Research paper

Physiological and morphological responses of *Tamarix ramosissima* and *Populus euphratica* to altered groundwater availability

J. Li[1,4], B. Yu[1,2], C. Zhao[1], Robert S. Nowak[3], Z. Zhao[1], Y. Sheng[1] and J. Li[1,2]

[1]State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, Xinjiang, China; [2]Graduate School, Chinese Academy of Sciences, Beijing, China; [3]Department of Natural Resources & Environmental Science, University of Nevada Reno, Reno, NV, USA; [4]Corresponding author (lijun@ms.xjb.ac.cn)

Riparian plants in arid areas are subject to frequent hydrological fluctuations induced through natural flow variation and water use by humans. Although many studies have focused on the success of *Tamarix ramosissima* Ledeb. in its invaded ranges, its major competitor in its home range, *Populus euphratica* Oliv., historically has dominated riparian forests where both species occur naturally. Thus, identifying ecophysiological differences between *T. ramosissima* and its co-evolved competitor under varying hydrological conditions may help us understand how flow regimes affect dominance in its home range and promote invasion in new ranges. We examined ecophysiological responses of *T. ramosissima* and *P. euphratica*, which are both native to the Tarim River Basin, northwest China, to experimental alterations in groundwater. Seedlings of both species were grown in lysimeters, first under well-watered conditions and then exposed to different groundwater treatments: inundation, drought, and relatively shallow, moderate and deep groundwater. Under inundation, *T. ramosissima* showed little growth whereas *P. euphratica* died after ~45 days. Droughted seedlings of both species suffered from considerable water stress evidenced by slow growth, decreased total leaf area and specific leaf area, and decreased xylem water potential (ψ), maximum photosynthetic rate and carboxylation efficiency. Both species had better ecophysiological performances under shallow and moderate groundwater conditions. When groundwater declined below rooting depth, seedlings of both species initially experienced decreased ψ, but ψ of *T. ramosissima* recovered late in the experiment whereas *P. euphratica* maintained decreased ψ. This ability of *T. ramosissima* to recover from water deficit might result from its rapid root elongation and subsequent ability to acquire groundwater, which in turn likely provides ecophysiological advantages over *P. euphratica*. Our results suggest that recent groundwater declines along the Tarim River could facilitate *T. ramosissima* more due to its rapid response to changed groundwater availability. This trait may also help the success of *T. ramosissima* as it invaded riparian ecosystems in southwestern USA.

Keywords: groundwater use, net CO_2 assimilation, riparian, root distribution, plant growth, Tarim River.

Introduction

Riparian zones have a highly variable physical environment, including frequent groundwater fluctuations that range from inundation in the flooding season to drought in the dry season (Naiman and Décamps 1997). This disturbance regime, of which the timing, frequency, intensity and duration are determined by flow regime, greatly influences reproduction, survival, growth, community structure and even patterns of riparian vegetation (Friedman and Lee 2002, Corenblit et al. 2009, Stromberg et al. 2010). To survive disturbances, riparian plants evolved adaptive traits that include both life-history strategies that are synchronized with flow patterns and

morphological adaptations that provide benefits when distur-
bances occur (Lytle and Poff 2004, Merritt et al. 2010). For
example, seed release of willows and cottonwoods often syn-
chronizes with timing of flood recession, which provides ideal
germination and initial growth conditions (Blom 1999).
Environmental fluctuations can favor different species at differ-
ent times, thus promoting coexistence (Hutchinson 1961).
Therefore, riparian plants are expected to exhibit differences in
individual adaptive traits in response to the disturbance regime
(from inundation to groundwater rise/decline, to drought), i.e.,
some species may be more adaptive to one disturbance
whereas some are more adaptive to another.

Because natural flow variability increases with increased
aridity, riparian plant communities in arid regions should expe-
rience a greater range and higher frequency in groundwater
variation. One particular example is the riparian forest along
the Tarim River, a 1321-km-long inland river located in the
Tarim Basin, which is the most arid basin in China. The Tarim
riparian forest currently is dominated by *Populus euphratica*
Oliv. (Zhang et al. 2005). Commonly, *Populus* seedlings
become established on bare, moist and newly deposited sedi-
ment near the active river channel. As the alluvial plain evolves
through channel meandering and narrowing, a transverse (i.e.,
perpendicular to the channel) gradient in *Populus* stand age
develops, where younger stands are nearer to the channel
(Han et al. 2007). This pattern in the Tarim riparian corridor of
increased *P. euphratica* population age with increased distance
from the active channel suggests that the riparian plant com-
munity structure is determined by succession at the seedling
stage because *Tamarix ramosissima* Ledeb., which is the sub-
dominant species in this region and *P. euphratica*'s only possi-
ble competitor, also becomes established on newly deposited
sediment near the active river channel. Thus, *P. euphratica* and
T. ramosissima share the same establishment niche (Zhao and
Yin 2005). Our investigations along the Tarim riparian corridor
also show that *P. euphratica* and *T. ramosissima* seedlings had
strong positive association, both establishing on alluvial flats
near to the channel (Figure 1).

The shift from *T. ramosissima* and *P. euphratica* co-domi-
nance in seedling community to *P. euphratica* dominance in
riparian forest along the Tarim River suggests that *P. euphratica*
is possibly more adaptive to the riparian habitats than *T. ramo-
sissima* after their establishments. This is quite different from
observations in the southwestern USA, where *T. ramosissima*
establishes dense stands that exclude native species
(DiTomaso 1998). Actually, as a seedling *Populus* outcompetes
Tamarix in the USA, suggesting that interspecific competition is
not the mechanism for the initial invasion of *Tamarix* (Sher
et al. 2000, 2002, Sher and Marshall 2003). Dynamics of
plant seedling communities are more sensitive to environmental
fluctuations (Norden et al. 2007), and subtle interspecific
differences in growth that result from different responses

Figure 1. A seedling community with similar abundance of *P. euphrat-
ica* (narrow leaves) and *Tamarix* (scale-like leaves) located in the Tarim
River riparian zone. Photo credit: J. Li (August 2008).

to hydrological fluctuations during early community succession
may increase over time, and consequently determine the
future structure of the mature population (Sher and Marshall
2003). Thus, comparing seedling responses to hydrological
fluctuations is ecologically important for understanding mecha-
nisms of community succession in highly variable riparian
environments.

Now *Tamarix* occupies most riparian corridors in the south-
western USA, displacing native *Populus* and *Salix* plants and
becoming the dominant or subdominant species in these
riparian ecosystems (Busch and Smith 1995, Cleverly et al.
1997, Smith et al. 1998, Friedman et al. 2005, Bhattacharjee
et al. 2009, Merritt and Poff 2010). Ecophysiological traits
have been extensively compared between *T. ramosissima*
and *Populus* plants (see the review by Glenn and Nagler
2005). Previous work shows that *Tamarix* is more salt- (Glenn
et al. 1998, Vandersande et al. 2001), drought- (Busch et al.
1992, Pockman and Sperry 2000) and fire (Busch and Smith
1995)-tolerant than native riparian plants in the southwest-
ern USA, and these traits may contribute to the success of
Tamarix in its invaded range. However, with flood distur-
bance *Tamarix* seedling growth and survival are influenced
by densities of its neighbors, i.e., the native *Populus* and
Salix, while growth and survival of the natives are not cor-
related with *Tamarix* densities (Sher et al. 2002). Another
work shows that first-year cottonwood seedlings can survive
fall flooding better than *Tamarix* (Gladwin and Roelle 1998).
More work indicates that flow regime alterations caused by
extensive water diversions likely favor *Tamarix* establishment
more than the flooding-dependent native *Populus* (Busch
and Smith 1995, Poff et al. 1997, Scott et al. 1997, Sher
et al. 2000, Glenn and Nagler 2005). In case of the Tarim
River, the riparian forests historically have been dominated
by *P. euphratica* despite the co-occurrence of *T. ramosissima*.
Thus, we speculate that *P. euphratica* has adaptive advan-
tages over *T. ramosissima*, especially at the seedling stage as

these two species cope with their highly variable riparian habitats. Considering that *P. euphratica* co-evolved in the same environment with *T. ramosissima* whereas North American cottonwoods did not, understanding how *P. euphratica* and *T. ramosissima* seedlings differ in their responses to hydrological fluctuations may provide information useful for understanding the success of *T. ramosissima* in southwestern US riparian corridors that underwent a rapid alteration of hydrological conditions in the past century.

