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# Water adaptive traits of deep-rooted C<sub>3</sub> halophyte (*Karelinia caspica* (Pall.) Less.) and shallow-rooted C<sub>4</sub> halophyte (*Atriplex tatarica* L.) in an arid region, Northwest China

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**Abstract:** This paper focused on the water relations of two halophytes differing in photosynthetic pathway, phenotype, and life cycle: *Karelinia caspica* (Pall.) Less. (C<sub>3</sub>, deep-rooted perennial Asteraceae grass) and *Atriplex tatarica* L. (C<sub>4</sub>, shallow-rooted annual Chenopodiaceae grass). Gas exchange, leaf water potential, and growth characteristics were investigated in two growing seasons in an arid area of Xinjiang to explore the physiological adaptability of the two halophytes. Both *K. caspica* and *A. tatarica* showed midday depression of transpiration, indicating that they were strong xerophytes and weak midday depression types. The roots of *A. tatarica* were concentrated mainly in the 0–60 cm soil layer, and the leaf water potential ( $\psi_L$ ) increased sharply in the 0–20 cm layer due to high soil water content, suggesting that the upper soil was the main water source. On the other hand, *K. caspica* had a rooting depth of about 1.5 m and a larger root/shoot ratio, which confirmed that this species uptakes water mainly from deeper soil layer. Although *A. tatarica* had lower transpiration water consumption, higher water use efficiency (WUE), and less water demand at the same leaf water potential, it showed larger water stress impact than *K. caspica*, indicating that the growth of *A. tatarica* was restricted more than that of *K. caspica* when there was no rainfall recharge. As a shallow-rooted C<sub>4</sub> species, *A. tatarica* displayed lower stomatal conductance, which could to some extent reduce transpiration water loss and maintain leaf water potential steadily. In contrast, the deep-rooted C<sub>3</sub> species *K. caspica* had a larger root/shoot ratio that was in favor of exploiting groundwater. We concluded that C<sub>3</sub> species (*K. caspica*) tapes water and C<sub>4</sub> species (*A. tatarica*) reduces water loss to survive in the arid and saline conditions. The results provided a case for the phenotype theory of Schwinning and Ehleringer on halophytic plants.

**Keywords:** *Karelinia caspica*; *Atriplex tatarica*; root/shoot ratio; leaf water potential; stomatal conductance; transpiration

About 45% of the world's agricultural land, which occupies 38% of the land that human resides (Bot *et al.*, 2000), is subjected to continuous or frequent droughts. Soil salinity is usually high in arid regions with shallow groundwater table. Drought and salinity are two widespread environmental factors limiting plant growth and ecological sustainability (Chen and Jiang, 2010). Under these conditions, soil water availability to plants is reduced, inducing a wide range of perturbations at cellular and whole-plant levels that

result in inhibition of plant growth and eventually deterioration of ecological environment.

Plant species growing in arid regions have acquired strategies to adapt to drought and saline environments. In arid and semi-arid ecosystems, distinct life forms are observed to utilize soil moisture in various ways (Noy-meir, 1973; Cody, 1986). As an example, Leffler *et al.* (2004) noticed that for two species having similar

Received 2012-04-04; accepted 2012-07-30

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rooting depths, *Artemisia tridentata* grew well when water was available in the upper soil layer, while *Chrysothamnus nauseosus* performed better when water was available in the lower soil layer. Plant water use strategies are closely related to phenotype, which can be unveiled from plant water use characteristics under arid and saline environments.

Leaf water potential ( $\Psi_L$ ) is a driving force for the movement of liquid water through plants, and has been widely used as an indicator of plant water status (Hsiao, 1973). By controlling stomatal conductance,  $\Psi_L$  affects transpiration, photosynthesis, and root water uptake (Campbell, 1985). Water potential gradient between leaves and soil tends to be equilibrated with water loss by transpiration (Jarvis, 1976). Changes in transpiration rate also cause  $\Psi_L$  changes, and ion accumulation in roots and leaf cellular expansion may complicate the relationship between  $\Psi_L$  and transpiration rate (Farquhar and Sharkey, 1982). Normally  $C_4$  grasses have lower stomatal conductance and water potential deficits, and higher leaf photosynthetic rate and water use efficiency (WUE) than  $C_3$  grasses (Taylor *et al.*, 2010). Photosynthesis of a  $C_4$  grass is highly sensitive to water stress and can be compensated by  $CO_2$ -concentrating mechanism under relatively low intercellular  $CO_2$  concentrations. When  $C_4$  plants experience drought in their natural environment, elevated  $CO_2$  concentration alleviates the effect of water stress (Ghannoum, 2009). Although the  $CO_2$ -concentrating mechanism offers  $C_4$  photosynthesis a greater buffering capacity against  $CO_2$  shortages, the biochemistry of  $C_4$  photosynthesis is even more sensitive to water stress than that of  $C_3$  photosynthesis, and it remains questionable whether the higher WUE of  $C_4$  plants results in greater tolerance to water stress than  $C_3$  species (Ghannoum, 2009). The influences of water shortage on leaf water potential and gas exchange are reasonably well understood (Boyer, 1976; Biran *et al.*, 1981; Chen and Jiang, 2010), but much remains to be explored about leaf water potential and water physiological characteristics among  $C_3$  and  $C_4$  plants under arid environments.

