Changes of xylem hydraulic efficiency and native embolism of *Tamarix ramosissima* Ledeb. seedlings under different drought stress conditions and after rewatering

M. Ayup, X. Hao, Y. Chen*, W. Li, R. Su

Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China
State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China

Received 28 January 2011; received in revised form 28 April 2011; accepted 11 May 2011

**Abstract**

To understand the factors controlling the survival of native *Tamarix ramosissima* Ledeb. in an extreme drought zone, the Tarim River Basin in northwestern China, we studied the impact of drought stress and water recovery treatments on hydraulic traits. These traits included initial hydraulic specific conductivity (Ks (init)), maximum hydraulic specific conductivity (Ks (max)) and native embolism (PLC, %) of lateral root, main stem and twigs, as well as the xylem anatomical structures of lateral roots and twigs of two-year old *T. ramosissima* seedlings. Results showed that drought stress and water recovery treatments had significant impacts on Ks (max) value of lateral root, Ks (init) value and native embolism rate of all different organs (p<0.01). Severely drought stress treatment induced a significant decrease in Ks (init) values of all organs (p<0.05), however, the values of Ks (max) in lateral root increased significantly (p<0.01). The native embolism rate increased with the intensity of soil drought stress in all different organ and short-term re-watering had only significant impacts on embolism recovery for lateral roots (p<0.01), embolism recovered 20% as compared to severely water stressed seedlings. Lateral roots had a larger mean vessel diameter (d mean, d h) and lower vessel density (VD) compared to the twigs, and their Ks (max) values were strongly correlated with xylem vessel diameter.

© 2011 SAAB. Published by Elsevier B.V. All rights reserved.

**Keywords:** Drought resistance; Native embolism; Xylem anatomy; Xylem hydraulic conductivity

1. Introduction

The impact of drought on the hydraulic traits of plants has drawn increasing attention. According to the cohesion–tension theory (Tyree, 1997; Steudle, 2001), water moves through the xylem under tension (negative pressure) during transpiration. Therefore, rapid transpiration during the drought season increases the risk of xylem cavitation. Cavitation is the abrupt change of water from liquid form to vapor under tension (Cruiziat et al., 2002). Once a conduit cavitates, it becomes air-blocked and is no longer available for water transport (Tyree and Sperry, 1989; Zimmermann, 1983).

Plant responses to drought are species specific, and depend on the plants’ hydraulic strategy (Breda et al., 2006; Awad et al., 2010). Research has demonstrated that plants can adjust their xylem hydraulic traits of withstanding seasonal drought or acclimatize to drought stress conditions through developing more resistant xylem to drought induced cavitation (Hacke et al., 2000; Ladjal et al., 2005; Stiller, 2009; Beikircher and Mayr, 2009; Awad et al., 2010), reducing root hydraulic conductance (KRL, kg s⁻¹ m⁻² MPa⁻¹) (Triflo et al., 2004), maintaining high hydraulic efficiency in stems and roots (Nardini and Pitt, 1999), and also by increasing whole plant leaf specific conductivity (KL .Pl, mmol m⁻² s⁻¹ MPa⁻¹) (Cinnirella et al., 2002; Shumway et al., 1991).

*Tamarix ramosissima* Ledeb. is one of the dominant desert phreatophyte shrub species native to the Tarim River Basin in northwestern China. Tamarix species and their hybrids are known collectively as saltcedar (Devitt et al., 1997; Lesica and DeLuca, 1994).
In its native range, T. ramosissima maintains a wide distribution across the range of Eurasia (Baum, 1978; Sexton et al., 2002). T. ramosissima provides remarkable ecological and economic benefits to arid areas in northwestern China, and is also an aggressive alien plant in riparian ecosystems of the southwestern United States. Therefore, many researchers have tried to identify traits that aid in its drought resistance as well as its strong invasive ability (Sexton et al., 2002; Gries et al., 2003; Pratt and Black, 2006; Devitt et al., 1997; Bruelheide et al., 2010; Johnson et al., 2010).