Our central objective was to evaluate ecophysiological and growth traits of *P. euphratica* and *T. ramosissima* seedlings in response to typical hydrological scenarios that frequently occur along the Tarim riparian forest. In particular, we addressed two hypotheses: (i) *P. euphratica* and *T. ramosissima* seedlings exhibit different trait responses under different groundwater scenarios that allow for long-term coexistence of the species under natural conditions. (ii) Trait responses of *P. euphratica* seedlings are more beneficial than those of *T. ramosissima* seedlings and allow *P. euphratica* to dominate the Tarim riparian corridor. These hypotheses were tested by assessing physiological and morphological traits of *P. euphratica* and *T. ramosissima* seedlings grown in lysimeters that simulated variable riparian habitats.

Materials and methods

Plant materials

Populus euphratica, a tree species, and *T. ramosissima*, a shrub species, are phreatophytic and native to central Eurasia. *Populus euphratica* seeds are often released between July and September, which coincides with the flooding period of the Tarim River, whereas *T. ramosissima* produces seeds for a longer time period, from May to September. Both species produce tiny, wind- and water-dispersed seeds that germinate on moist sites newly created by floods, and thus they exploit the same riparian habitat for establishment. This habitat similarity provides an opportunity for interspecific competition, especially at the seedling stage: seedlings of whichever species grows more rapidly and first develops dense stands will most likely be the better competitor and suppress the other species. Thus, our studies focused on 3-year-old *P. euphratica* and *T. ramosissima* seedlings, 50 ± 5 cm in height, because seedlings at this stage are just entering a rapid growth stage, but neither species has developed dense stands (Figure 1).

In August 2005, seeds of each species were collected from a natural population established in the riparian zone of the Tarim River, and then sown in a nursery at the Aksu Water Balance Station, Chinese Academy of Sciences (40°27′N, 80°45′E, hereafter Aksu Station). Aksu Station is ~30 km north of the source of the Tarim River and is where experiments were conducted. On 24 March 2009, seedlings that met the above-mentioned size requirements were selected and transplanted into lysimeters designed for simulating hydrological conditions in riparian corridors.

Experimental design

To simulate hydrologic fluctuations in riparian habitats, we modified lysimeters that have been widely used in experimental studies of groundwater table effects on plants (Mueller et al. 2005). Each lysimeter was a 1.2 m tall × 0.3 m inner diameter PVC pipe that was closed at the bottom with a drain valve. When drain valves were open, water flowed freely out of lysimeters, and lysimeters lacked a water table. To impose water table treatments, the drain valve was closed and water was added to lysimeters through a 2 cm diameter tube that was inserted vertically just above the lysimeter bottom so that lysimeters could be watered from the bottom up. Bottoms of lysimeters were filled with a 10 cm layer of cobblestone <2 cm in diameter, which allowed the water table to rise evenly when watered. A discharge valve was installed at specific heights to control the water table within each lysimeter. The remainder of each lysimeter was filled with loamy (sand : silt : clay averaged 20 : 75 : 5) and loosely structured soil that was collected from the soil surface of a riparian site where both *P. euphratica* and *T. ramosissima* were present. We did not add any fertilizer to lysimeters because low nutrient availability typically occurs in Tarim riparian zones (Fan et al. 2005).

One seedling was transplanted into each lysimeter on 24 March 2009. To reduce transplant shock after transplanting and allow all seedlings a short period of establishment, soils in all lysimeters initially were well-watered. Each week, water was added from the soil surface until it flowed out through the open drain valve. On 4 July, we initiated experimental treatments by closing the drain valve, opening the discharge valve and manually watering through the irrigation tube to attain a range of hydrologic scenarios. Five hydrologic treatment scenarios were used: no groundwater table, soil inundation, and depth to groundwater (DGW) at deep (100 cm DGW), moderate (60 cm DGW) and shallow (20 cm DGW) groundwater conditions. Each hydrologic treatment had five replications per species, and an additional five alternates for each species were prepared in case of transplant failure. Thus, the total experimental design included 60 lysimeters: 2 species × 5 treatments × 5 replications + 10 alternates. Lysimeters were randomly placed in outdoor troughs at Aksu Station to keep them upright. Dried reeds were laid around the upper part of each lysimeter to protect it from sunlight and avoid over-heating. Although Aksu Station has an annual mean precipitation <50 mm, we used a rainfall shelter to exclude confounding effects of rainfall on the lysimeter hydrologic treatments.

During the treatment period, water addition occurred every afternoon (4–6 p.m. local time). For the inundation treatment, water depth above the soil surface within lysimeters

was kept >10 cm, varying from 10 to 12 cm as a result of evapotranspiration. For the no water table treatment, we simply stopped watering during the corresponding treatment period, which effectively led to a drought treatment in these lysimeters. The experiment ended and seedling biomass was harvested in early September, which was the end of the growing season when leaves of both species had begun to turn yellow in the field.

Data collection

Right before initiation of treatments on 4 July, pre-treatment measurements of aboveground and belowground biomass were obtained by destructive harvest of three randomly selected seedlings for each species from the 10 alternates. Soil in lysimeters was removed at 5-cm intervals to obtain roots layer by layer, and then fresh roots were scanned for calculation of root length density within the entire soil column in lysimeters. From treatment onset to 4 September, aboveground stem diameter and height of each seedling were documented every 10 days.

Assimilation rate–internal CO_2 concentration $(A - C_i)$ response was determined using an LI-6400 portable photosynthesis system (LI-COR Corp., Lincoln, NE, USA) with a 2 cm × 3 cm chamber equipped with a light source (6400-02B; LI-COR Corp.). Leaves measured were the youngest mature ones and were in full exposure to sunlight. Measurements were made between 10:00 and 14:00 h local time on clear days over a 25-day sampling period in August. During $A - C_i$ measurements, a CO_2 injecting tank was attached to the Li-Cor system to control cuvette CO_2 concentration (C_a), which was initially maintained at 200 µmol mol^{-1} for 5 min to stimulate stomatal opening. Then C_a was controlled at 50, 100, 200, 300, 400, 600, 800, 1000, 1200 and 2000 µmol mol^{-1}, and gas exchange properties were logged at each C_a until the system reached a stable point defined as coefficient of variation <1%. In-chamber photosynthetic photon flux density (PPFD) was maintained at light saturation that was previously determined by photosynthetic light-response curves of each species (2500 µmol m^{-1} s^{-1} for *P. euphratica* and 1800 µmol m^{-1} s^{-1} for *T. ramosissima*). Temperature and relative humidity within the cuvette were respectively controlled at 30 °C and 30%, which was similar to ambient conditions. Immediately after measurement, leaves within the cuvette were cut and then photographed with a 1.3 × 10^7 pixel digital camera (Canon 5D, Canon Inc., Tokyo, Japan), such that leaf area in the cuvette for each measurement could be calculated from these photographs using Image Pro Plus software (Media Cybernetics Inc., MD, USA). For cylindrical leaves of *T. ramosissima*, we calculated actual leaf surface area as the photographic projected area ×π/2, as Chen and Black (1992) suggested. $A - C_i$ response measurement was repeated on three or four individuals of each species under each treatment. The data were fitted

with non-linear least-squares regression to an exponential function $y = a(1-\exp^{-bx}) + c$, from which maximum photosynthetic rate (A_{max}) and carboxylation efficiency (CE) were calculated (Jacob et al. 1995).

