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SPECIAL FEATURE

Trends in isotope ecology

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Responses of the carbon and oxygen isotope compositions of desert plants to spatial variation in soil salinity in Central Asia

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Abstract We examined the isotopic parameters in two C_3 species (*Artemisia diffusa* H. Krasch and *Tamarix hispida* Willd.) and a C_4 species [*Haloxylon aphyllum* (Minkw.) Iljin.] growing or planted in soils with different levels of salinity in a Central Asian desert. The oxygen isotope ratios of stem water ($\delta^{18}O_{stem}$) in *T. hispida* and *H. aphyllum* distributed in high-salinity zones were similar to the $\delta^{18}O$ of artesian water ($\delta^{18}O_{artesian}$) and different from that in *A. diffusa* distributed in lower-salinity zones. This indicates that *T. hispida* and *H. aphyllum* depend on water with low salinity in the deeper soil layer, whereas *A. diffusa* depends on water in the shallower soil layer that would be affected by salt accumulation. The carbon isotope composition of leaf organic matter ($\delta^{13}C_{om}$) and oxygen isotope enrichment in leaf organic matter above stem water ($\Delta^{18}O_{om}$) were lower in *A. diffusa* than in the other species. The responses of $\delta^{13}C_{om}$ and $\Delta^{18}O_{om}$ to soil salinity observed for *T. hispida* suggest that the species decreased its transpiration rate and increased its intrinsic water-use efficiency in response to increasing soil salinity. The $\delta^{13}C_{om}$ and $\Delta^{18}O_{om}$ of *H. aphyllum* were higher than those of the C_3 species, and were not correlated with soil salinity, suggesting that *H. aphyllum* reduced its salt uptake by decreasing transpiration—even though it was able to access less saline water in the deeper soil layer. These results indicate that the water-use strategy of desert plants in high-salinity environments can be assessed based on their carbon and oxygen isotope ratios.

Keywords Salt tolerance · *Tamarix hispida* · *Artemisia diffusa* · *Haloxylon aphyllum* · Water source · Water-use efficiency · Transpiration rate

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Introduction

Soil salinization has damaged the natural vegetation in Central Asian deserts, even though most of the native species are salt-resistant. The response of native species to soil salinity should be examined to predict the impact of soil salinization on natural vegetation. Salt-tolerant plants adapt to high-salinity environments by various mechanisms (Gorham 1996; Flowers and Colmer 2008). Some plants obtain less saline water by growing only during the rainy season when the salinity at the soil surface decreases, or extending their roots close to the groundwater table (Xu and Li 2006). Some plants exclude excess salt using specific organs such as salt glands (Scholander et al. 1962), and others use succulent leaves to protect their cytoplasmic enzymes from high salinity by accumulating salts in vacuoles (Wyn Johns and Gorham 2002). In addition, some plants enhance osmotic pressure by accumulating compatible solutes in their cells (Sanada et al. 1995; Ghoulam et al. 2002). Most mechanisms are related either to the protection of photosynthetic machinery from salt or the maintenance of water uptake in high-salinity environments, which affects water-use efficiency, defined as the ratio of growth to water consumption, or the ratio of photosynthesis to transpiration.

The carbon isotope composition ($\delta^{13}C$) of plant material is related to the intrinsic water-use efficiency in C_3 plants (Farquhar et al. 1989). Leaf organic matter in

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C_3 plants is less ^{13}C-enriched than is source CO_2 due to C_3 photosynthesis (Farquhar et al. 1989). ^{13}C discrimination during photosynthesis ($\Delta^{13}C_{om}$) has the following relationship with the ratio of intercellular to atmospheric CO_2 (C_i/C_a), known as the intrinsic water-use efficiency (Farquhar et al. 1989):

$$\Delta^{13}C_{om} = \frac{\delta^{13}C_{air} - \delta^{13}C_{om}}{1 + \delta^{13}C_{om}} \approx \delta^{13}C_{air} - \delta^{13}C_{om} = a + (b - a)\frac{C_i}{C_a} \quad (1)$$