Most studies have focused on the effects of groundwater depth on the performance of T. ramosissima (Gries et al., 2003; Bruelheide et al., 2010; Vonlanthen et al., 2010). Recently, Pockman and Sperry (2000) and Pratt and Black (2006) studied the stem xylem hydraulic traits of T. ramosissima in the Sonoran desert and west-central Idaho. However, their studies focused solely on stems. Xylem water transport capacity of the whole plant under different drought stress conditions has not yet been examined.

In this study, the response of T. ramosissima seedlings to short-term drought stress and water recovery treatment and how hydraulic and native embolism differ in different organs, including lateral root, main stem and twigs were studied in the Tarim River Basin in northwestern China. The xylem anatomical structure of lateral roots and twigs and the relationship with hydraulic conductivity were discussed. The aim of this study was to determine how hydraulic efficiency and native embolism are different between various organs and affected by short-term drought stress.

2. Material and methods

2.1. Study sites and plant material

The study was carried out at in situ ecological observation station on the lower reaches of the Tarim River, between the Taklamakan and the Kuruke deserts in northwestern China. The climatic conditions are extremely arid with an average annual precipitation between 17 and 42 mm, potential annual evaporation of 2500 and 3000 mm, and average diurnal temperature ranging from 13 to 17 ºC. Thirty, 2-year old seedlings of Tamarix ramosissima Ledeb. were collected from a natural stand along the bank of the Tarim River, southern Xinjiang, China, in March 2010. Seedlings were carefully excavated to limit damage to the root system and planted in cylindrical PVC plastic pipes (height=0.8 m, diameter=0.3 m) and filled with natural soil on delivery to the in situ station. The seedlings were cultivated to PVC pipe outside at the in situ station on 15th of March, 2010 and allowed to recover from transplanting until to 17th of July, 2010 before the water treatment experiment was begun. Irrigation was provided once a week via full irrigation in order to maintain moisture levels close to field capacity throughout the cultivation period.

2.2. Water treatment experiment

Water treatment began on July 17, 2010. The thirty seedlings were divided into five sets of six seedlings and subjected to five different water regimes. The first set of seedlings was used as a control (T0), and was maintained with optimal moisture levels, i.e. 70–100% of field capacity (FC) throughout the water treatment period. The second set of seedlings was moderately water stressed (T1), where FC was maintained within 40–60%. The third set of seedlings was severely water stressed (T2), where FC was maintained within 20–40%. This set of seedlings was not irrigated throughout the water treatment period (after 17–19 days without irrigation, more than half of leaves turned yellow).

The fourth set of seedlings was re-watered after being moderately water stressed (T1R). Initially, water treatment maintained FC at the same level as T1 seedlings (10 days of stress treatment), then the seedlings were rewatered (10–13 days of full watering before measurement) and maintained close to FC 70–100%. The fifth set of seedlings was re-watered after being severely water stressed (T2R). Initially, water treatment maintained FC at the same level as T2 seedlings, and then the seedlings were fully irrigated (18–25 days of full watering before measurement) and maintained close to FC 70–100%. Volumetric water content of the surface soil (0–10 cm) was checked using a soil moisture meter (HH2 Moisture Meter, US) every morning throughout the water treatment period, and then samples were watered depending on their assigned watering regime. Due to the climatic conditions (extremely dry climate with high evaporative demand, annual precipitation is less then 50 mm) of study area, the growth status of seedlings (leaf color) and the amount of water we irrigated were also considered while maintaining the ideal water conditions of seedlings.

T0, T1, T2 seedlings hydraulic traits were began to measure after 10 days of water treatment (on 27th of July). Because measuring plants hydraulic conductivity is a time-consuming task, only two seedlings in the same treatment group were harvested on each measuring day and each treatment group was processed into three days, which means, T1 treatment group were fully irrigated (18–25 days of full watering before measurement) and maintained close to FC 70–100%. Volumetric water content of other treatment groups.