Plant water status was determined by measuring predawn (ψ_{pd}) and midday (ψ_{md}) xylem water potentials (ψ) with a PMS Model 1000 (PMS Instrument Co., Albany, OR, USA) pressure chamber. ψ_{pd} and ψ_{md} were measured about half an hour before sunrise and at solar noon, respectively. Because suitable branches for water potential measurements were lacking at the beginning of the hydrologic treatments, we only measured plant water status twice (on 17 July and 30 August, i.e., ~2 and ~8 weeks after treatment initiation, respectively) during the treatments, and for each time, three replicates were taken for each species under each treatment.

At the end of the experiment, three seedlings of each species for each treatment were harvested to measure both aboveground and belowground biomass. For aboveground biomass, leaves and branches were separated, dried and weighed for the entire plant. In addition, fresh leaves from three randomly selected branches of each harvested seedling were gently extended onto a white board, and then photographed for determining total leaf surface area of each branch. Average specific leaf area (SLA) of each harvested seedling was obtained from the ratio of average leaf surface area to average dry biomass for each of the three randomly selected branches. The total leaf area (TLA) of each seedling was estimated as average SLA × total harvested leaf biomass. For belowground harvests, we first longitudinally cut the lysimeter wall, removed the wall and measured the depth at which roots were mainly developed. Then, the whole soil cylinder was soaked with water for a few hours to facilitate removal of whole root systems from the loamy soils with a spray nozzle. All biomass was dried in an oven at 65 °C for 72 h and then weighed.

Gravimetric soil water content was measured at the end of the experiment. Soil in each lysimeter, with the exception of inundation treatment, was sampled from soil surface to the experimental groundwater table (to 100 cm deep for drought treatment) at 10 cm depth increments.

Data analysis

Interspecific differences in root length density at each soil depth prior to treatment onset were determined by *t*-tests. Analysis of variance was used to determine sensitivity of physiological and morphological traits to hydrological scenarios. Plant growth was compared by two-way repeated-measures analysis of variance (ANOVA). A two-way ANOVA was applied to determine the species and treatment as well as their interaction effects on SLA, TLA, biomass A_{max}, CE and ψ. If a significant effect (defined as $P < 0.05$) occurred, then a least significant difference (LSD) post hoc test was used to deter-

mine which hydrological treatments differed for each species. All statistical tests and descriptive statistics were performed using SPSS 13.0 (SPSS Inc., Chicago, IL, USA).

Results

Root length distribution prior to treatment

Prior to the onset of treatment when seedlings of both species were well watered from the soil surface, root distribution within lysimeters differed between *P. euphratica* and *T. ramosissima* (Figure 2). Total root length density peaked at 35 cm depth for *P. euphratica*, compared with 20 cm for *T. ramosissima*. *Populus euphratica* had a greater rooting depth (80 vs. 60 cm) than its counterpart, and had significantly greater root length density in topsoil and below 30 cm. Total root length over the entire soil profile did not differ significantly between species (data not shown).

Soil water content distribution within lysimeters

At the end of the experiment, soil water profiles in lysimeters containing either with *P. euphratica* or with *T. ramosissima* differed significantly ($P < 0.05$, ANOVA) among hydrological treatments (Figure 3). Overall, soil water content at any one depth decreased with increasing DGW. However, soils close to the groundwater table for *P. euphratica* were wetter than those for *T. ramosissima* under 60 and 100 cm DGW.
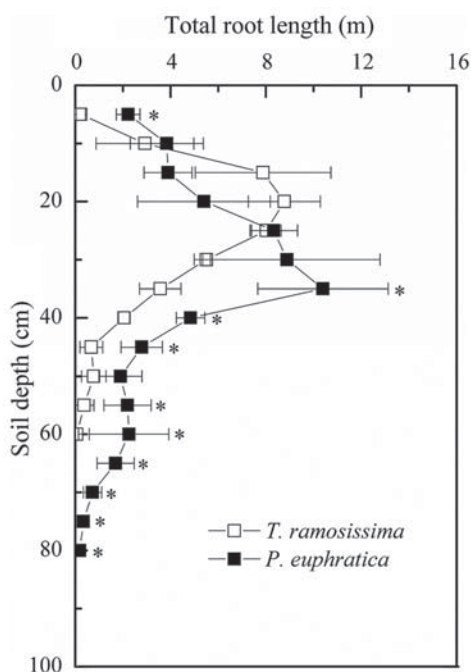
Figure 2. Total root length distributions of *P. euphratica* and *T. ramosissima* within lysimeter soil profiles, prior to the onset of treatment. Error bars represent the standard deviation of the mean of three measurements. An asterisk indicates a significant difference ($P < 0.05$; *t*-test) between species at corresponding soil depth.
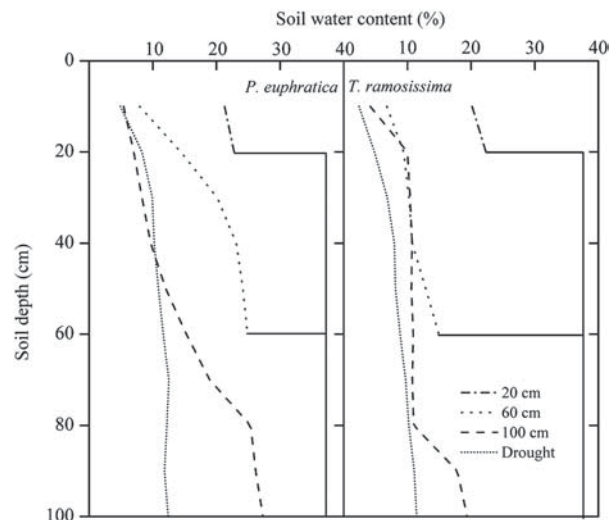
Figure 3. Soil water content within soil profiles in lysimeters ($N = 3$) grown with *P. euphratica* (left) and *T. ramosissima* (right) at the end of 60-day treatments with depth to groundwater at 20, 60 and 100 cm and without any groundwater (drought treatment). Solid line indicates that soils at the corresponding depths were water-saturated due to inundation (gravimetric saturated soil water content is 38–43% for the site where soil was collected).

Plant growth and biomass accumulation

Growth (Figure 4) and biomass accumulation (Tables 1 and 2) of *P. euphratica* and *T. ramosissima* seedlings significantly varied between species and among treatments. *Populus euphratica* seedlings grown under inundation conditions started to defoliate after ~20 days of treatment and then died one plant after another until all plants were dead at ~45 days. In contrast, *T. ramosissima* seedlings tolerated inundation and even showed a slight, persistent increase in height and diameter over the experiment. Our daily observations indicated that *T. ramosissima* seedlings developed vegetative roots above the soil surface after ~2 weeks of inundation, but *P. euphratica* did not. This ability by *T. ramosissima* to produce new roots may be partially responsible for the difference in survival under inundation between the two species.

Under shallow (20 cm DGW) and moderate (60 cm DGW) groundwater treatments, both species grew rapidly, achieving ~70 cm growth in height (>1 cm per day) during the 60-day experiment period. Although height and diameter growth of the two species were similar for these two DGW treatments (Figure 4), *T. ramosissima* seedlings had significantly greater aboveground and total biomass at the end of the experiment than *P. euphratica* (Table 2). Greater aboveground biomass for *T. ramosissima* was due in part to more new branch development. The greatest aboveground biomass accumulation rate approached 5 g day^{-1} for *T. ramosissima* at 60 cm DGW compared with 3 g day^{-1} for *P. euphratica* at 20 cm DGW.