*Karelinia caspica* (Pall.) Less. and *Atriplex tatarica* L. are typical halophytes in Northwest China and are widespread in the salt marsh, Gobi desert and barren

lands. *K. caspica* is a  $C_3$  herbaceous perennial halophyte of the Asteraceae family and has succulent leaves and massive taproot. *A. tatarica* is a  $C_4$  halophytic annual herb of the Chenopodiaceae family with well-developed superficial root systems. They are edible for cattle, sheep, and camels in areas where local forage is insufficient. Although the two halophytes are often subjected to soil and atmospheric water deficits as well as to high soil salinity, they can survive and exhibit strong vitality in an arid and saline environment. What are the adaptive mechanisms of the deep-rooted  $C_3$  halophyte *K. caspica* and shallow-rooted  $C_4$  halophyte *A. tatarica* to an arid and saline environment? Are there differences in physiological mechanisms between the two halophytes?

In this study, a field research was conducted to study the leaf water potential and adaptive traits of *K. caspica* and *A. tatarica* under arid and saline habitats. Plant growth, gas exchange, and water relations in two successive growing seasons were investigated.

## 1 Materials and methods

### 1.1 Study area

The study area is located in the alluvial plain of Manas River Basin (44°42'54.3"N, 85°22'42.6"E), Xinjiang Uygur autonomous region of Northwest China. The area exhibits typical arid features. The average annual precipitation and potential evaporation are 136.9 and 1,876.8 mm, respectively. The annual average temperature is 7.3°C, and accumulative temperature ( $\geq 10^\circ\text{C}$ ) is 2,627°C. The average annual sunshine hours are 2,828.2 h, and average annual frost-free period is 163 days.

The experimental area is about 20 m×20 m, and has a shallow groundwater table of 2.5 m. Soil water moves upward by evapotranspiration, and salts are left in the topsoil (Cui and Shao, 2005). Cotton was planted in the 1980s. Crop land has been abandoned because of salinization. The site has mixed halophyte species, including *K. caspica*, *Kochia scoparia*, *A. tatarica*, *Populus euphratica*, *Tamarix chinensis*, and *Achnatherum splendens*. The soil type was chloride-sulfate saline soil, with pH 7.83–7.89, and electrical conductivity (EC, soil to water ratio is 1:5) 3.7–4.2 dS/m.

## 1.2 Plant species

The dominant plant species are halophytes and salt-tolerant xerophytes, with 36 plant families and over 120 genera. The studied *K. caspica* and *A. tatarica* are native to Xinjiang, and are also distributed in some other parts of Asia (e.g. Iran, Mongolia, and Turkey). Both species are distributed widely in Manas River Basin. They are different in photosynthetic pathway (C<sub>3</sub> vs. C<sub>4</sub>; Wang, 2007), phenotype (deep-rooted vs. shallow-rooted), and life form (perennial vs. annual). The growing season lasts from April to October. That is, plants revive in early April, bloom in July and August, bear fruits in September, and wilt before the first frost.

## 1.3 Methods

Five *K. caspica* plants and five *A. tatarica* plants with similar height and growth stage were selected for this study. The distance between *K. caspica* and *A. tatarica* plants was less than 10 m. For gas exchange and leaf water potential measurements, younger, intact and expanded leaves in the crowns of the plants were used. Diurnal variations were monitored every two hours from 7:30 to 19:30 on 20 August, 2010 and 2011 when the plants reached their respective maximum biomass. Each measurement was repeated three times. The shoots were harvested after diurnal variation measurements were finished. Plants were oven-dried at 80°C for 72 h and then weighted.

Photosynthetic rate ( $P_n$ ), transpiration rate ( $Tr$ ), and stomatal conductance ( $g_s$ ) were measured using a portable photosynthesis system (Li-6400, Licor Inc., Lincoln, NE, USA) equipped with an aperture of 0.785 cm<sup>2</sup>. The inner environment of the leaf chamber was controlled automatically, and daily variations of leaves were measured under the following conditions: molar air flow per unit leaf area of 200 mmol/(m<sup>2</sup>·s), atmospheric pressure of 96–98 kPa, water vapor pressure (inside chamber) of 1.5–2.0 MPa, relative humidity (inside chamber) of 20%–60%, maximum photosynthetic photon flux density at leaf surface of 1,800 μmol/(m<sup>2</sup>·s), and maximum leaf temperature of 38°C.

$\Psi_L$  measurement was made with a portable pressure chamber (SKPM 1400, Skye Instruments, Landrindod Wells, UK). It was conducted near the leaves where gas exchange was measured. The leaves were excised

at the leaf collar and covered by the leaf holder until the measurement was complete. The equilibrium pressure that squeezed liquid out of the cut leaf collar cross-section was recorded as leaf water potential.