After 10 days of water treatment, full irrigation was conducted (on 27th of July) for T1R, T2R seedlings. Re-irrigation period was 10–13 days for T1 seedlings and 18–25 days for T2R seedlings according to these plants recovering status (leaves turned from yellow to green).

Seedlings were first placed in dark plastic bags to ensure zero transpiration, then, the PVC plastic pipes were broken open and measured the water content of different soil layers (0, 20 cm, 40 cm, 60 cm, 80 cm), before carefully excavating the root system of seedlings. Roots were immediately placed in a bucket filled with little amount of tap water, and fine root tips were cut underwater to prevent refilling of embolized vessels and to prepare for measurement of hydraulic traits.

2.3. Xylem hydraulic conductivity and embolism measurement

Xylem hydraulic specific conductivity (kg m⁻¹ s⁻¹ MPa⁻¹) and native embolism were measured on 4–6 cm long lateral root, main stem and twig segments using a XYLEM ®xylem embolism meter (Bronkhorst, Montigny-les-cormeilles,
The hydraulic conductivity and PLC values were measured with a prototype of the new XYLEM system (INRA license, http://www.instructec.fr) following Sperry and Tyree (1988). In the laboratory, 3–5 of yellow lateral roots (2 < d < 4 mm), main stems (5 < d < 7 mm), and twigs (2 < d < 4 mm) of each *T. ramosissima* seedlings were subsequently harvested under water and their ends cut with a sharp razor blade. The main root (black color with > 5 mm diameter) or coarse lateral root (deep red color with > 5 mm diameter) of *T. ramosissima* was short and complex, and it was very difficult to obtain reliable data, so we didn’t consider the hydraulic traits data of main and coarse lateral root. 4–6 cm long segment was re-cut underwater (mean ± SD of sample segment length, diameter and segment numbers of each organ which were measured as hydraulic traits are given in Table 1). The basal cut end was then immediately attached to the hydraulic apparatus. The hydraulic pressure head was adjusted to avoid refilling of embolized vessels. For measurement of hydraulic conductivity, we chose 0.5 kPa for roots, and 1 kPa for stems and twigs (INRA license, http://www.instructec.fr).

An air perfusion technique was used to determine the maximum vessel length of twigs. The distal end of the twig sections were placed underwater while air was supplied at the proximal end at a pressure of 0.1 MPa. The twig was recut a few cm from the submerged end until the first bubbles appeared in the water (Zimmermann and Jeje, 1981; Choat et al., 2003). The maximum vessel length was defined as the remaining twig length. Test results showed that the maximum vessel length of *Tamarix ramosissima* Ledeb. seedling twigs was 23 ± 1.3 cm (mean ± SD, N = 8), (total sample length 35 ± 1 cm). Long sampling needed longer time to remove the embolism and it caused plugging problems during measurement (segment conductance declined after each flush). Subsequently, we preferred to work on relatively short samples and also added 1 mM CaCl2 to the perfusion solution to reduce the artificial pectin effects (Ryden et al., 2000).

Initial conductivity (*Kinit*: kg.s⁻¹ MPa⁻¹) of the segments was measured by gravitation perfusion with a 10 mM KCl and 1 mM CaCl2 filtered (0.22 μm) solution (pH 6) at low pressure (0.5 kPa for root and 1 KPa for stem and twig K measurement). Afterwards, samples flushed at high pressure (at 150 KPa) with the same solution used *Kinit* measurement. Maximum conductivity (*Kmax*: kg.s⁻¹ MPa⁻¹) was then measured. Both diameter (with bark) and length of each segment were measured by a vernier scale, and calculated segment cross-sectional area. Specific conductivity was then calculated as *Ks* = k (kg.s⁻¹ MPa⁻¹) × segment length (m)/segment cross-sectional area (m²). Finally, percentage loss of hydraulic conductivity was computed as (Eq. (1))

\[
PLC = 100 \left(1 - \frac{k_s(\text{init})}{k_s(\text{max})}\right)
\]

(1)

