leaf-to-air VPD-response measurements were performed on 3 randomly selected seedlings of each species in each mixture pool, and 7 in *P. euphratica* monoculture and 6 in *T. ramosissima* monoculture.

For determination of stomatal conductance (g_s) in response to leaf-to-air VPD, we set the reference CO₂ at 400 $\mu\text{mol/mol}$, and the photosynthetic photon flux density (PPFD) at ambient level that ranged between 1,100 and 1,600 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$. We obtained within-cuvette leaf-to-air VPD gradient through controlling relative humidity (RH), of which the values were targeted to the following levels in the order of 20%, 15%, 10%, 20%, 30%, 40%, 50%, 60%, 70% and 80%. It should be noted that the cuvette RH>90% was difficult to be achieved due to low ambient air RH

at the study site. This was also true for the cuvette RH <5% in cases of the seedlings with high leaf transpiration. During each measurement, we did not log the gas exchange parameters until g_s had stabilized for 15–20 min. Subsequent measurement on each RH value was logged after g_s had stabilized at least 2 min. Leaves within the cuvette were cut immediately after the measurement, and then scanned for measuring the leaf area that was used to recalculate gas exchange parameters in the Li-Cor system.

1.4 Data analysis

The harvested seedlings were used to calculate the means for individual above-ground biomass and the leaf mass proportion to above-ground biomass for each species in each pool. Competitive effects were assessed with t -tests, in which the means of individual above-ground biomass from 7 mixture pools were compared with the means of the corresponding species from monoculture pools. The t -test was also used for determining the difference in leaf biomass allocation and plant water status. We used a competition index, termed relative yield (RY), expressed as the proportion of individual above-ground biomass of each species in mixture to that in monoculture, to evaluate the competitive effects of one species on the other (Weigelt and Jolliffe, 2003). RY difference between species was determined by ANOVA. Relative growth rate (RGR), calculated by $RGR = ((\text{plant height at time } n+1) - (\text{height at time } n)) / (\text{height at time } n)$, was applied to characterize growth changes of both species in mixture or in monoculture. For detecting the sensitivity of g_s to leaf-to-air VPD, we fitted the relationship between g_s and \ln -transformed leaf-to-air VPD with linear models, in which the higher slope indicates higher g_s sensitivity. The difference in g_s sensitivity was tested using analysis of covariance (ANCOVA). Leaf-level water use efficiency (WUE) was calculated by $WUE = P_n / T_r$, where P_n is net photosynthesis rate and T_r is transpiration rate. All statistical tests were performed using SPSS 13.0 (SPSS Inc., Chicago, IL, USA).

2 Results

2.1 Competition effects

Overall, the individual above-ground dry mass of *T. ramosissima* was several times greater than that of *P. euphratica*, regardless of in mixture or in monoculture (Fig. 2a). For *P. euphratica*, the individual above-ground dry mass was significantly greater ($P < 0.01$) in monoculture than in mixture, whereas an opposite pattern was found for *T. ramosissima* ($P < 0.01$). RY for *P. euphratica*, averaged 0.44, was significantly ($P < 0.01$) lower than that of *T. ramosissima*, averaged 1.34, indicating that *T. ramosissima* was a stronger competitor in the experiment (Fig. 2a). *T. ramosissima* also had significantly higher proportion of dry mass allocated to leaf than *P. euphratica* in both monoculture and mixture. Within species, *P. euphratica* showed no significant difference in leaf mass proportion between treatments, while *T. ramosissima* had a significantly higher value in mixture pools (Fig. 2b).

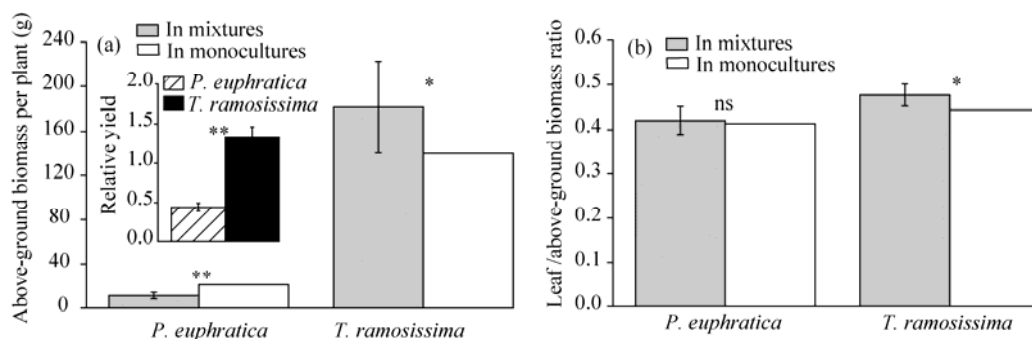


Fig. 2 The effect of competition on above-ground dry mass per plant (a) and leaf mass allocation (b) for *P. euphratica* and *T. ramosissima* in the experiment. Error bars indicate SE. An asterisk indicates significant difference within paired bars at $P < 0.05$ level (t -test), and double asterisks at $P < 0.01$ level. The small panel in Fig. 2a indicates a significantly ($P < 0.01$) higher relative yield of *T. ramosissima* seedlings.