Water stress impact on species (WSIS) can reflect the extent to which plant growth is restricted. WSIS is calculated by the following equation (Vertovec *et al.*, 2001):

$$WSIS = \int_{t_0}^{t_x} \Psi_L \cdot dt.$$

Where  $dt$  is the time interval at which  $\Psi_L$  is measured. The leaf water potential measurement was conducted every 2 hours from 7:30 to 19:30.

Relationships between leaf water potential and relative water content were determined in the laboratory. Leaves were packed with aluminum foil, frozen, and brought to the laboratory right away. The samples were then placed in deionized water overnight. After the determination of the saturated weight, leaf water potential was measured immediately. The measurements were repeated until leaf water potential was less than the minimum value observed in the field. The leaves were then dried at 75°C for 72 h and weighed. Relative water content (RWC) of shoots was determined as  $RWC = ((FM - DM) / (SM - DM)) \times 100\%$ , where FM, DM, and SM are fresh mass, dry mass, and saturated mass, respectively.

Leaf area ratio (LAR) was determined by dividing the leaf mass by its specific leaf area. Leaf pictures were recorded using a camera (NIKON P60) in coordinate paper, and then leaf area was calculated using the Digimizer image analysis software (version 3.1.2.0; MedCalc Software, Mariakerke, Belgium).

The amount of water consumption per plant was estimated from transpiration rate (mmol H<sub>2</sub>O/(m<sup>2</sup>·s) × leaf area (m<sup>2</sup>) × time (s)). WUE was determined by dividing shoot dry weight by water consumption per plant (Wu *et al.*, 2004).

Roots were sampled on the basis of soil horizons (0–10, 10–20, 20–40, 40–60, 60–80, 80–100, 100–120, 120–150 cm), and soil samples were collected at the same time. Immediately after harvesting, roots were washed to get rid of soil particles with tap water. The roots were scanned by spreading them carefully in a thin layer of water on a transparent tray. Root

surface area for each soil horizon was then analyzed and calculated using the root analysis system (winRHIZO, Regent Instruments Inc., Quebec, Canada) (Pro, 2004).

The gravimetric water content of the soil was measured by drying in an oven at 105°C for 48 h. Soil volumetric water content was determined by multiplying mass water content with bulk density. The EC of 1:5 soil water extract was determined with a DDS-308A conductivity meter (Shanghai Precision & Scientific Instrument Inc., Shanghai, China).

#### 1.4 Statistical analysis

We were interested mainly in the factors that affected the leaf water potential of both halophytes. Correlation analyses were performed to evaluate the relationships between leaf water potential, stomatal conductance and transpiration rate, and between leaf water potential, soil volumetric water content and soil electrical conductivity. The differences in growth attributes and water consumption characteristics between the two species were examined with the two-way analysis of variance (ANOVA). Statistical analyses were performed using the SPSS Statistical Software (SPSS software v. 17.0; SPSS Inc., Chicago, IL, USA).

## 2 Results

### 2.1 Climatic condition

As shown in Fig. 1, daily mean air temperature and

precipitation in plant growth periods were higher in 2011 than in 2010. The minimum air temperature, −0.17°C in 2010 and 0.77°C in 2011, appeared in April, and the maximum air temperature, 31.99°C in 2010 and 31.65°C in 2011, occurred in July. The annual mean air temperature was 1.3°C greater in 2011 than in 2010. The annual precipitations were 78.2 mm and 112.5 mm in 2010 and 2011, respectively. The largest amount of monthly precipitation, 24.3 mm and 41.2 mm, appeared in April 2010 and May 2011, respectively.

### 2.2 Photosynthetic characteristics and leaf water potential

Daily variation of photosynthetic characteristics and leaf water potential on 20 August, 2010 and 2011 were shown in Fig. 2. As a  $C_4$  species, *A. tatarica* exhibited larger  $P_n$  than *K. caspica*, especially at noon (Fig. 2a). The maximal  $P_n$  of *A. tatarica* occurred at about 13:00, which was 8 and 9.4  $\mu\text{mol H}_2\text{O}/(\text{m}^2\cdot\text{s})$  larger than that of *K. caspica* in 2010 and 2011, respectively. For both species,  $g_s$  and  $Tr$  displayed “double peaks” at daytime (Figs. 2b, c). The first peak appeared at 11:30, when  $g_s$  of *K. caspica* was 0.2 and 0.3  $\text{mol H}_2\text{O}/(\text{m}^2\cdot\text{s})$  larger than that of *A. tatarica*, and the  $Tr$  of *K. caspica* was 1.8 and 2.9  $\text{mmol H}_2\text{O}/(\text{m}^2\cdot\text{s})$  greater than that of *A. tatarica*. In the early morning and evening when  $g_s$  and  $Tr$  were low, the two halophytes showed similar  $g_s$  and  $Tr$  values. The diurnal variation of  $\Psi_L$  displayed single-peak curves (Fig. 2d). The negative peak appeared at 15:30 at which  $\Psi_L$  of *A. tatarica* was 0.5 and