### 2.4. Lateral root vulnerability curve

A yellow lateral root vulnerability curve was determined by measuring percentage loss of hydraulic conductivity (PLC, %) due to embolism over a range water potential (Ψ) reached during dehydration by the bench drying method (Sperry and Tyree, 1988). Vulnerability curve was fitted with an exponential sigmoidal equation (Eq. (2) given on Pammenter and Vander Willigen (1998):

\[
PLC = 100 \left(1 + \exp\left(a(\Psi - \Psi_{50})\right)\right)
\]

(2)

Where PLC is the percent loss of hydraulic conductivity, Ψ is the corresponding water potential (MPa) and parameter *a* is related to the curve slope. Ψ₅₀ corresponds to Ψ at 50% loss of conductivity.

The water potential was measured with a HR-33 T Dew Point Microvolt-meter made by the U.S WESCO Company. PLC (%) was measured by using the XYLEM ® xylem embolism meter with the same procedure described above. Root samples were collected on the same day of the measurement of seedlings hydraulic traits. Before dawn, 2–4 yellow lateral roots (length = 20–25 cm, diameter = 2–4 mm) of each seedling were harvested underwater, and then placed immediately into plastic bags containing aluminum foil. In laboratory (28 °C–36 °C), these were allowed to dehydrate between 0.25 h to 4 h. Before testing, roots were tightly wrapped in dark plastic bags for 2–2 h (wet root) or overnight (dry root) to allow equilibration of water potential. For measurements, samples were dissected into two parts, one was used for PLC (%) determination, and one

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Mean ± Standard deviation of sample length, outer diameter, and sample numbers (N) of different organ of the <em>Tamarix ramosissima</em> Ledeb. seedlings.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Water treatment</strong></td>
<td><strong>T0</strong></td>
</tr>
<tr>
<td><strong>Lateral root</strong></td>
<td></td>
</tr>
<tr>
<td>Sample length (mm)</td>
<td>49.8 ± 5.5</td>
</tr>
<tr>
<td>Outer diameter (mm)</td>
<td>2.8 ± 0.5</td>
</tr>
<tr>
<td>N</td>
<td>52</td>
</tr>
<tr>
<td><strong>Main stem</strong></td>
<td></td>
</tr>
<tr>
<td>Sample length (mm)</td>
<td>44.2 ± 6.3</td>
</tr>
<tr>
<td>Outer diameter (mm)</td>
<td>6.4 ± 1.1</td>
</tr>
<tr>
<td>N</td>
<td>25</td>
</tr>
<tr>
<td><strong>Twigs</strong></td>
<td></td>
</tr>
<tr>
<td>Sample length (mm)</td>
<td>38.6 ± 1.9</td>
</tr>
<tr>
<td>Outer diameter (mm)</td>
<td>2.7 ± 0.4</td>
</tr>
<tr>
<td>N</td>
<td>24</td>
</tr>
</tbody>
</table>
was used for measurement of water potential. After dissecting, one part was immediately re-cut under distilled water to 4–6 cm in length, and attached to the XYLEM meter for PLC (%) measurement. Another part (maintained in a plastic bag while the other parts were attached to the XYLEM system) was also divided into 3 parts, and a 0.5-cm long slice was cut from the middle of each part. The root slices were placed in the C-52 sample chamber of the Dew Point Microvolt-meter and conducted water potential measurement. The water potential of each root sample was determined taking the average value of the three root slices. Finally, water potential ($\Psi$) and embolism values (PLC, %) from lateral roots were plotted on the same graph to produce the vulnerability curve.