The temporal patterns of RGR were distinct between species during the experiment (Fig. 3). *T. ramosissima* exhibited little difference in RGR between monoculture and mixture, with the value peaking in the first 3 weeks following treatment initiation, and then declining to a low level in the late stage of the experiment. In comparison, the RGR of *P. euphratica* increased with time following the treatment initiation, but exhibited an initial value greatly lower than that of *T. ramosissima* in the same stage. The RGR value for monoculture peaked one week later than for mixture, resulting in an extended period of higher growth rate for *P. euphratica* in monoculture.

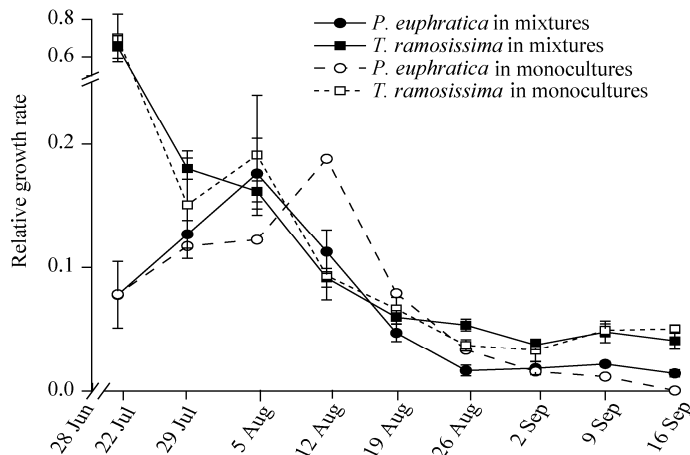


Fig. 3 Relative growth rate for *P. euphratica* and *T. ramosissima* in mixture and monoculture pools. Values are means \pm SE calculated from 7 mixture pools.

2.2 Plant water status

There was no difference either in ψ_{pd} or ψ_{md} between monoculture and mixture for *P. euphratica* (Fig. 4). For *T. ramosissima*, monoculture seedlings displayed a significantly ($P<0.01$) lower ψ_{md} but a similar ψ_{pd} in comparison to mixture ones.

2.3 Leaf gas exchange

Net photosynthesis rate (P_n) was higher in *P. euphratica* than in *T. ramosissima* throughout the obtained leaf-to-air VPD range, regardless of treatments (Fig. 5). As leaf-to-air VPD increased, the P_n for *P. euphratica* seedlings in monoculture slightly decreased, while the P_n for those in mixture tended to be constant. But there was no significant difference between treatments within the overlapped leaf-to-air VPD range. For *T. ramosissima*, the P_n exhibited little fluctuation over the obtained leaf-to-air VPD range, with the seedlings in mixture having slightly higher values than those in monoculture.

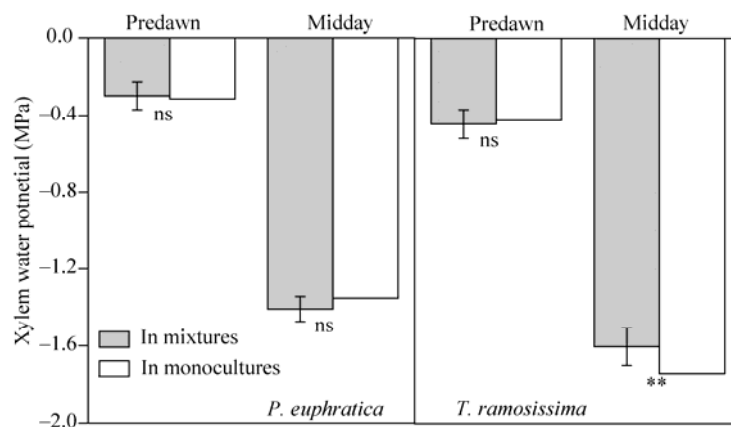


Fig. 4 Predawn and midday xylem water potential for *P. euphratica* and *T. ramosissima* seedlings in mixture and monoculture. Values are means \pm SE. Double asterisks indicate significant difference within paired bars at $P<0.01$ level and ns indicates no significant difference.