The greatest difference between species occurred for the deep groundwater treatment (100 cm DGW), where
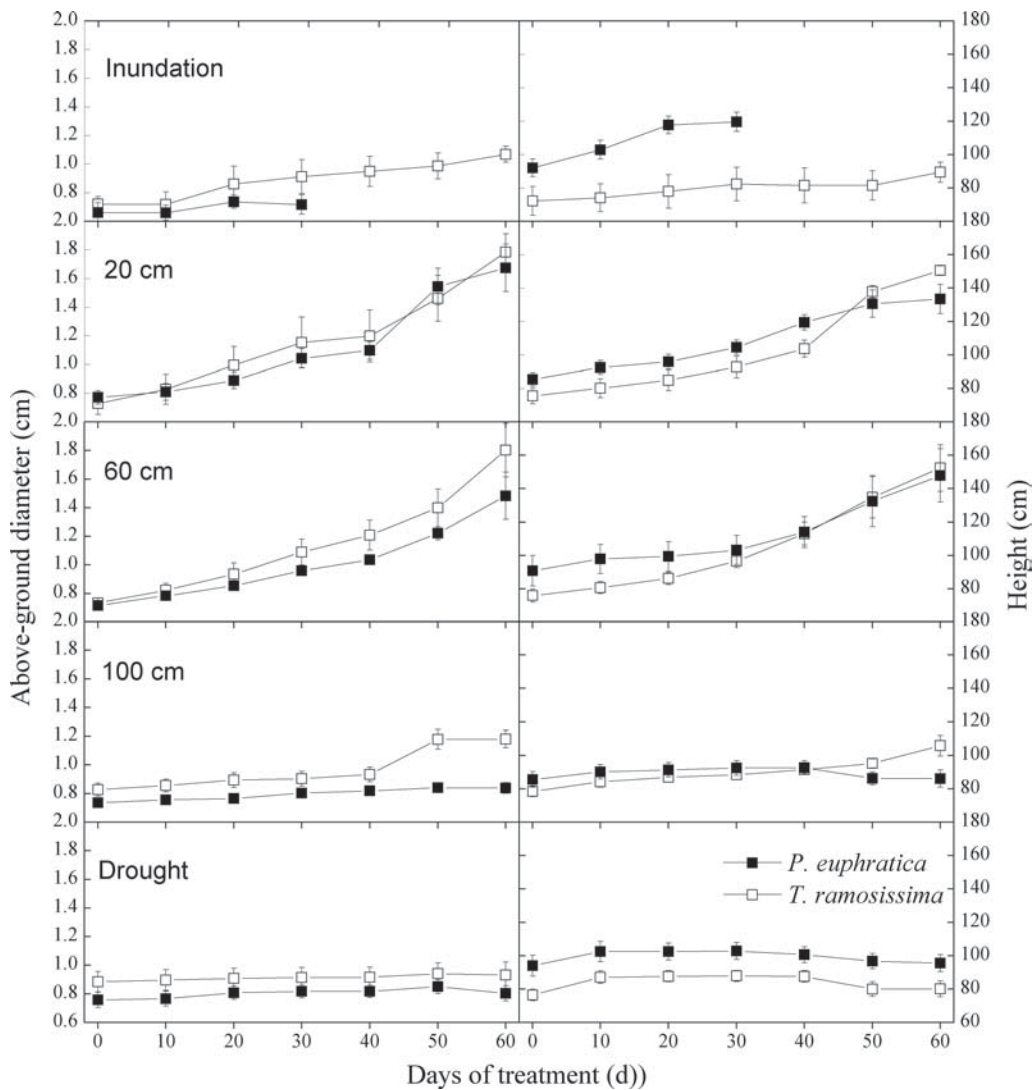
Figure 4. Change in shoot diameter and height during the experiment for *P. euphratica* (filled symbols) and *T. ramosissima* (open symbols) grown under inundation, 20, 60 and 100 cm DGW, and drought treatments. Error bars represent the standard deviation of the mean (*N* = 5).

T. ramosissima seedlings at the end of the experiment were about 7, 2 and 4 times greater in aboveground, belowground and total biomass, respectively, than *P. euphratica* (Table 2). Diameter and height growth (Figure 4) of *P. euphratica* seedlings for the 100 cm DGW treatment were nominal over the entire experiment, whereas *T. ramosissima* seedlings had an evident growth spurt during the last 20 days of the treatment period.

Tamarix ramosissima in the drought treatment also had significantly greater aboveground biomass accumulation than *P. euphratica* (Table 2). For both species, biomass measurements for the drought treatment were significantly lower than the other treatments. As with the 100 cm DGW treatment, diameter and height of *P. euphratica* grown in the drought treatments were relatively unchanged over the experiment (Figure 4).

Morphological traits

Seedlings also significantly varied in SLA and TLA between species and among treatments (Table 1). Specific leaf area of *P. euphratica* seedlings grown at moderate (60 cm) DGW was significantly greater than that at all other hydrological treatments (Figure 5), with SLA of the shallow (20 cm DGW) treatment intermediate and with the deep (100 cm DGW) and drought treatment lowest. *Tamarix ramosissima* seedlings grown at 60 cm DGW also had the greatest SLA, but in contrast to *P. euphratica*, SLA of *T. ramosissima* grown at 100 cm DGW was intermediate to those at shallow and moderate groundwater, and SLA of the drought treatment was significantly lower than all other treatments (Figure 5). Differences in TLA among treatments also differed between species. For *P. euphratica*, shallow and moderate groundwater treatments had significantly greater TLA than deep groundwater and

Table 1. Two-way ANOVA for growth, morphological and ecophysiological traits of *P. euphratica* and *T. ramosissima* grown under different hydrological treatments ($N = 3$). Biomass and leaf area (SLA, TLA) data collected at end of treatment period; leaf gas exchange data collected in August; water potential data (ψ_{pd} and ψ_{md}) were collected 2 times: early in the treatment (20 July) and near the end of the treatment (30 August).

Factor	Species		Hydrological treatment		Species × hydrological treatment	
	F	P	F	P	F	P
Aboveground biomass	21.1	<0.01	17.1	<0.01	2.7	0.08
Belowground biomass	3.9	0.06	20.7	<0.01	4.5	0.02
Total biomass	14.7	<0.01	18.5	<0.01	2.9	0.07
R/S ratio	44.7	<0.01	10.6	<0.01	3.9	0.03
SLA	33.6	<0.01	12.2	<0.01	4.1	0.03
TLA	24.2	<0.01	10.0	<0.01	2.8	0.07
ψ_{pd} on 20 July	35.4	<0.01	50.0	<0.01	16.2	<0.01
ψ_{md} on 20 July	25.5	<0.01	23.4	<0.01	3.3	0.04
ψ_{pd} on 20 August	166.2	<0.01	380.6	<0.01	127.1	<0.01
ψ_{md} on 20 August	112.9	<0.01	139.6	<0.01	57.2	<0.01
CE	38.9	<0.01	52.9	<0.01	4.0	0.01
A_{max}	12.9	<0.01	40.8	<0.01	2.1	0.13

SLA, specific leaf area; TLA, total leaf area; CE, carboxylation efficiency; A_{max}, maximum CO_2 assimilation rate; R/S, root/shoot ratio; ψ_{pd}, predawn xylem water potential; ψ_{md}, midday xylem water potential.

Table 2. Aboveground, belowground, total dry biomass and root/shoot ratio at the end of the experiment for *P. euphratica* and *T. ramosissima* seedlings grown under varying hydrological treatments.