2.5. Anatomical measurement

Xylem anatomical observations were made on yellow lateral roots and twigs of well-watered (T0) and the moderately water stressed/re-watered seedlings (T1R) used for measurement of hydraulic traits. Cross-sections were taken from 1–2 year old twigs and lateral roots, and immediately fixed in a solution consisting of formalin, acetic acid and ethanol (5:5:90 v/v). Using a slide microtome, 6–8 $\mu$m thin sections were transversally cut from these samples, the sections were double-stained with (1%) safranine and (1%) fast green, and observed under a light microscope (Olympus, BX51) equipped with a digital camera (Olympus DP70). The measurement of mean vessel diameters (measured in two directions), vessel densities and vessel number distributions were done on individual micrographs from each of 13 different lateral roots and 6 twigs of T. ramosissima. The number of vessels measured per section varied between 180 and 395 for lateral roots and 260 and 357 for twigs. The mean hydraulic conduit diameter ($d_h$) was calculated from the individual diameter (according to Sperry and Hacke 2004) (Eq. (3)):

$$d_h = \frac{\sum d^5}{\sum d^4}$$

3. Results

The mean soil water content with different soil layers (0, 20 cm, 40 cm, 60 cm, 80 cm) of 5 water treatment groups were given Fig. 1. The mean soil water content (0–80 cm) of T0, T1, T2, T1R and T2R treatment groups were 23.72±1.02%, 15.47±0.92%, 9.47±1.72%, 25.45±3.96% and 26.29±1.79%, Mean±SE respectively.

The two drought stress and two re-watering treatments had significant impacts on initial hydraulic specific conductivity, $k_s$ (init) of lateral root, main stem and twigs ($p<0.05$) and on maximum hydraulic specific conductivity (conductivity with embolism removed), $k_s$ (max), of lateral roots of Tamarix ramosissima Ledeb. seedlings ($p<0.01$) (Table 2).

Under moderate drought stress treatment (T1), the value of $k_s$ (init) and $k_s$ (max) in T. ramosissima seedlings lateral root, main stem and twigs all decreased in general, but there was no significant difference between the well-watered (T0) and moderately stressed (T1) seedlings ($p>0.05$) (Fig. 2, Fig. 3).

After the severely drought stress treatment (T2), the value of $k_s$ (init) in lateral root, main stem and twigs all decreased significantly ($p<0.05$) (Fig. 2), however, the value of lateral root $k_s$ (max) increased significantly ($p<0.01$) (Fig. 3), the $k_s$ (max) value increased for about 45% as to the value of well-watered (T0) seedlings.

After re-watering treatment, no significant difference was observed between T2R and T2, T1R and T1 treatment groups in lateral root, main stem and twigs both $k_s$ (init) and $k_s$ (max) value ($p>0.05$), except for the value of $k_s$ (init) in main stem and twigs between T1R and T1 treatment groups ($p<0.05$) (Fig. 2, Fig. 3).

Table 2

<table>
<thead>
<tr>
<th>Different organ</th>
<th>ANOVA results</th>
<th>$k_s$(max)</th>
<th></th>
<th></th>
<th>$k_s$(init)</th>
<th></th>
<th></th>
<th>PLC (%)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sum of square</td>
<td>df</td>
<td>F</td>
<td>Sig</td>
<td>Sum of square</td>
<td>df</td>
<td>F</td>
<td>Sig</td>
<td>Sum of square</td>
<td>df</td>
</tr>
<tr>
<td>Lateral root</td>
<td>Between groups</td>
<td>542.683</td>
<td>4</td>
<td>10.263</td>
<td>0.0001</td>
<td>17.15</td>
<td>4</td>
<td>2.799</td>
<td>0.031</td>
<td>15204.7</td>
</tr>
<tr>
<td></td>
<td>Within groups</td>
<td>1216.2</td>
<td>92</td>
<td>125.62</td>
<td>0.001</td>
<td>125.62</td>
<td>82</td>
<td>14.84</td>
<td>0.0001</td>
<td>47248.7</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>1758.88</td>
<td>96</td>
<td>142.77</td>
<td>0.0001</td>
<td>142.77</td>
<td>86</td>
<td>15.34</td>
<td>0.0001</td>
<td>65453.4</td>
</tr>
<tr>
<td>Main stem</td>
<td>Between groups</td>
<td>3.6605</td>
<td>4</td>
<td>0.799</td>
<td>0.529</td>
<td>3.085</td>
<td>4</td>
<td>4.968</td>
<td>0.001</td>
<td>5577.84</td>
</tr>
<tr>
<td></td>
<td>Within groups</td>
<td>92.7351</td>
<td>81</td>
<td>12.728</td>
<td>0.001</td>
<td>12.728</td>
<td>82</td>
<td>15.813</td>
<td>0.001</td>
<td>5577.84</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>96.3956</td>
<td>85</td>
<td>15.813</td>
<td>0.001</td>
<td>15.813</td>
<td>86</td>
<td>27000.5</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>Twigs</td>
<td>Between groups</td>
<td>6.579</td>
<td>4</td>
<td>2.154</td>
<td>0.087</td>
<td>0.792</td>
<td>4</td>
<td>2.862</td>
<td>0.028</td>
<td>11626.5</td>
</tr>
<tr>
<td></td>
<td>Within groups</td>
<td>39.425</td>
<td>90</td>
<td>6.087</td>
<td>0.087</td>
<td>6.087</td>
<td>88</td>
<td>30619.4</td>
<td>90</td>
<td>1238.3</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>46.004</td>
<td>94</td>
<td>6.879</td>
<td>0.087</td>
<td>6.879</td>
<td>92</td>
<td>42245.9</td>
<td>94</td>
<td>1238.3</td>
</tr>
</tbody>
</table>