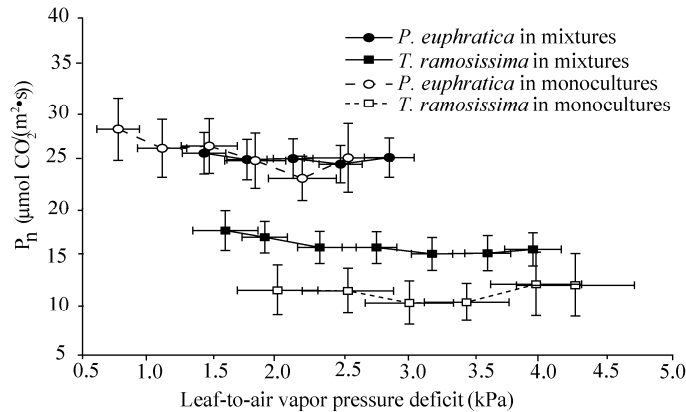


Fig. 5 Relationship between net photosynthetic rate (P_n) and leaf-to-air vapor pressure deficit for *P. euphratica* and *T. ramosissima* in mixture and monoculture. Values are means \pm SE.

For both species stomatal conductance (g_s) declined linearly with the ln-transformed leaf-to-air VPD. Relationships between g_s and $\ln(\text{leaf-to-air VPD})$ were strong ($R^2=0.80$) for each species under each treatment (Fig. 6). The slope in the fitted models, as an indicator of the stomatal sensitivity to leaf-to-air VPD, differed between treatments for *P. euphratica*, with a significantly ($P<0.01$) higher value in mixture than in monoculture (0.78 vs 0.44). In comparison, it was similar between mixture and monoculture for *T. ramosissima*.

Leaf transpiration rate (T_r) in both species increased in response to increasing leaf-to-air VPD. At a given leaf-to-air VPD, *P. euphratica* had a higher T_r in monoculture than in mixture, while *T. ramosissima* showed an opposite pattern (Fig. 7a). Leaf water use efficiency (WUE) for both species declined rapidly in lower leaf-to-air VPD levels, and declined slightly over the higher values (Fig. 7b). For each species, WUE was greater in mixture than in monoculture, with the difference tending to be smaller with increasing leaf-to-air VPD.

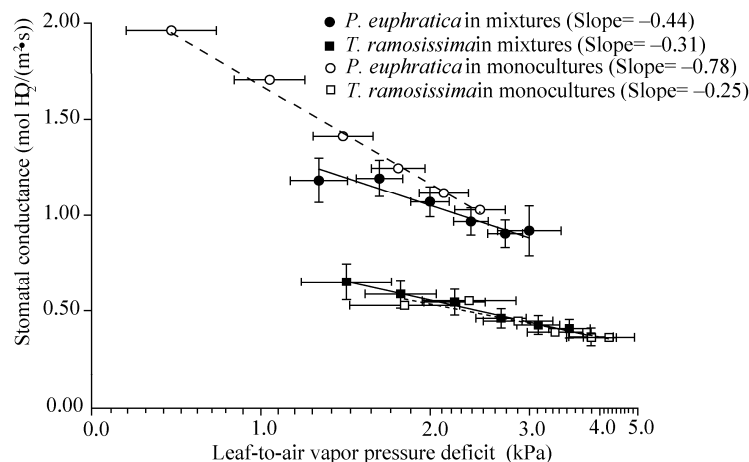


Fig. 6 Stomatal conductance in relation to leaf-to-air vapor pressure deficit for *P. euphratica* and *T. ramosissima* in mixture and monoculture. Slope of each fitted line represents stomatal sensitivity to leaf-to-air vapor pressure deficit. Values are means \pm SE. Note the ln-transformed scale in x-axes.