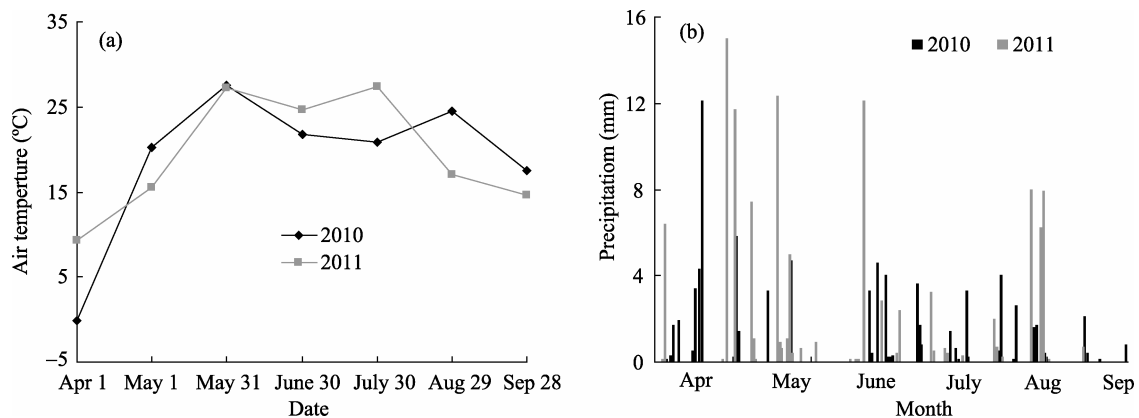
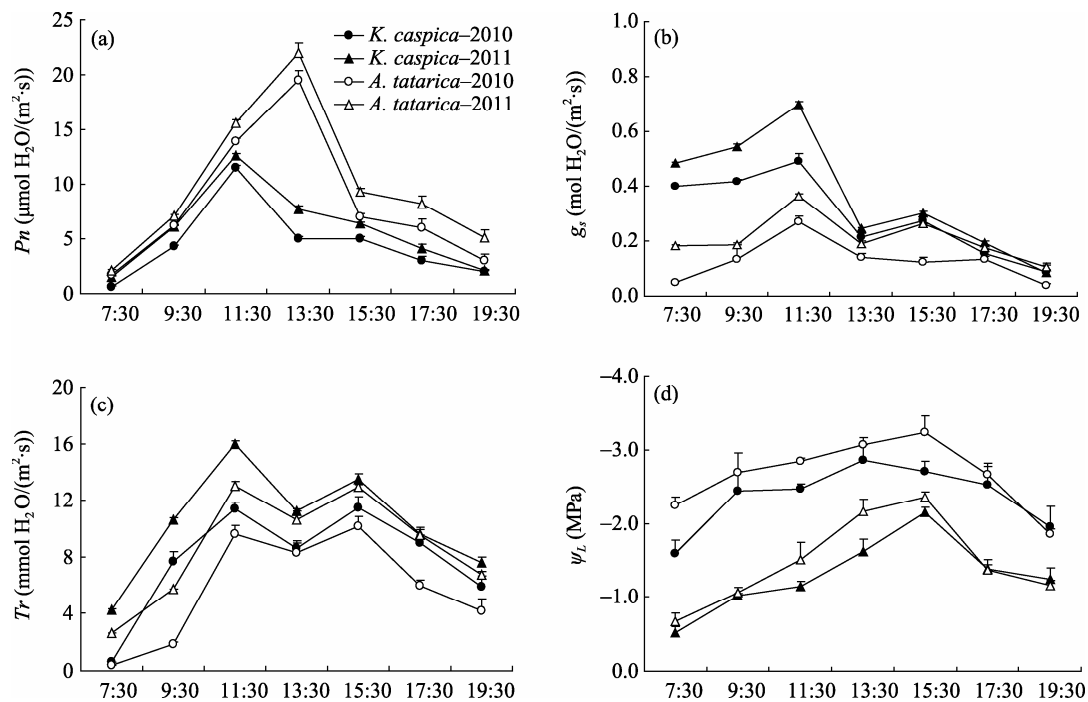


Fig. 1 Daily mean air temperature (a) and monthly precipitation (b) during 2010 and 2011 in the study area