Fig. 1. The mean soil water content with different soil layers of 5 water treatment groups of T. ramosissima Mean±SE.
The \( k_s \) (init) value in main stem and twigs of T1R seedlings kept decreasing after the short-term re-watering treatment (Fig. 2).

In all five treatments, the native embolism rate (PLC, %) of the lateral roots, main stems and twigs, all varied significantly \((p<0.01)\) (Table 2). The native PLC value of moderately drought stressed (T1) seedlings for all the different organs increased to some extent as comparing to the well-watered (T0) seedlings, but we didn’t observe a significant difference between these two treatment group in native PLC value \((p>0.05)\). After the severely drought stress treatment (T2), the native PLC value of lateral root, main stem and twigs all increased significantly \((p<0.01)\) (Fig. 4), and there was a significant difference between well-watered (T0) and severely drought stressed (T2) seedlings in native PLC value \((p<0.01)\) (Fig. 4).

The relationships between native PLC value of \( T. ramosissima \) seedlings’ different organ and mean soil water content \((0–80 \text{ cm})\) in PVC pipes of T0, T1, T2 water treatment groups are given in Fig. 5. The native PLC value of lateral root, main stem, and twigs increased with the intense of soil drought stress. When mean soil water content was 23.72±1.02%, native PLC value of lateral root, main stem, twigs was 55.70±6.8, 63.94±4.8, 51.28±7.7 PLC (mean±SE) respectively, and it increased to 88.51±7.7, 85.32±3.0, 80.85±2.8 PLC while mean soil water content dropped to 9.47±1.72%, respectively (Fig. 5).

After the re-watering treatment, only the lateral root embolism recovered to a greater degree than the other organs. There was significant difference between the severely drought stressed (T2) seedlings and the severely water stressed/rewatered (T2R) seedlings lateral root native PLC value \((p<0.05)\), embolism recovered for about 20% as to the severely drought stressed (T2) seedlings (Fig. 4).

The lateral root \((2 \leq \text{diameter} \leq 4 \text{ mm})\) vulnerability curve was steep, mostly increasing between \(-2 \) and \(-4 \text{ MPa}\). The PLC increased sharply above \(-2 \text{ MPa}\) xylem water potential, a water potential of \(-2.99 \text{ MPa}\) gave 50 PLC. The PLC was 90–99 at between \(-4 \text{ Mpa}\) and \(-6 \text{ MPa}\) xylem water potential (Fig. 6).

The mean vessel diameters and densities of the twigs and lateral roots of 2-year old \( T. ramosissima \) seedlings in T0 and T1R treatment groups are given in Table 3. We did not observe a significant difference between the T0 and T1R treatment group seedlings lateral root and twigs mean vessel diameter \((d_{\text{mean}})\), hydraulic diameter \((d_h)\) and densities \((\text{VD})\) \((P>0.05)\), respectively (Table 3).