3 Discussion

Although competition is considered important in structuring plant communities, it is difficult to predict the outcome of competitive interactions for many plant communities (Connell, 1983). This situation may be, for a given community, resulted from the lack of our understanding

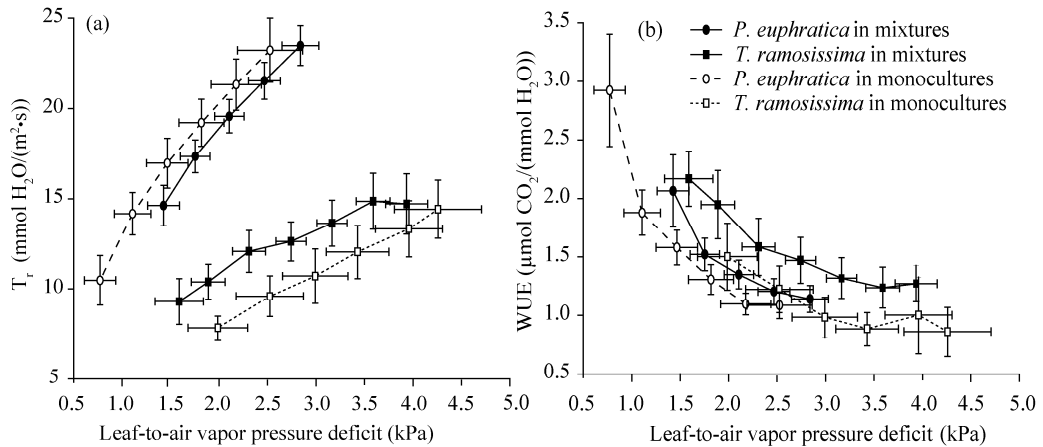


Fig. 7 Transpiration rate (a) and water use efficiency(WUE, b) responses to leaf-to-air vapor pressure deficit in *P. euphratica* and *T. ramosissima*. Values are means \pm SE.

in the role of competition: when, how and at which stage of life cycle of plants does competition determine community structure (Fowler, 1986). Indeed, this is true in case of our study, as *T. ramosissima* as the stronger competitor, evidenced by its higher RY (Fig. 2a), is contrary to the field observations. *T. ramosissima* exhibited a lower leaf-level transpiration (Fig. 7a) associated with a lower leaf-level P_n (Fig. 5) and a similar WUE (Fig. 7b) compared to *P. euphratica*. However, the increased slope of the linear model between g_s and \ln -transformed leaf-to-air VPD in *P. euphratica* under intra-specific competition (Fig. 6) indicates that *P. euphratica* is more sensitive in stomatal response to leaf-to-air VPD increase. This suggests that, even with unlimited groundwater availability, g_s would decrease at a larger degree to control water loss from leaves when air surrounding them becomes drier. Conversely, the inert stomatal response to leaf-to-air VPD in *T. ramosissima* allows the g_s to decrease less under higher transpiration demand. Therefore, our expectation that the stronger competitor under high groundwater availability is associated with greater water use is largely supported. Overall, our results provide the strong evidences that the direct competition at early stage do not determine the structure of the late-successional communities along the Tarim riparian zones.

The competitive advantages of *T. ramosissima* over *P. euphratica* in our experiment involve several aspects in eco-physiology. Firstly, although with a lower leaf-level transpiration (Fig. 7a), *T. ramosissima* allocated higher proportion of biomass to leaf (Fig. 2b) in comparison to *P. euphratica*, indicating that *T. ramosissima* tends to increase its leaf area on the individual basis, a trait allowing fast growth for plants. These results are consistent with the findings from the *T. ramosissima* invaded riparian ecosystems in the southwestern USA, in which *T. ramosissima* has a comparable leaf-level water use but a greatly higher individual leaf area, and thus leading to the greater water use compared to the native phreatophytes (Sala et al., 1996). Secondly, in contrast to the sensitive stomatal response of *P. euphratica* to leaf-to-air VPD (Fig. 6), the inert stomatal response allow *T. ramosissima* seedlings to maintain relatively stable stomatal conductance during periods of high evaporative demand, as long as water availability for uptake is sufficient. Because stomata are controlled by the balance between water supply and loss, again, these results confirm that *T. ramosissima* is able to compensate water loss from leaves through uptake when groundwater is highly available (Sala et al., 1996), possibly due to an efficient hydraulic architecture. Inevitably, decrease in stomatal conductance in response to leaf-to-air VPD leads to decreased carbon gain (Ocheltree et al., 2013). In the long run, the optimal stomatal control is to maximize the carbon gain for given amount of water use (Buckley, 2005). Thus under the high water availability in our experiment, the inert stomatal response to leaf-to-air VPD as a water-spender strategy used by *T. ramosissima* has competitive advantage over the conservative water-use strategy by *P. euphratica*. Another important aspect is that *T. ramosissima* had a rapid growth in response to groundwater amelioration, as evidenced by its greater RGR than *P. euphratica* in the initial weeks following groundwater treatment (Fig. 3). To a large degree, this can be explained by the rapid root system responses of *T. ramosissima* to groundwater alterations (Li et al., 2013), which allows *T. ramosissima* to access to groundwater earlier than *P. euphratica*.

once groundwater depth is altered. Field observations also support that the growth of *P. euphratica* is more dependent on groundwater than that of *T. ramosissima* (Gries et al., 2003). Therefore, the stronger competitiveness of *T. ramosissima* in our experiment can be partly, if not fully, attributed to its inert stomatal response to leaf-to-air VPD, higher mass allocation to leaf and rapid response to groundwater alterations.