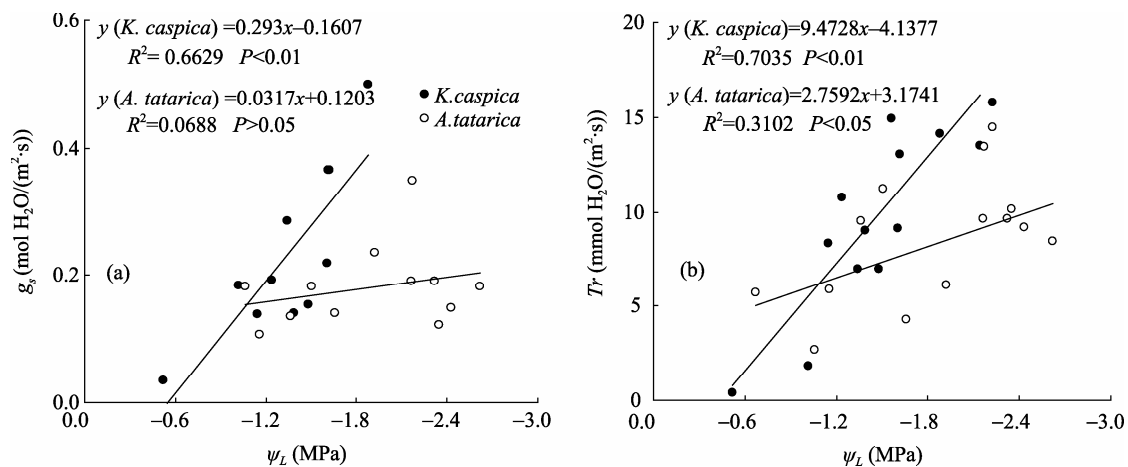
0.2 MPa lower than that of *K. caspica*. In both 2010 and 2011, *K. caspica* showed greater  $g_s$ ,  $Tr$ , and  $\Psi_L$ , and lower  $P_n$  values than *A. tatarica*. The higher mean air temperature and larger precipitation in 2011 resulted in greater  $P_n$ ,  $g_s$ ,  $Tr$ , and  $\Psi_L$  values than that in 2010.

$Tr$  and  $g_s$  showed a similar trend in responses to reduced  $\Psi_L$  for both species (Fig. 3). However, *K. caspica*

displayed larger  $Tr$  and  $g_s$  as compared to *A. tatarica* at the same  $\Psi_L$  value. In addition, the slopes of the  $\Psi_L$ - $Tr$  and  $\Psi_L$ - $g_s$  regression lines of *K. caspica* were greater than those of *A. tatarica*. These results indicate that with decreasing leaf water potential, *A. tatarica* exhibited preferable stomatal control. The lower stomatal conductance reduced transpiration water loss effectively, and leaf water potential was maintained steadily.



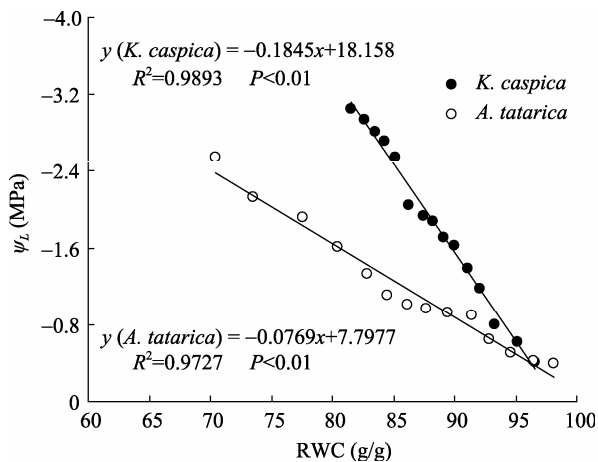
**Fig. 2** Diurnal variation of photosynthetic rate ( $P_n$ ) (a), stomatal conductance ( $g_s$ ) (b), transpiration rate ( $Tr$ ) (c), and leaf water potential ( $\Psi_L$ ) (d) in *K. caspica* and *A. tatarica* on August 20, 2010 and 2011



**Fig. 3** Relationships between stomatal conductance ( $g_s$ ) (a), transpiration rate ( $Tr$ ) (b), and leaf water potential ( $\Psi_L$ ) of *K. caspica* and *A. tatarica*

### 2.3 Plant water and growth characteristics

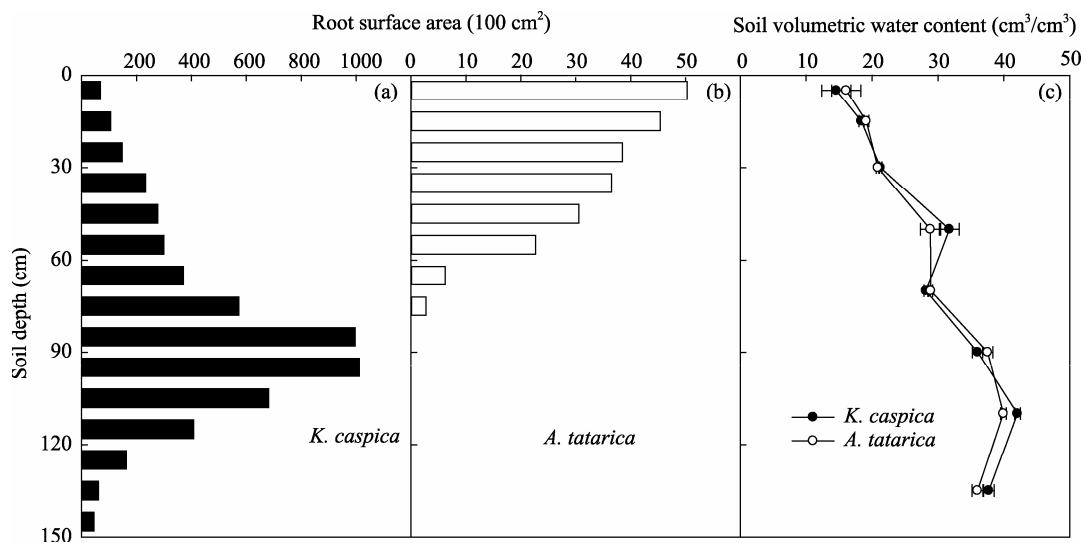
Figure 4 shows the relationship between leaf water potential and leaf relative water content (RWC) of *K. caspica* and *A. tatarica*. In general, with increasing leaf relative water content,  $\Psi_L$  of *K. caspica* decreased more rapidly than that of *A. tatarica*, indicating that *K. caspica* had larger RWC than *A. tatarica* at a given water potential. At the maximal RWC, the two species had similar leaf water potentials.