	Inundation	20 cm	60 cm	100 cm	Drought
Aboveground biomass (g)					
P. euphratica	—	203.9 ± 92.4a	182.7 ± 117.4a	25.1 ± 6.7b	16.8 ± 4.1b
T. ramosissima	108.2 ± 20.4c	333.8 ± 56.9a	448.7 ± 157.4a	216.8 ± 26.5b	29.0 ± 1.3d
Belowground biomass (g)					
P. euphratica		141.4 ± 14.3a	153.5 ± 55.4a	50.4 ± 15.6b	23.0 ± 4.9c
T. ramosissima	13.6 ± 2.8c	96.9 ± 37.4b	231.3 ± 79.7a	144.2 ± 15.6ab	19.0 ± 4.2c
Total biomass (g)					
P. euphratica	—	345.3 ± 106.6a	336.2 ± 172.6a	75.4 ± 18.1b	39.8 ± 8.9c
T. ramosissima	121.7 ± 23.2c	430.8 ± 94.3ab	680.0 ± 236.3a	360.9 ± 12.4b	48.1 ± 4.7d
Root/shoot ratio					
P. euphratica	—	0.78 ± 0.29b	0.94 ± 0.22b	2.07 ± 0.65a	1.38 ± 0.09a
T. ramosissima	0.13 ± 0.01c	0.28 ± 0.07b	0.52 ± 0.04a	0.68 ± 0.17a	0.66 ± 0.14a

Values are mean ± SE of three measurements. Different letters indicate significant differences between treatments for each species determined by an LSD post hoc test ($P < 0.05$) after significant treatment effects were determined with a two-way ANOVA.

drought treatments, whereas all three groundwater treatments for *T. ramosissima* were not significantly different from each other but significantly greater than the drought treatment. Furthermore, *T. ramosissima* had greater TLA than *P. euphratica*, especially in the 100 cm DGW treatment (Figure 5).

Rooting depth of *P. euphratica* and *T. ramosissima* seedlings exhibited high plasticity across treatments (Figure 6). Root systems of plants grown under the drought treatments were less developed than other treatments, with roots of *P. euphratica* extending deeper than *T. ramosissima* (compare 'a' in Figure 6a and b) and producing greater biomass (Table 2). An important phenomenon was that root systems of *P. euphratica* seedlings did not reach the groundwater in the 100 cm DGW treatment.

In comparison, *T. ramosissima* seedlings rooted >1 m in depth in the 60 and 100 cm DGW treatments (Figure 6), reaching the cobble layer in the lysimeters. Root biomass of *T. ramosissima* was greater than that of *P. euphratica* for these two treatments (Table 2). At 20 cm DGW, both species had shallow rooting depth with most of their absorbing roots distributed just above the controlled DGW (Figure 6).

The root/shoot ratio was affected by species and treatments as well as their interaction (Table 1). Root/shoot ratios of both species tended to increase with increasing DGW, with highest values in the 100 cm DGW treatment (Table 2). Root/shoot ratios of *P. euphratica* were usually more than twice those of *T. ramosissima*, especially for 100 cm DGW treatment where

ratios of *P. euphratica* seedlings exceeded 2.0 because below-ground biomass increased to a greater extent than above-ground biomass.

Physiological traits

Pre-dawn (ψ_{pd}) and midday (ψ_{md}) xylem water potentials on both sampling dates were significantly affected by species and hydrological treatments as well as their interaction (Table 1). On 20 July (16 days after the onset of hydrological treatments), ψ_{pd} of *P. euphratica* grown in deep groundwater and drought treatments was significantly lower than that grown in inundation, shallow and moderate groundwater treatments (Figure 7).

ψ_{md} showed a similar pattern, but with no significant difference detected among seedlings grown in shallow, moderate and deep groundwater. Similarly, both ψ_{pd} and ψ_{md} of *T. ramosissima* seedlings grown in deep groundwater and drought treatments were lower than those in inundation, shallow and moderate groundwater treatments (Figure 7). On 30 August, both ψ_{pd} and ψ_{md} of *P. euphratica* seedlings grown in deep groundwater and drought treatments were significantly lower than those grown in shallow and moderate groundwater. For *T. ramosissima*, both ψ_{pd} and ψ_{md} of seedlings grown in varying groundwater treatments were similar and significantly higher than those in the drought treatment (Figure 7).

The main effects of species and treatments were significant for CE and A_{max}, along with the species × treatment effect for CE (Table 1). Carboxylation efficiency in *P. euphratica* seedlings grown in the 100 cm DGW treatment was reduced by ~25% compared with those grown in 20 and 60 cm DGW treatments but was ~3 times higher than that of the drought treatment (Figure 8). A_{max} of *P. euphratica* seedlings showed a different pattern among treatments, with the greatest value in the 100 cm DGW treatment. For *T. ramosissima*, CE and A_{max} showed similar patterns among treatments: they were not significantly different among 20, 60 and 100 cm DGW treatments, but these three treatments had significantly ($P < 0.05$) greater values than inundation and drought treatments (Figure 8).

Discussion

Populus euphratica and *T. ramosissima* seedlings varied greatly in growth, in biomass accumulation and allocation, and in morphological and physiological traits in response to simulated groundwater scenarios. It should be noted that the lysimeter that we used has been criticized for overestimating water use by plants (Shafroth et al. 2005); here it is appropriate since we did not focus on water use. Our experiment was designed to simulate the range of hydrological conditions that *P. euphratica* and *T. ramosissima* seedlings are likely to experience along the Tarim River as well as within most other riparian ecosystems,
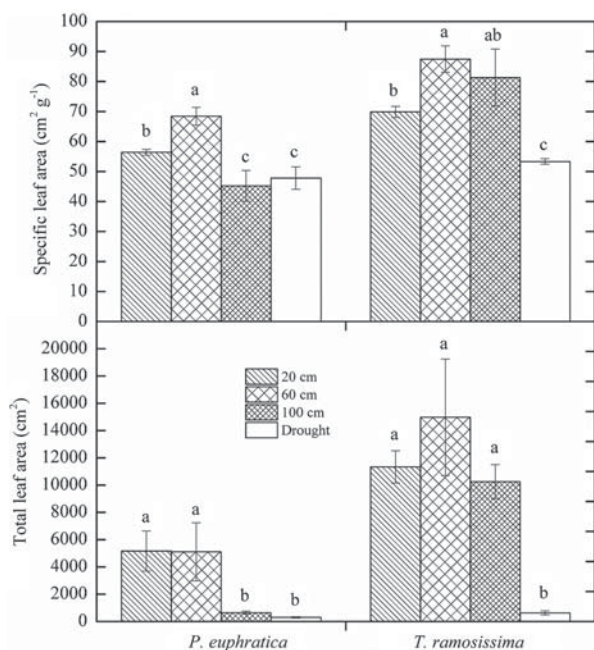