where $\delta^{13}C_{air}$ and $\delta^{13}C_{om}$ are the $\delta^{13}C$ in atmospheric CO_2 and leaf organic matter (‰), respectively, a is a fractionation factor due to the smaller diffusivity of $^{13}CO_2$ through the stomata (=4.4 ‰, Farquhar et al. 1989), b is the fractionation factor caused by rubisco and phosphoenolpyruvate carboxylase (=27 ‰, O'Leary et al. 1981), and C_i and C_a are the intercellular and atmospheric CO_2 concentrations (μmol mol^{-1}), respectively. Increasing intrinsic water-use efficiency is associated with decreasing $\Delta^{13}C_{om}$, and when the $\delta^{13}C_{air}$ is spatially uniform at a site, it is associated with increasing $\delta^{13}C_{om}$. Positive correlations have been found between substrate salinity and $\delta^{13}C_{om}$ in both salt-tolerant (Guy et al. 1980; Farquhar et al. 1982; Sobrado 1999) and salt-sensitive species (Seemann and Critchley 1985). These reports indicate that salt stress decreases C_i via stomatal closure and consequently increases intrinsic water-use efficiency.

On the other hand, the oxygen isotope composition ($\delta^{18}O$) of plant material reflects leaf evaporative conditions, the responses of leaf transpiration to environmental conditions, and the $\delta^{18}O$ of source water (Farquhar et al. 1998, 2007). Compared to source water, leaf water is more enriched in ^{18}O due to transpiration, because the diffusivity of $H_2^{18}O$ is smaller than that of $H_2^{16}O$, and the vapor pressure of $H_2^{18}O$ is lower than that of $H_2^{16}O$ (Farquhar et al. 1998). Furthermore, the $\delta^{18}O$ of plant materials, including cellulose, reflects the ^{18}O enrichment of leaf water due to the exchange of oxygen atoms between the medium water and carbonyl oxygen (Sternberg and DeNiro 1983). The ^{18}O enrichment of plant materials to source water ($\Delta^{18}O_{om}$) is defined as:

$$\Delta^{18}O_{om} = \frac{\delta^{18}O_{om} - \delta^{18}O_{sw}}{1 + \delta^{18}O_{sw}} \approx \delta^{18}O_{om} - \delta^{18}O_{sw} \quad (2)$$

where $\delta^{18}O_{om}$ and $\delta^{18}O_{sw}$ are the $\delta^{18}O$ of leaf organic matter and source water (‰), respectively. Decreasing transpiration is associated with increasing $\Delta^{18}O_{om}$ in plants growing under the same conditions and evaporative demands (Barbour et al. 2000; Farquhar et al. 2007). Salt stress decreases transpiration via stomatal closure in salt-tolerant species (Ball and Farquhar 1984; Brugnoli and Lauteri 1991; Lin and Sternberg 1993; Maricle et al. 2007) and in salt-sensitive species (Brugnoli and Lauteri 1991). Thus, salt stress may affect the $\delta^{18}O_{om}$ as well as the $\delta^{13}C_{om}$. Moreover, the $\delta^{18}O$ of source water ($\delta^{18}O_{sw}$) must be determined for each plant because each plant may have a different water source, which also affects salt uptake. The $\delta^{18}O$ of stem water is assumed to be equal to that in source water because no change in the $\delta^{18}O$ of water is observed during uptake before it reaches the leaves (Yakir 1992).

We, therefore, hypothesized that intrinsic water-use efficiency, transpiration, and source water, which are essential to our understanding of how desert plants adapt to high-salinity environments, can be estimated based on the $\delta^{13}C$ and $\delta^{18}O$ in leaf organic matter and the $\delta^{18}O$ in stem water. To test this hypothesis, we examined these isotopic parameters in three dominant plants growing, or planted, in soils with different levels of salinity in a Central Asian desert.

Materials and methods

Study site and plant materials

This study was conducted in the Kyzylkum Desert, located at the center of the Republic of Uzbekistan (41°05′N, 64°52′E). This region has a typical inland arid climate with hot, dry summers and cold winters; the annual mean temperature is 11.4 °C, and the annual mean precipitation, which occurs mainly from November to May, is 120 mm. Seven experimental plots with different vegetation types were established at the study site over a length of 7 km (Shuyskaya et al. 2012). Three dominant species were analyzed in this study: *Artemisia diffusa* H. Krasch (C_3 species), *Tamarix hispida* Willd. (C_3 species), and *Haloxylon aphyllum* (Minkw.) Iljin (C_4 species). *Artemisia diffusa*, which is a dominant native vegetative species, was distributed in plots 2 and 3, *T. hispida*, which is frequently found after salinization, was distributed in plots 1, 5, 6, and 7, and *H. aphyllum*, which is a native vegetative species, was planted in all plots as a sand shield.