**Fig. 4** Relationship between leaf water potential ( $\Psi_L$ ) and leaf relative water content (RWC) of *K. caspica* and *A. tatarica* as determined from two leaves

Figure 5 shows the vertical distribution of root surface area for *K. caspica* and *A. tatarica*, along with soil volumetric water content on 20 August 2010. In the 80–100 cm layer, root surface area of *K. caspica* accounted for 49.4% of the total root surface area, indicating that the roots of *K. caspica* were distributed primarily in this layer. On the other hand, the roots of *A. tatarica* distributed mainly in the 0–60 cm soil layer (Fig. 5b), and the root surface area in the 0–20 cm layer took up 41.1% of the total. On 20 August 2010, soil volumetric water content increased with soil depth (Fig. 5c), and the maximum water content appeared in the 100–120 cm soil layer. Clearly the maximum rooting density of *K. caspica* matched the maximum water content layer, suggesting that the major water source of *K. caspica* came from the deeper soil layer.

The root/shoot ratios of *K. caspica* were 1.3 and 0.8 in 2010 and 2011, respectively, 16.8% and 40.2% greater than that of *A. tatarica* (Table 1). In addition, *K. caspica* had a leaf area ratio of 127.1 g/cm<sup>2</sup> and 74.6 g/cm<sup>2</sup> in 2010 and 2011, respectively, 2.3 and 1.3 times that of *A. tatarica*. As a consequence, water consumption of *K. caspica* was 2.1 and 1.5 times larger than that of *A. tatarica*. However, the WUE of *K. caspica* was 64.4% and 71.7% lower than that of *A. tatarica* in 2010 and 2011, respectively (Table 1).



**Fig. 5** Vertical distribution of root surface area of *K. caspica* (a) and *A. tatarica* (b) and soil volumetric water content ( $\theta_v$ ) (c) on 20 August 2010

## 2.4 Leaf water potential, soil water, and salinity

For the two species,  $\Psi_L$  of *A. tatarica* increased sharply with the soil water content in 0–20 cm layer (Fig. 6a,  $P<0.01$ ), indicating that upper soil water was the main water source for *A. tatarica*. Compared to that of *K. caspica*, the leaf water potential of *A. tatarica* was more sensitive to changes in soil electrical conductivity in the 0–20 cm layer (Fig. 6b), suggesting that the growth of *A. tatarica* was more influenced by salinity in the topsoil. However, for *K. caspica*, the  $\Psi_L$  remained quite stable with changes of soil water and salinity in 0–20 cm layer.

## 2.5 Water stress impact on the two halophytes

The WSIS is related to precipitation frequency and intensity (Sanchez-Diaz and Kramer, 1971; Vertovec *et al.*, 2001; Xu and Li, 2006). In our case, there were 2.3, 3.2, and 0 mm rainfalls respectively before the monitoring days of 26 June 2010, 27 July 2010, and 20 August 2011. Since there was no precipitation the day before 20 August 2011, it was more representative to assess the water stress impact on *K. caspica* and *A. tatarica*. In general, the im-

pacts of water stress on *A. tatarica* were significantly greater than on *K. caspica* (Fig. 7), which indicates that *A. tatarica* was more sensitive to water stress than *K. caspica* when there was less or no rainfall recharge. When the rainfall was 7 mm on 17 August 2010, water stress impact on *K. caspica* and *A. tatarica* did not differ significantly. It indicated that 7 mm precipitation could ease the water stress of *A. tatarica* but had no significant effect on the *K. caspica* growth.