Lateral roots had larger mean vessel diameters \((d_{\text{mean}})\), and mean hydraulic diameter \((d_h)\) than twigs; however, mean vessel
density (VD) was lower in roots (93.61 ± 8.21, mean ± SE) than twigs (114.40 ± 10.43, mean ± SE) (Table 3). The mean vessel diameter \((d_{mean})\), mean hydraulic diameter \((d_h)\) was significantly different between lateral roots and twigs \((p < 0.01)\). The \(k_{s(\text{max})}\) value of lateral root and twigs were closely correlated with their \(d_{mean}\) and \(d_h\) respectively \((r^2 = 0.955, r^2 = 0.987)\).

The distribution of vessel diameters in roots and twigs of \(T. ramosissima\) are given Fig. 7. The number of vessels with diameters between 10 and 70 \(\mu m\) accounted for 95.68% of the total vessel numbers in roots (Fig. 7, lateral root). In twigs, diameters between 15 and 50 \(\mu m\) vessel numbers occupied 95.86% of the total vessel numbers in twigs (Fig. 7, twigs).

4. Discussion

Widespread plant species must show physiological and structural plasticity to deal with contrasting water balance conditions (Poyatos et al., 2007). The results of this study revealed that variation of root system hydraulic traits in drought stress and re-watering conditions may be one of the important factors underlying the survival of \(T. ramosissima\) in extremely dry climates and variable water environments such as the Tarim River Basin in northwestern China.

4.1. Variation of maximum hydraulic specific conductivity \((k_{s(\text{max})})\) under different water treatments

Changing of hydraulic conductivity as a response to different environmental condition seems to vary between species. Mature ponderosa pine trees grown in dry sites had higher hydraulic conductivity than trees growing in cool and moist sites (Maherali and DeLucia, 2000). Similar results have been found for \(Eucalyptus camaldulensis\) seedlings, which were from different climatic origins (Franks et al., 1995). Conversely, xylem hydraulic conductivities were higher in trees on mesic sites than in trees on xeric sites in four eucalyptus clones (Vander Willigen and Pammenter, 1998). Likewise, for \(Vitis vinifera\) (Schultz and Matthews, 1988; Lovisolo and Schubert, 1998), \(Quercus rubra\) and \(Liriodendron tulipfera\) seedlings (Shumway et al. 1993), maximum hydraulic conductivity was positively correlated with the soil water availability. For \(C. libani\) (Armut Alani, Turkey), a moderate soil drought applied for 10 weeks induced a reduction of hydraulic conductivity (Ladjal et al., 2005).

In the present case, the short–term moderately drought stress treatment resulted in a decrease in \(k_{s(\text{max})}\) value of \(T. ramosissima\)'s different organ in general (Fig. 3), but we didn’t observe a significant difference between T0 and T1 treatment group. Interestingly, the severe drought stress treatment induced a significant increase in \(k_{s(\text{max})}\) for the lateral root \((p < 0.01)\) (Fig. 3). The severely drought stressed period for

### Table 3

<table>
<thead>
<tr>
<th>Organ of (T. ramosissima)</th>
<th>lateral roots</th>
<th>twigs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>T0</td>
<td>T1R</td>
</tr>
<tr>
<td>Mean diameters ((d_{mean}, \mu m))</td>
<td>36.31 ± 1.79</td>
<td>33.64 ± 1.37</td>
</tr>
<tr>
<td>Mean hydraulic diameter ((d_h, \mu m))</td>
<td>55.59 ± 3.57</td>
<td>52.86 ± 2.75</td>
</tr>
<tr>
<td>Vessel densities (\text{n/mm}^{-2})</td>
<td>100.07 ± 15.53</td>
<td>88.09 ± 8.18</td>
</tr>
</tbody>
</table>
T2 seedlings was about 17–19 days, and this is a comparatively shorter period. However, *T. ramosissima* is a wide spread phenotype shrub species native to Tarim River Basin in china and aggressive alien plant to the southern united status. That means it might have quite strong adaptive ability to different habitat; secondly, the root system, especially lateral root (2 mm < d < 4 mm), is not only the main water and nutrition absorbing organ, but also is more fragile to drought induced–cavitation than coarse or main roots, therefore, lateral root is extremely sensitive to any changes in soil water conditions. Besides, as to the study area, the annual precipitation is less then 50 mm, the survival of *T. ramosissima* mainly relies on the groundwater, so, the underground ecosystem might be more active then the aboveground. The increase in xylem hydraulic conductivity of lateral roots under severely drought stress conditions may help to mitigate the increase of water tension in xylem. This is helpful in meeting the high evaporation demands of the whole plant, and may preventing occurrences of catastrophic cavitations in xylem which leads to dieback of *T. ramosissima*.