Sampling and measurement procedures

Sample collection was conducted in the seven plots in the summers of 2007 and 2008. Soil samples were collected from 0 to 120 cm deep at 20-cm intervals. After the fresh weights (FW) of the soil samples collected in 2007 were measured, the samples were oven-dried and re-weighed (DW). The soil water content (SWC) was given by $(FW - DW)/DW \times 100$(g water/g soil %). Soluble salts were extracted from 100 mg of the air-dried soil samples collected in 2008 using distilled water, and the concentration of Na^+ in the solution was analyzed using an atomic-adsorption spectrometer (Model 207; Hitachi, Tokyo, Japan) at the K. A. Timiriazev Plant Physiology Institute, Russian Academy of Science, Russia. Artesian water was collected at the wells of plots 1 and 5. Stem samples with well-developed periderm

were collected from three individuals of each species in 2008. Water was cryogenically extracted from the stem samples in the laboratory at Mie University, Japan. Leaf samples were also collected from three individuals of each species in 2007 and 2008, and then oven-dried at 70 °C for 48 h and finely ground.

The carbon and oxygen isotope ratios were expressed in standard delta notation (‰) relative to the VPDB (Vienna Pee Dee belemnite) and VSMOW (Vienna Standard Mean Ocean Water) standards, respectively:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{18}\mathrm{O} = \frac{R_{\mathrm{sample}}}{R_{\mathrm{standard}}} - 1 \quad (3)$$

where R_{sample} and R_{standard} represent the $^{13}C/^{12}C$ or $^{18}O/^{16}O$ of the samples and the standard, respectively. The $\delta^{18}O$ in the artesian water ($\delta^{18}O_{\mathrm{artesian}}$) and the stem water ($\delta^{18}O_{\mathrm{stem}}$) were analyzed using an isotope ratio mass spectrometer (MAT252; Thermo Fisher Scientific, Rockford, IL, USA) at the Center for Ecological Research, Kyoto University, Japan. The precision of the analyses was ±0.08 ‰. Because ^{18}O discrimination does not occur during water uptake by plants, the $\delta^{18}O_{\mathrm{stem}}$ reflects that of the source water (Yakir 1992). Many studies estimate the depth from which plants absorb water by comparing the $\delta^{18}O_{\mathrm{stem}}$ with the $\delta^{18}O$ of a potential source water (Dawson 1993; Greaver and Sternberg 2006). However, as we could not collect soil water or groundwater, we determined differences in source water among the three species by comparing their $\delta^{18}O_{\mathrm{stem}}$ values. The $\delta^{13}C$ in the leaf samples ($\delta^{13}C_{\mathrm{om}}$) was analyzed using a continuous flow system with an elemental analyzer and an isotope ratio mass spectrometer (Flash2000 and Delta-S; Thermo Fisher Scientific) at the Field Science Education and Research Center, Kyoto University. The precision of the analyses was ±0.05 ‰. The $\delta^{13}C$ in atmospheric CO_2 ($\delta^{13}C_{\mathrm{air}}$) was assumed to be uniform over the seven plots where the air was well mixed because the canopies were fully open. The $\delta^{18}O$ in the same leaf samples ($\delta^{18}O_{\mathrm{om}}$) was also analyzed using a continuous flow system with a pyrolysis-type elemental analyzer and an isotope ratio mass spectrometer (TC/EA and Delta-plus-XP; Thermo Fisher Scientific) at the Research Institute for Humanity and Nature, Japan. The precision of the analyses was ±0.34 ‰. The $\delta^{18}O_{\mathrm{stem}}$ was used for $\delta^{18}O_{\mathrm{sw}}$ in Eq. (2), following Yakir (1992), to calculate $\Delta^{18}O_{\mathrm{om}}$. The $\delta^{18}O_{\mathrm{stem}}$ was only measured in 2008, whereas the $\delta^{18}O_{\mathrm{om}}$ was measured both in 2007 and 2008. We assumed that the $\delta^{18}O_{\mathrm{sw}}$ of the plants would not change during the 2 years.

Data analyses

Relationships between the environmental conditions and isotopic parameters were analyzed by ordinary least-squares regression. Differences in isotopic parameters among species and plots were tested by an analysis of variance using SPSS software (SPSS Japan Inc., Tokyo, Japan). Results were considered statistically significant at $p < 0.05$.