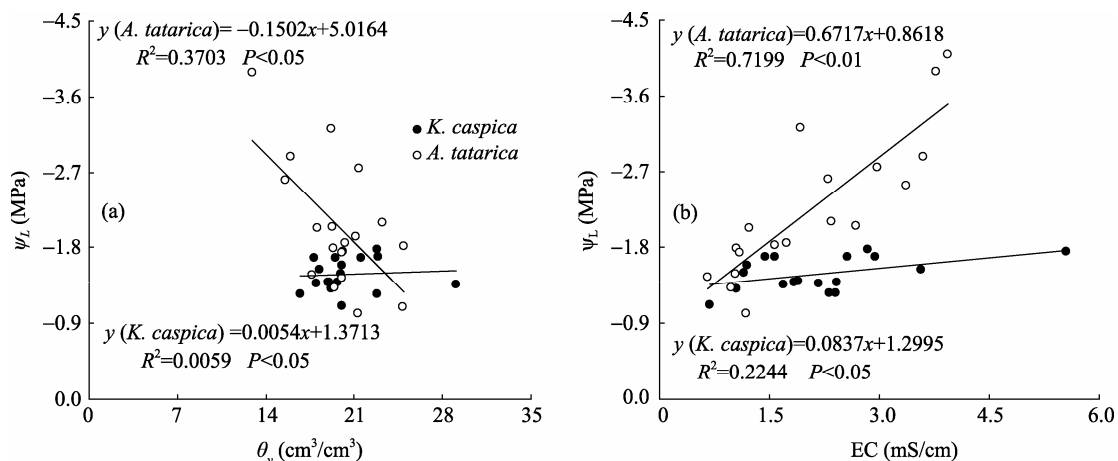
## 3 Discussion

*K. caspica* and *A. tatarica* are typical halophytes widely distributed in Manas River Basin. Both the two species displayed a lower transpiration rate and stomatal conductance at midday. According to Dong *et al.* (1994), *K. caspica* and *A. tatarica* are classified into strong xerophytes and weak midday depression type. Stomata closure limits the transportation of CO<sub>2</sub> as the raw material of photosynthesis. The higher CO<sub>2</sub> concentration generated by the CO<sub>2</sub>-concentrating mechanism in the bundle sheath of C<sub>4</sub> plants contributes to

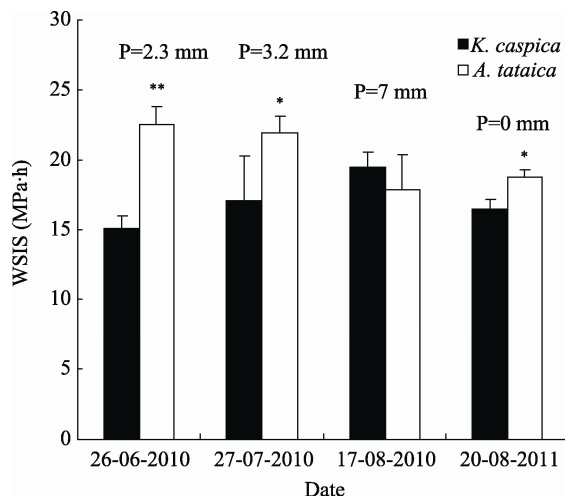
**Table 1** Growth and water consumption characteristics of *K. caspica* and *A. tatarica* on 20 August, 2010 and 2011

Year	Species	Root/shoot ratio	Leaf area ratio (g/cm <sup>2</sup> )	Amount of water consumption (g/plant)	Water use efficiency (kg/m <sup>3</sup> )
2010	<i>K. caspica</i> (Perennial)	1.3±0.06**	127.1±6.4**	182.2±15.2**	1.2±0.05
	<i>A. tatarica</i> (Annual)	0.6±0.05	55.4±5.3	88.2±6.0	3.3±0.2*
2011	<i>K. caspica</i> (Perennial)	0.8±0.08*	74.6±8.2*	186.4±20.1*	1.5±0.1
	<i>A. tatarica</i> (Annual)	0.6±0.02	57.7±1.6	126.8±18.4	5.3±0.1**

Note: \* and \*\* indicate significance at  $P<0.05$  and  $P<0.01$  level, respectively.



**Fig. 6** Relationships between leaf water potential ( $\Psi_L$ ) and soil volumetric water content ( $\theta_v$ ) (a), and soil electrical conductivity (EC) (1:5 soil to water ratio) (b) in the 0–20 cm layer



**Fig. 7** Water stress impact on species (WSIS) of *K. caspica* and *A. tatarica* during 2010 and 2011. P means precipitation. \* and \*\* indicate significance between *K. caspica* and *A. tatarica* at  $P < 0.05$  and  $P < 0.01$  level, respectively.

the suppression of apparent photorespiration as well as the saturation of photosynthesis at a lower ambient  $\text{CO}_2$  concentration. As a  $\text{C}_4$  halophyte, *A. tatarica* had the advantage of using  $\text{CO}_2$  at a lower concentration to keep a higher photosynthetic rate compared to  $\text{C}_3$  halophyte *K. caspica*. This is essential for adaptation to the drought habitat (Taylor *et al.*, 2011). Stomatal closure is the main cause for transpiration decline as water stress develops (Farquhar and Sharkey, 1982). Our results indicated that the lower stomatal conductance of  $\text{C}_4$  halophyte *A. tatarica* helped to reduce the transpiration water loss and to some degree maintained leaf water potential steadily.