The effect of drought on xylem anatomy has been analyzed in several recent studies (Schume et al., 2004; February and Manders, 1999; Ladjal et al., 2005), which suggests that drought–induced changes of hydraulic conductivity is related to the changes of conduit size. Unfortunately, in this study, we have only randomly chosen the well-watered (T0) and moderately drought stressed-rewatered (T1R) groups for lateral root and twigs anatomical measurement. Consequently, in terms of relationship between changes in hydraulic conductivity and xylem conduit size, we didn’t observe any difference between these two treatment groups (Table 3). Further studies are therefore needed to find out the effects of drought on wood anatomy and its associations with changes in hydraulic conductivity.

4.2. Variation of native embolism under different water treatments

A high native embolism rate of *T. ramosissima* stems was reported; mean native embolism in different season was between 46.95-86.90 PLC (Pockman and Sperry, 2000). In the present study, native embolism value of each organ was also high: the mean native embolism of lateral roots, main stems and twigs of control plants fluctuated around 50–70 PLC (Fig. 4). Each organ had different levels of native embolism rate, with lateral roots and twigs possessing smaller embolism levels compared to woody stems in control plants (Fig. 4). Severely drought stress treatments increased the native embolism rate of whole plant xylem with lateral roots having the highest embolism levels (88%) compared to other organs (Fig. 4; Fig. 5).

In the root systems of woody plants, field studies showed significant embolism during drought with recovery occurring following rain (Domec et al., 2006). In this study, after the short-term water recovery treatment, severely water stressed seedlings lateral root embolism recovered greatly than the other organs (Fig. 4). The previously embolized vessels during the severely drought stress treatment in woody stems and twigs, did not respond quickly to the short-term water recovery treatment.

4.3. Relations between maximum hydraulic conductivity and xylem anatomical structure

In the present study, lateral roots had the highest maximum hydraulic specific conductivity and twigs had the lowest values under different water treatment conditions (Fig. 3). The maximum xylem-specific conductivity of each species correlated well with their vessel diameter, higher conductivities being associated with larger vessel diameters (Zimmermann, 1983; Ewers et al., 1989; Vander Willigen et al., 2000). This association was also observed in this study. The anatomical structure of xylem in lateral roots and twigs in *T. ramosissima* revealed that lateral roots had larger mean vessel diameters (d_{mean}d_{h}), than twigs (Table 3) and the maximum hydraulic conductivity were closely correlated with their vessel diameter (r² > 0.95).

Overall, we can conclude that the native embolism value of *T. ramosissima’s* all different organs increased with the intensity of drought stress, and lateral root embolism can recover greatly after short-term re-irrigation; lateral root changes its maximum hydraulic conductivity under severely drought stress conditions. This supports the hypothesis that *T. ramosissima* root system might be able to change its hydraulic traits in response to different water stress conditions, and this might be one of the important factors underlying its survival in extremely dry climates and variable water environments such as the Tarim River Basin in northwestern china.

Acknowledgements

This study was funded by National Natural Science Foundation of China (Grant No. 91025025), Knowledge Innovative Project of Chinese Academy of Science (Grant No.KZCX2-Yw-Q10-3-3), and West Light Foundation of the Chinese academy of science (Grant No.RCPY200903).

References