Figure 5. Specific leaf area and TLA at the end of the experiment for *P. euphratica* and *T. ramosissima* seedlings grown in 20, 60 and 100 cm DGW and drought treatments. Letters indicate significant differences among treatments for each species determined by an LSD post hoc test ($N = 3$, $P < 0.05$) after significant treatment effects were determined with a two-way ANOVA.
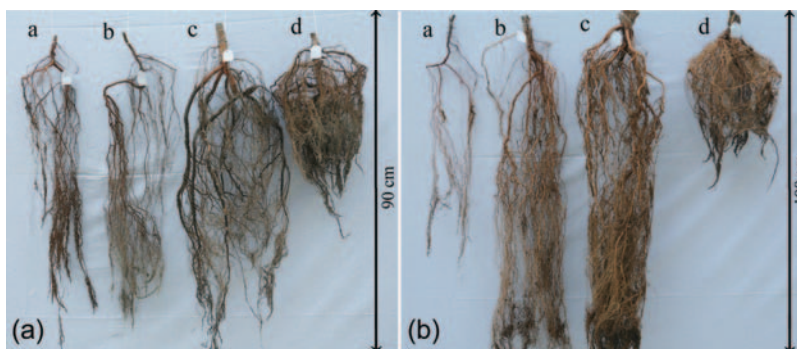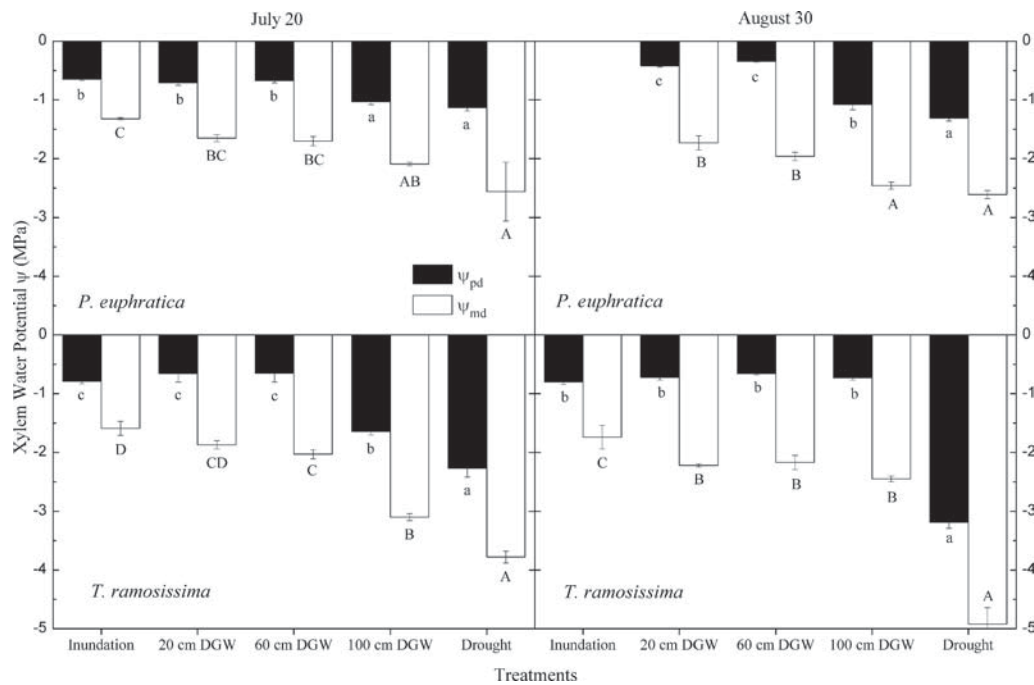

Figure 6. Whole root systems of *P. euphratica* (a) and *T. ramosissima* (b) grown in drought (a), 100 (b), 60 (c) and 20 (d) cm DGW hydrological treatments.

Figure 7. Predawn (ψ_{pd}) and midday (ψ_{md}) xylem water potential for *P. euphratica* and *T. ramosissima* seedlings grown under different hydrological treatments. Data were collected 2 times: early in the treatment (20 July) and near the end of the treatment (30 August). Values are mean ± 1 SE ($N = 3$). Lowercase and capital letters indicate significant ($P < 0.05$) differences for ψ_{pd} and ψ_{md}, respectively, between treatments within each panel by an LSD post hoc test after significant species and treatment effects were determined with a two-way ANOVA.
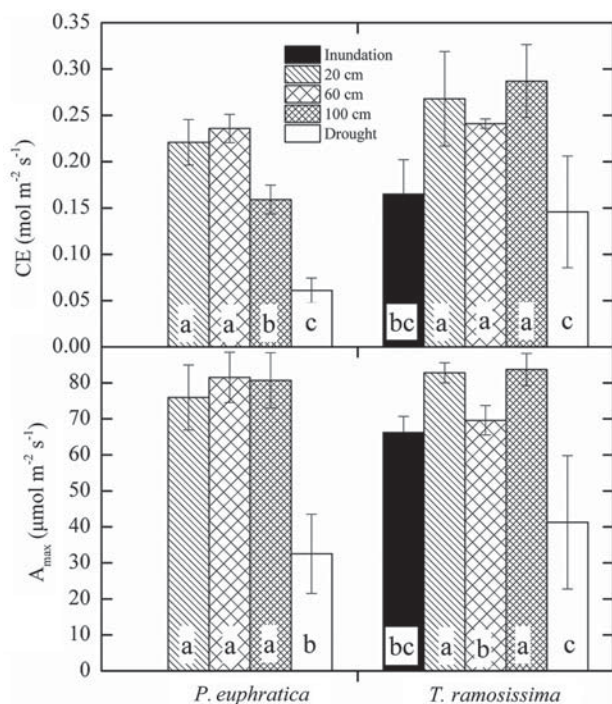

Figure 8. Carboxylation efficiency and maximum CO_2 assimilation rate (A_{max}) of *P. euphratica* and *T. ramosissima* grown under different hydrological treatments. Letters indicate significant differences among treatments for each species determined by an LSD post hoc test ($N = 3$ or 4, $P < 0.05$) after significant treatment effects were determined with a two-way ANOVA.

i.e., between the extremes of drought (no additional water input) and inundation as well as to various DGWs where the groundwater table is above, near or below the rooting depth of the seedlings prior to treatments (Figure 2). Our focus was not the first stage in vegetation recolonization of flood plains, i.e., how seeds germinate and seedlings initially grow, but rather the second stage, i.e., how established seedlings respond to subsequent alterations in hydrological conditions.

During the short duration (60 days) of the experimental treatments, both species grew rapidly under shallow (20 cm) and moderate (60 cm) groundwater treatments, but *T. ramosissima* had greater aboveground biomass accumulation. Especially under the deep (100 cm) groundwater treatment, *T. ramosissima* performed better than *P. euphratica*, as evidenced by all of the ecophysiological traits we measured. Furthermore, *T. ramosissima* was much more tolerant of extreme hydrological conditions (e.g., drought and inundation) than *P. euphratica*. Therefore, whereas we accept our first hypothesis that *P. euphratica* and *T. ramosissima* adapt to groundwater fluctuations in different ways, we reject our second hypothesis that *P. euphratica* has distinct growth advantages over *T. ramosissima*.

Rapid growth is a life-history trait widely observed for riparian species (Lytle and Poff 2004, Corenblit et al. 2009). Our data show that seedlings of both species can grow ~1 m (from 0.5 to 1.5 m) in height in one season. However, rapid growth occurs only under favorable hydrological conditions when

groundwater table is maintained near the rooting depth of growing seedlings. When groundwater is not available, as shown in the drought treatment, both species show little growth, reduced shoot elongation, leaf senescence, reduced leaf area and poor ecophysiological performance such as reduced photosynthesis and ψ, similar to the results from fields that riparian plants exhibit poor ecophysiological performances in response to groundwater decline (Scott et al. 1999, Horton and Clark 2001, Amlin and Rood 2003, Chen et al. 2011).