Results

Soil moisture and salinity

The mean water content in soil at a depth of 0–120 cm ranged from 1.5 to 7.8 g water/g soil % (Fig. 1a). Plots 1–4 had similar water contents, while plots 5–7 had higher water contents (Fig. 1a). The mean Na^+ concentration in the soil at 0–120 cm deep ranged from 0.1 to 9.0 mg eq/100 g soil (Fig. 1b). The Na^+ concentration was lower in plots 2 and 3, at which natural vegetation dominated (Fig. 1b). The highest concentration was observed in plot 7 (Fig. 1b), particularly at the soil surface (56.6 mg eq/100 g soil; not shown in Fig. 1b).

Plant water source

The mean $\delta^{18}O_{\mathrm{stem}}$ was significantly higher in *A. diffusa* than in the other species ($p < 0.01$) (Table 1). No difference was observed in $\delta^{18}O_{\mathrm{stem}}$ between *T. hispida* and *H. aphyllum* growing in the same plots ($p = 0.076$) (Table 1), indicating that *T. hispida* and *H. aphyllum* depended on the same water source. The $\delta^{18}O_{\mathrm{stem}}$ values of *T. hispida* and *H. aphyllum* were similar to those of $\delta^{18}O_{\mathrm{artesian}}$ in plots 1 and 5 (Fig. 2). Assuming that the $\delta^{18}O_{\mathrm{artesian}}$ was equal to the $\delta^{18}O$ in the groundwater of this area, *T. hispida* and *H. aphyllum* may depend on

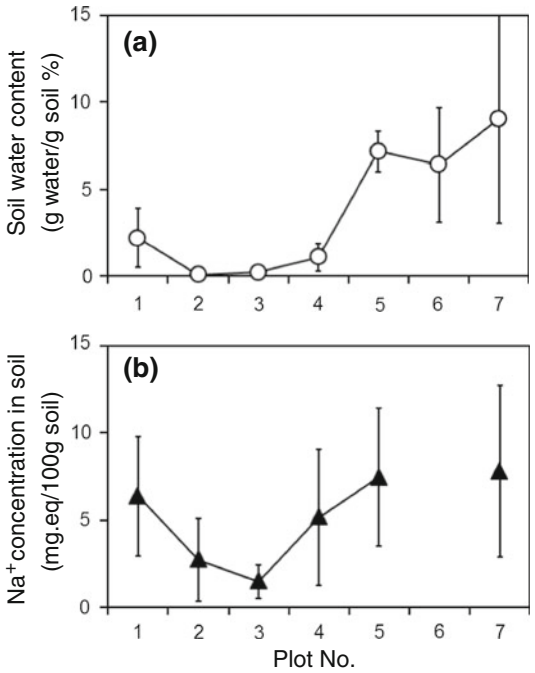

Fig. 1 Mean water content (**a**) and Na^+ concentration (**b**) in the soil at 0–120 cm deep in each experimental plot. *Error bars* represent the standard deviation of the mean

Table 1 Mean values of the isotopic parameters for *Artemisia diffusa*, *Tamarix hispida*, and *Haloxylon aphyllum*

Parameter	*Artemisia diffusa*	*Tamarix hispida*	*Haloxylon aphyllum*
$\delta^{13}C_{om}$ (‰)	-27.35 ± 0.82^{a} ($n = 11$)	-25.35 ± 1.26^{b} ($n = 24$)	-12.43 ± 0.49^{c} ($n = 39$)
$\delta^{18}O_{stem}$ (‰)	-1.60 ± 0.43^{a} ($n = 4$)	-10.48 ± 0.86^{b} ($n = 12$)	-9.17 ± 1.98^{b} ($n = 18$)
$\delta^{18}O_{om}$ (‰)	31.13 ± 1.73^{a} ($n = 11$)	30.77 ± 2.98^{a} ($n = 24$)	47.35 ± 3.07^{b} ($n = 39$)
$\Delta^{18}O_{om}$ (‰)	32.73 ± 1.83^{a} ($n = 11$)	41.25 ± 2.98^{b} ($n = 24$)	56.02 ± 2.85^{c} ($n = 36$)

Values are mean ± standard deviation and values with the same subscript do not differ significantly ($p < 0.05$)

water in the deep layer of the soil, at least in plots 1 and 5. The $\delta^{18}O_{stem}$ was higher in *A. diffusa* than in *H. aphyllum* in the same plots (Fig. 2), indicating that the *A. diffusa* water source was different from that of *H. aphyllum* and could not be water from the deep soil layer.