Stomatal sensitivity, an important role in the survival and success for a plant in competition, is affected by several environmental factors (Aasamaa and Söber, 2011). Although the mechanism of stomatal response to leaf-to-air VPD has not been fully understood (Addington et al., 2003), the stomatal sensitivity to leaf-to-air VPD has shown to change considerably for plants experiencing soil water deficit at varying degrees (Bovard et al., 2005). Here, seedlings of both species in our experiment were grown under high groundwater, and the similar ψ between treatments for *P. euphratica* (Fig. 4) suggests that the competition did not affect its water status. Thus, while the difference in stomatal sensitivity between species can be explained by species variation, the decreased stomatal sensitivity in mixture *P. euphratica* (Fig. 6) can not be explained by the plant water status. As hydraulic conductance increases with viscosity, a lower temperature resulting from shading would cause a decrease in hydraulic conductance for water movement to leaves (Mott and Peak, 2010). Under constant leaf-to-air VPD, g_s increases in response to leaf temperature (Fredeen and Sage, 1999), consistent with the increased T_r (Fig. 7a) and g_s (Fig. 6) in *P. euphratica* in monoculture pools. Therefore, because stomatal sensitivity is related to a common spectrum of maximum g_s (Ocheltree et al., 2013), the decreased stomatal sensitivity in *P. euphratica* in mixture may be caused by the shading by its competitor, which affects the whole-plant conductance through temperature alterations.

The unexpected outcome of our experimental competition could be related to our choice of young seedlings (3 years old): *P. euphratica* seedlings may need a few more years of growth to be more competitive. However, early competition from *T. ramosissima* is inevitable for *P. euphratica* due to the overlap of their establishment niches. Thus, how *P. euphratica* goes through the early competition against *T. ramosissima* becomes a key issue for understanding the early succession of the riparian plants along the Tarim River. Now it is known that *T. ramosissima* has both ruderal and stress tolerant characteristics (Glenn and Nagler, 2005), and, as a facultative phreatophyte, is able to use both groundwater and soil water (Busch and Smith, 1995). With these eco-physiological advantages, *T. ramosissima* is expected to be more competitive than *P. euphratica* in other conditions such that *P. euphratica* seedlings were excluded soon when no groundwater was available (Fig. 1b). Thus, our results suggest that explaining the success of *P. euphratica* should combine the integrative effects of environment fluctuations at a community level, which highlights the importance of the tradeoffs between costs and benefits of plant adaptations to long-term flow regimes (Lytle and Poff, 2004). For example, the higher biomass allocation to roots can allow plants to suffer less from flooding and drought, and enhance the ability to resprout at the cost of above-ground biomass reduction (Barrat-Segretain, 2001). Similarly, rapid growth may have the cost of more biomass loss during stressful periods such as drought and flooding (Sparks and Black, 1999; Rood et al., 2000). These tradeoffs suggest, from a perspective of long-term effects, that disturbances induced by hydrological fluctuations may favor *P. euphratica* more than *T. ramosissima* at early-successional stage through growth slowing, biomass losing or mortality, and thus weakening competition and preventing earlier space occupation by *T. ramosissima*. Hence the combined effects of varying hydrological conditions on the plant interaction are worthy of further work to warrant a general understanding of plant community structuring in riparian zones.

4 Conclusions

Our experiments show that *T. ramosissima* seedlings could exhibit competitive advantages over *P. euphratica* when groundwater is highly available. *T. ramosissima* benefits from its rapid responses to groundwater alterations, as well as a water-spender strategy including the inert stomatal response to leaf-to-air VPD and the higher mass allocation to leaf. Result of the experimental competition is inconsistent to the fact that *P. euphratica* is the final dominator in fields, suggesting that competition exclusion is not the mechanism for structuring the plant communities along the Tarim riparian zones. As seedling communities close to active channel suffer from disturbances

imposed by hydrological fluctuations, the disturbance-induced competition lessening may favor *P. euphratica* going through the early competition against *T. ramosissima*. Our study highlights the importance of the mediation by environmental fluctuations in community structuring in riparian zones.

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