As with many riparian trees, P. euphratica and T. ramosissima are phreatophytic and rely heavily on groundwater (Busch and Smith 1995, Shafroth et al. 1998, Horton and Clark 2001), and access to groundwater is important for riparian tree growth (Stromberg and Patten 1990). In the short duration of our experiment, T. ramosissima seedlings reached groundwater in the 100 cm DGW treatment (Figure 6) whereas P. euphratica did not, even though T. ramosissima was relatively shallow rooted at the start of the experimental treatments (Figure 2). This result provides evidence that T. ramosissima is able to reach groundwater more rapidly than P. euphratica when the groundwater table declines below their initial rooting depths, evidence that is consistent with faster root elongation of Tamarix in response to declining groundwater reported by Horton and Clark (2001). Cottonwood seedlings also show the ability to increase root elongation when groundwater declines gradually, but similar to the 100 cm DGW P. euphratica, they exhibit reduced growth as a result from drought stress when an abrupt groundwater decline occurs because the rate of moisture zone decline is more rapid than the rate of root elongation (Rood et al. 2000). Tamarix is known to be a facultative phreatophyte that is able both to use groundwater and associated capillary fringe and to extract water from unsaturated soils (Everitt 1980, Busch and Smith 1995). Lower soil water content close to the groundwater table for 60 and 100 cm DGW lysimeters grown with T. ramosissima (Figure 3) also suggests that T. ramosissima extracted more soil water from soils. This attribute may help T. ramosissima access rapidly declining groundwater and may be a possible reason for field observations that Tamarix becomes more abundant with increasing DGW (Zhu et al. 2011). The rapid response of T. ramosissima root systems to decreased groundwater availability also may contribute to its invasive success in riparian ecosystems of the southwest USA, where natural flow regimes were intensively altered over the 20th century (Cleverly et al. 1997, Merritt and Poff 2010). These altered flow regimes coincided with the rapid invasion of Tamarix (Friedman et al. 2005), and Tamarix has the highest dominance along rivers with the most altered flow regimes (Merritt and Poff 2010). In terms of relative dominance between P. euphratica and T. ramosissima along the Tarim River, rapid response of T. ramosissima to declined groundwater may improve its advantage over P. euphratica, given the groundwater decline along the Tarim River in recent decades (Chen et al. 2006).

Ecophysiological characteristics of riparian plants are often studied along gradients of DGW (Rood et al. 2003, Hao et al. 2010, Chen et al. 2011) or between dry and wet seasons (Horton et al. 2001a, 2001b) to understand DGW thresholds for riparian vegetation. Our data provide evidence that the ecophysiological performances of riparian plants are dependent upon the context of groundwater fluctuations and the rapidness of plant response to altered groundwater tables. For example, both P. euphratica and T. ramosissima showed decreased ψ soon after DGW was decreased to 100 cm (July 20), but ψ of T. ramosissima recovered to those at shallower groundwater by the end of the experiment (30 August) whereas P. euphratica did not (Figure 7). Lower ψ of T. ramosissima than P. euphratica under drought condition is similar to the pattern where Tamarix has lower ψ_{pd} than native Populus competitors in dry years (Horton et al. 2001a) or at greater DGW (Gries et al. 2003). These results suggest that Tamarix is more drought tolerant than Populus and better able to extract water from relatively dry soils. The flexible rooting ability of Tamarix could also explain why Tamarix shows reduced gas exchange at 3 m DGW (Horton et al. 2001a) whereas it is still vigorous at 7–8 m DGW (Stromberg 1998): previously shallow-rooted riparian plants can exhibit weak ecophysiological performance even at a relatively shallow groundwater condition (e.g., 3 m DGW), but if given sufficient time to grow deep roots under deep DGW (e.g., 7–8 m DGW), they can appear vigorous under those deep DGW conditions.

The monoculture in our experiment limits our understanding of interspecific interaction between P. euphratica and T. ramosissima. However, our results raise an interesting question: how can P. euphratica currently be the dominant species in Tarim River riparian forests if T. ramosissima consistently grew more and adapted better to hydrological fluctuations? In all treatments, P. euphratica had greater root/shoot ratios than T. ramosissima especially in the 100 cm DGW treatment. In the 100 cm DGW treatment, aboveground biomass of P. euphratica seedlings hardly increased while root biomass doubled during the experiment (Table 2), suggesting that a large proportion of photosynthetic end products were allocated belowground. This allocation strategy, at the cost of possible reduction of aboveground biomass (Barrat-Segretain 2001, Karrenberg et al. 2002), may be an adaption to variable riparian habitats: plants often lose part of their aboveground biomass during floods and droughts (Usherwood et al. 1997), whereas allocation to root biomass enhances resprouting ability during favorable times (Barrat-Segretain 2001). Greater allocation to root systems also may increase the ability of P. euphratica to absorb limited soil resources such as N and other nutrients. However, optimal allocation might be determined by magnitude and frequency of flow events (Lytle and Poff 2004) that control fluctuations of water environment in riparian zones. Assuming that current dominance of P. euphratica along the Tarim River benefitted

from its biomass allocation strategy that evolved during historical hydrological regimes, more recent hydrological regimes marked by reductions in both magnitude and frequency of flooding (Chen et al. 2003) may facilitate *T. ramosissima* more than *P. euphratica*, causing a possible shift in future dominance to *T. ramosissima* at newly developed point bars along the Tarim River. Thus, to understand the current dominance of *P. euphratica* in Tarim River riparian forests is worthy of further work, on the one hand, on the benefits of biomass allocation and competitive effects between *P. euphratica* and *T. ramosissima* in relation to varying hydrological conditions, and on the other hand, on the long-term field observation of seedling communities with similar abundance of *P. euphratica* and *T. ramosissima* under given hydrological conditions.

Conclusions

Our study showed that ecophysiology of *T. ramosissima* responds more rapidly than that of *P. euphratica* to altered groundwater availability, either increased or decreased. Thus, we predict that increased dominance of *Tamarix* might occur along the riparian corridor of the Tarim River where hydrological conditions have been altered intensively over the past few decades. Further research should focus on the importance of biomass allocation strategy and interspecific interactions relative to water environment fluctuations in riparian zones that result from flow regime changes.

Acknowledgments

We would like to thank Yong Zhang, Shaoyong Jiang, Bin Huang, Heng Wei, Xun Cao, Peng Wang and Xiaojuan Sun for their assistance during the experiments.

Conflict of interest

None declared.

Funding

References

Amlin NM, Rood SB (2003) Drought stress and recovery of riparian cottonwoods due to water table alteration along Willow Creek, Alberta. Trees 17:351–358.

Barrat-Segretain MH (2001) Biomass allocation in three macrophyte species in relation to the disturbance level of their habitat. Freshw Biol 46:935–945.

Bhattacharjee J, Taylor JP, Smith LM, Haukos DA (2009) Seedling competition between native cottonwood and exotic saltcedar: implications for restoration. Biol Invasions 11:1777–1787.

Blom C (1999) Adaptations to flooding stress: from plant community to molecule. Plant Biol 1:261–273.

Busch DE, Smith SD (1995) Mechanisms associated with decline of woody species in riparian ecosystems of the Southwestern US. Ecol Monogr 65:347–370.

Busch DE, Ingraham NL, Smith SD (1992) Water uptake in riparian phreatophytes of the southwestern United States: a stable isotope study. Ecol Appl 2:450–459.

Chen JM, Black TA (1992) Defining leaf area index for non-flat leaves. Plant Cell Environ 15:421–429.

Chen Y, Cui W, Li W, Chen Y, Zhang H (2003) Utilization of water resources and ecological protection in the Tarim River. Acta Geogr Sin 58:215–222.

Chen Y, Chen Y, Xu C, Li W (2011) Photosynthesis and water use efficiency of *Populus euphratica* in response to changing groundwater depth and CO$_2$ concentration. Environ Earth Sci 62:119–125.

Chen YN, Zilliacus H, Li WH, Zhang HF, Chen YP (2006) Groundwater level affects plant species diversity along the lower reaches of the Tarim River, Western China. J Arid Environ 66:231–246.

Cleverly J, Smith S, Sala A, Devitt D (1997) Invasive capacity of *Tamarix ramosissima* in a Mohave Desert floodplain: the role of drought. Oecologia 111:12–18.