Long-term trends in intrinsic water-use efficiency

In the C_3 species, $\delta^{13}C_{om}$ was significantly higher in *T. hispida* than in *A. diffusa* ($p < 0.01$) (Table 1), indicating that *T. hispida* had a higher intrinsic water-use efficiency than *A. diffusa*. The $\delta^{13}C_{om}$ of *T. hispida* was significantly higher in plot 7, which had the highest soil Na^{+} concentration, compared to that in plots 1 and 5 ($p < 0.05$). The $\delta^{13}C_{om}$ of the C_4 species, *H. aphyllum*, ranged from −13 to −12 ‰.

Long-term transpiration trends

$\delta^{18}O_{om}$, which reflects ^{18}O enrichment during transpiration as well as the $\delta^{18}O$ of source water ($\delta^{18}O_{sw}$), was significantly higher in *H. aphyllum* than in the C_3 species ($p < 0.01$) (Table 1). $\Delta^{18}O_{om}$, which was calculated by $\delta^{18}O_{om}$ and $\delta^{18}O_{stem}$ with the assumption that $\delta^{18}O_{stem}$ varied little from 2007 to 2008, was significantly higher in *H. aphyllum* ($p < 0.01$) and lower in *A. diffusa* than in *T. hispida* ($p < 0.01$) (Table 1). Theory suggests that plants with higher transpiration rates have lower $\Delta^{18}O_{om}$ when they are grown under the same conditions of air temperature and humidity (Barbour et al. 2000; Farquhar et al. 2007). We assumed that there was no difference in atmospheric conditions between the plots. Thus, variation in $\Delta^{18}O_{om}$ between species or plots was expected to reflect a difference in transpiration. The $\Delta^{18}O_{om}$ data suggested that the long-term average transpiration rate may be higher in *A. diffusa* and lower in *H. aphyllum* than in *T. hispida*.

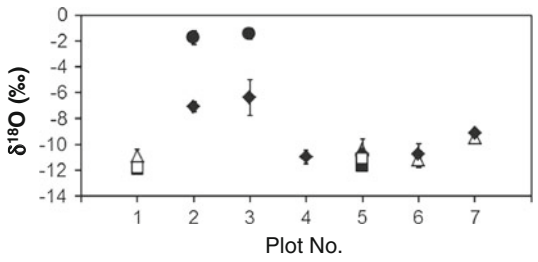

Fig. 2 The oxygen isotope ratio ($\delta^{18}O$) of stem water in *Artemisia diffusa* (*circles*), *Tamarix hispida* (*triangles*), and *Haloxylon aphyllum* (*diamonds*), and the $\delta^{18}O$ of artesian water in 2007 (*black squares*) and 2008 (*white squares*). *Error bars* represent the standard deviation of the mean

Discussion

Water-use strategy of *A. diffusa*

Artemisia diffusa was distributed only in zones of low soil moisture and salinity (Fig. 2). The higher $\delta^{18}O_{stem}$ indicates that the water source of *A. diffusa* was different from that of *T. hispida* and *H. aphyllum*. Roots of *A. diffusa* are distributed at a shallower depth (1.1–2.5 m) compared with those of the other two species (Gintzburger et al. 2003). These results indicate that *A. diffusa* depends on water in the shallower layers of the soil, and, therefore, was more affected by salt accumulation. This water-use characteristic would explain why *A. diffusa* was not distributed in higher-salinity zones, where much salt accumulated in the shallower soil layer. The amount of available water for *A. diffusa* was expected to be smaller than that for the other two species because of the shallower root distribution of *A. diffusa*. However, its lower $\delta^{13}C_{om}$ and $\Delta^{18}O_{om}$ suggest that *A. diffusa* has lower intrinsic water-use efficiency and a higher transpiration rate. *Artemisia diffusa* grows during the rainy season from March to June and stops activity during summer when there is less precipitation (Gintzburger et al. 2003). Therefore, the lower $\delta^{13}C_{om}$ and $\Delta^{18}O_{om}$ would indicate lower intrinsic water-use efficiency and a higher transpiration rate during the growing season when the water content in the upper soil layer is abundant. This phenological strategy may enable *A. diffusa* to survive in environments with low soil moisture.