Leaf water potential reflects plant physiological status under stressed conditions and can be used as an indicator of plant water status (Brown *et al.*, 1976; Jongdee *et al.*, 2002). The diurnal variation of leaf water potential in *K. caspica* and *A. tatarica* showed single-peak curves and was similar to that of *A. portulacoides* (O'Toole and Cruz, 1980; Neves *et al.*, 2008). The results showed that *A. tatarica* had lower leaf water potential, stomatal conductance and transpiration rate compared with *K. caspica*, and *A. tatarica* had less increment in stomatal conductance and transpiration rate than *K. caspica* with the decrease of leaf water potential, indicating that *A. tatarica* exhibited lower water consumption for transpiration and higher stomatal sensitivity to decreasing

leaf water potential. The change in stomatal conductance caused the change in leaf water potential by modifying transpiration rate (Farquhar and Sharkey, 1982). As an annual halophyte, *A. tatarica* has a small root/shoot ratio, and low transpiration rate can help plant to survive in the environment where available soil water is limited. Our results suggests that lower transpiration rate of *A. tatarica* was achieved by adjusting stomatal conductance that reduced water loss and maintained leaf water potential steadily. In addition, the results also indicated that the  $\text{C}_4$  halophyte *A. tatarica* required less water to maintain the same leaf water potential, and at the same time possessed higher water use efficiency as compared to  $\text{C}_3$  halophyte *K. caspica*. Our result was in accordance with the conclusion of Kalapos *et al.* (1996) who reported less water consumption and greater water use efficiency in  $\text{C}_4$  species *Tragus racemosus* considerably postponed the development of plants under water stress.

Root distribution is closely related to root water uptake (Gardner, 1964; Yu *et al.*, 2007). Deep soil water was the main water source for *K. caspica* (Zeng *et al.*, 2006). In our study area, groundwater depth is around 2.5 m and rises gradually in recently years due to field irrigation (Li *et al.*, 2008). As a perennial halophyte, *K. caspica* had a larger root/shoot ratio beneficial for uptaking deep soil water. Similar to  $\text{C}_3$  species *Triticum aestivum* (Kalapos *et al.*, 1996), it appears that deep-rooted *K. caspica* is able to exploit deeper soil water source in a more effective way. We indicated that water-saving species (*A. tatarica*) had a small root/shoot ratio, and prevented water deficit damage, decreasing water loss by closing their stomata and reducing the transpiration water loss; in contrast, water-consuming species (*K. caspica*) showed a large root/shoot ratio, and extracted water from soil to support high leaf gas exchange rates by increasing water absorption from deep soil, which was the same results with Levitt (1980). In addition, the results that different physiological behaviors appear to be related mainly to architectural traits were also found in the seedlings of seven Mediterranean species (Hernández *et al.*, 2010).

Just as the optimal phenotype theory (Schwinning and Ehleringer, 2001), our study implied that as a perennial halophyte, *K. caspica* used mainly deep soil



water and groundwater source, and it exhibited a larger root/shoot ratio, predominantly deep root system, and low stomatal sensitivity to decreasing leaf water potential. *A. tatarica* used primarily upper soil water; and as an annual plant, it displayed a small root/shoot ratio, and high stomatal sensitivity to decreasing leaf water potential. So our results provided a case for the phenotype theory of Schwinning and Ehleringer (2001) on halophytic plants.

Manas River Basin exhibits typical arid features with an extremely small amount of precipitation and great potential evaporation capacity. The plants grown in this region have been under a long period of water deficit. As a perennial halophyte, *K. caspica* used mainly deep soil water, and the small amount of precipitation rarely affected the growth of *K. caspica*. Our results indicated that *A. tatarica* showed higher water stress impact than *K. caspica*, indicating that the growth of *A. tatarica* was more limited than *K. caspica* when there was no rainfall recharge. Thus it was supported by the facts that *A. tatarica* had lower transpiration water consumption and less water demand than *K. caspica* when the same leaf water potential was maintained. It deserves further study on whether the C<sub>4</sub> species *A. tatarica* is more drought-tolerant

than the C<sub>3</sub> species *K. caspica* or not. In addition, soil salinity affects plant water absorption and leaf water potential, and ion accumulation in leaves helps to resist external salt stress (Belkheiri and Mulas, 2011).

## 4 Conclusion

The perennial C<sub>3</sub> species *K. caspica* possessed rich water supply from root absorption, while sparing water consumption was exhibited for the annual C<sub>4</sub> species *A. tatarica*. Combining with other results, we concluded that the abilities to tap water by deep roots help C<sub>3</sub> species (*K. caspica*) to adapt to the arid habitats. For the C<sub>4</sub> species (*A. tatarica*), economizing on water expenses by reduced stomatal conductance and less transpiration water loss in shoots is a strategy to survive in the arid environment.

## Acknowledgements

This research was supported by the National Basic Research Program of China (2009CB825101) and the Specialized Research Fund for the Doctoral Program of Higher Education of China (20110008110035). We are very grateful to the staff of Ecology Laboratory of the Shihezi University for their invaluable help in field sampling.

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