Corenblit D, Steiger J, Gurnell AM, Naiman RJ (2009) Plants intertwine fluvial landform dynamics with ecological succession and natural selection: a niche construction perspective for riparian systems. Glob Ecol Biogeogr 18:507–520.

DiTomaso J (1998) Impact, biology, and ecology of saltcedar (*Tamarix* spp.) in the southwestern United States. Weed Technol 12:326–336.

Everitt BL (1980) Ecology of saltcedar—a plea for research. Environ Geol 3:77–84.

Fan J, Liu M, Gao J, Kou J (2005) Preliminary study on soil nutrients, microorganisms and enzyme activities of characteristic fruit tree and *Populus euphratica* stands in upriver of Tarim river. Chin Agric Sci Bull 21:184–187.

Friedman JM, Lee VJ (2002) Extreme floods, channel change, and riparian forests along ephemeral streams. Ecol Monogr 72:409–425.

Friedman JM, Auble GT, Shafroth PB, Scott ML, Merigliano MF, Freehling MD, Griffin ER (2005) Dominance of nonnative riparian trees in western USA. Biol Invasions 7:747–751.

Gladwin DN, Roelle JE (1998) Survival of plains cottonwood (*Populus deltoides* subsp. *monilifera*) and saltcedar (*Tamarix ramosissima*) seedlings in response to flooding. Wetlands 18:669–674.

Glenn EP, Nagler PL (2005) Comparative ecophysiology of *Tamarix ramosissima* and native trees in western U.S. riparian zones. J Arid Environ 61:419–446.

Glenn E, Tanner R, Mendez S, Kehret T, Moore D, Garcia J, Valdes C (1998) Growth rates, salt tolerance, and water use characteristics of native and invasive riparian plants from the delta of the Colorado River, Mexico. J Arid Environ 40:281–294.

Gries D, Zeng F, Arndt SK, Bruelheide H, Thomas FM, Zhang X, Runge M (2003) Growth and water relations of *Tamarix ramosissima* and *Populus euphratica* on Taklamakan desert dunes in relation to depth to a permanent water table. Plant Cell Environ 26:725–736.

Han L, Wang HZ, Li ZJ (2007) Population structure and demography of *Populus euphratica* in upper and middle reaches of Tarim River. Acta Ecol Sin 27:1315–1322.

Hao X, Li W, Huang X, Zhu C, Ma J (2010) Assessment of the ground-water threshold of desert riparian forest vegetation along the middle and lower reaches of the Tarim River, China. Hydrol Process 24:178–186.

Horton JL, Clark JL (2001) Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings. For Ecol Manage 140:239–247.

Horton JL, Kolb TE, Hart SC (2001*a*) Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. Plant Cell Environ 24:293–304.

Horton JL, Kolb TE, Hart SC (2001*b*) Leaf gas exchange characteristics differ among Sonoran Desert riparian tree species. Tree Physiol 21:233–241.

Hutchinson GE (1961) The paradox of the plankton. Am Nat 95:137–145.

Jacob J, Greitner C, Drake DG (1995) Acclimation of photosynthesis in relation to Rubisco and non-structural carbohydrate contents and in situ carboxylase activity in *Scirpus olneyi* grown at elevated CO_2 in the field. Plant Cell Environ 18:875–884.

Karrenberg S, Edwards PJ, Kollmann J (2002) The life history of Salicaceae living in the active zone of floodplains. Freshw Biol 47:733–748.

Lytle DA, Poff NL (2004) Adaptation to natural flow regimes. Trends Ecol Evol 19:94–100.

Merritt DM, Poff NL (2010) Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers. Ecol Appl 20:135–152.

Merritt DM, Scott ML, Poff NL, Auble GT, Lytle DA (2010) Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. Freshw Biol 55:206–255.

Mueller L, Behrendt A, Schalitz G, Schindler U (2005) Above ground biomass and water use efficiency of crops at shallow water tables in a temperate climate. Agric Water Manage 75:117–136.

Naiman RJ, Décamps H (1997) The ecology of interfaces: riparian zones. Annu Rev Ecol Syst 28:621–658.

Norden N, Chave J, Caubère A, Châtelet P, Ferroni N, Forget PM, Thébaud C (2007) Is temporal variation of seedling communities determined by environment or by seed arrival? A test in a neotropical forest. J Ecol 95:507–516.

Pockman W, Sperry J (2000) Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. Am J Bot 87:1287–1299.

Poff NL, Allan JD, Bain MB, Darr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime: a paradigm for river conservation and restoration. BioScience 47:769–784.

Rood SB, Zanewich K, Stefura C, Mahoney JM (2000) Influence of water table decline on growth allocation and endogenous gibberellins in black cottonwood. Tree Physiol 20:831–836.

Rood SB, Braatne JF, Hughes FMR (2003) Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. Tree Physiol 23:1113–1124.

Scott ML, Auble GT, Friedman JM (1997) Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. Ecol Appl 7:677–690.

Scott ML, Shafroth PB, Auble GT (1999) Responses of riparian cottonwoods to alluvial water table declines. Environ Manage 23:347–358.

Shafroth PB, Auble GT, Stromberg JC, Pattern DT (1998) Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. Wetlands 18:577–590.

Shafroth PB, Cleverly JR, Dudley TL, Taylor JP, van Riper C III, Weeks EP, Stuart JN (2005) Control of *Tamarix* in the Western United States: Implications for water salvage, wildlife use, and riparian restoration. Environ Manage 35:231–246.

Sher AA, Marshall D (2003) Seedling competition between native *Populus deltoides* (Salicaceae) and exotic *Tamarix ramosissima* (Tamaricaceae) across water regimes and substrate types. Am J Bot 90:413–422.

Sher AA, Marshall D, Gilbert SA (2000) Competition between native Populus deltoides and invasive *Tamarix ramosissima* and the implications for reestablishing flooding disturbance. Conserv Biol 14:1744–1754.

Sher AA, Marshall D, Taylor J (2002) Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. Ecol Appl 12:760–772.

Smith S, Detitt D, Sala A, Cleverly J, Busch D (1998) Water relations of riparian plants from warm desert regions. Wetlands 18:687–696.

Stromberg J (1998) Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. J Arid Environ 40:133–155.

Stromberg JC, Patten DT (1990) Riparian vegetation instream flow requirements: a case study from a diverted stream in the eastern Sierra Nevada, California, USA. Environ Manage 14:185–194.

Stromberg JC, Tluczek MGF, Hazelton AF, Ajami H (2010) A century of riparian forest expansion following extreme disturbance: spatiotemporal change in *Populus/Salix/Tamarix* forests along the Upper San Pedro River, Arizona, USA. For Ecol Manage 259:1181–1189.

Usherwood JR, Ennos AE, Ball DJ (1997) Mechanical and anatomical adaptations in terrestrial and aquatic buttercups to their respective environments. J Exp Bot 48:1469–1475.

Vandersande MW, Glenn EP, Walworth JL (2001) Tolerance of five riparian plants from the lower Colorado River to salinity drought and inundation. J Arid Environ 49:147–159.

Zhang YM, Chen YN, Pan BR (2005) Distribution and floristics of desert plant communities in the lower reaches of Tarim River, southern Xinjiang, People's Republic of China. J Arid Environ 63:772–784.

Zhao FX, Yin LK (2005) Spatial distribution pattern and interspecific association of *Populus euphratica* and *Tamarix ramosissima* seedlings populations along desert inland river. Chin J Ecol 26:972–977.

Zhu JT, Yu JJ, Wang P, Wang ZY (2011) Quantitative classification and analysis of relationships between plant communities and their groundwater environment in the Ejin Desert Oasis of China. Chin J Ecol 35:480–489.