Physiological response of *T. hispida* to variations in soil salinity

Tamarix hispida was distributed in high-salinity zones and had a higher $\delta^{13}C_{om}$ and $\Delta^{18}O_{om}$ than *A. diffusa*, which was distributed only in less saline zones (Fig. 2). The $\delta^{13}C_{om}$ of *T. hispida* was higher in plot 7, where the soil moisture and salinity were high (Figs. 3, 4). However, previous studies have reported that a decrease in

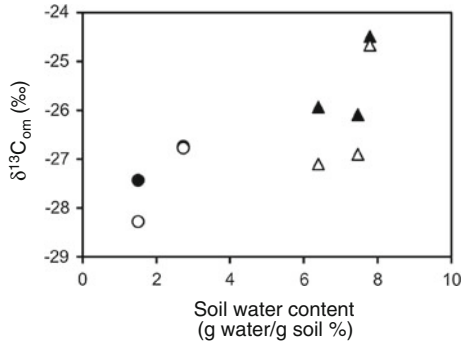

Fig. 3 The carbon isotope composition of leaf organic matter ($\delta^{13}C_{om}$) in *Artemisia diffusa* (*circles*) and *Tamarix hispida* (*triangles*) plotted against the mean water content in the soil at 0–120 cm deep. *White* and *black symbols* refer to the data for 2007 and 2008, respectively. *Error bars* represent the standard deviation of the mean

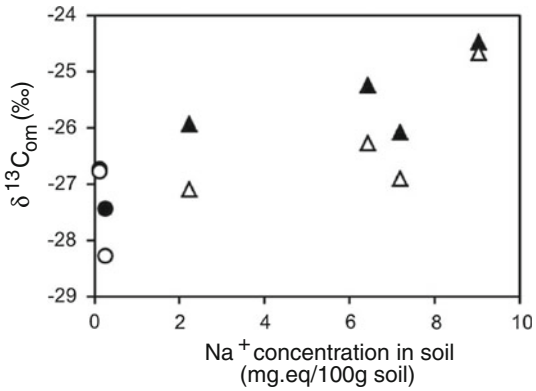

Fig. 4 The carbon isotope composition of leaf organic matter ($\delta^{13}C_{om}$) in *Artemisia diffusa* (*circles*) and *Tamarix hispida* (*triangles*) plotted against the mean Na^+ concentration in the soil at 0–120 cm deep. *White* and *black symbols* refer to the 2007 and 2008 data, respectively. *Error bars* represent the standard deviation of the mean

available water induces stomatal closure and enhances the intrinsic water-use efficiency, which results in an increase in $\delta^{13}C_{om}$ (Farquhar and Richards 1984). Previous studies have also reported positive correlations between soil salinity and $\delta^{13}C_{om}$ in some salt-tolerant species (Guy et al. 1980; Farquhar et al. 1982) and salt-sensitive species (Seemann and Critchley 1985); they concluded that low soil water potential due to high salinity decreased C_i through stomatal closure, resulting in ^{13}C enrichment in leaf organic matter. Therefore, the higher $\delta^{13}C_{om}$ found in *T. hispida* in plot 7 would be attributable to high soil salinity, not to high soil moisture. In contrast, a significant correlation was observed between soil salinity and $\Delta^{18}O_{om}$ in *T. hispida* in 2008 (Fig. 6). This observation suggests that the transpiration rate of *T. hispida* decreased slightly with increasing soil salinity, consistent with previous reports. There was no correlation between soil salinity and $\Delta^{18}O_{om}$ in 2007. This may have resulted from the assumption in the $\Delta^{18}O_{om}$ calculation that $\delta^{18}O_{stem}$ did not vary throughout the 2 years. The $\delta^{18}O_{stem}$ of *T. hispida* was similar to the $\delta^{18}O_{artesian}$ (Fig. 2), indicating that *T. hispida* could obtain less saline water from the deeper soil layer. *Tamarix hispida* in the Central Asian desert extends its roots to depths of 6–8 m and excludes excessive salt through salt glands (Gintzburger et al. 2003). *Tamarix ramosissima*, which dominates in areas of high salinity and high groundwater in the Central Asian desert, also extends its main and feeder roots close to the groundwater table (Xu and Li 2006; Xu et al. 2007). These observations suggest that *T. hispida* maintains low transpiration rates and increases its intrinsic water-use efficiency even in high-salinity zones because they depend on less saline water in the deeper soil layer and exclude excessive salt though salt glands.

Physiological adaptation of *H. aphyllum*

Haloxylon aphyllum is a native C_4 species that is planted in a wide range of salinity levels as a sand shelter (Figs. 4, 6). C_4 species tend to have lower transpiration rates and higher intrinsic water-use efficiencies relative to C_3 species. Therefore, it was expected that the intrinsic water-use efficiency of *H. aphyllum* would be higher than that of the C_3 species. The $\Delta^{18}O_{om}$ of *H. aphyllum* was higher than that of the C_3 species (Table 1), and was not significantly correlated with soil moisture or salinity (Figs. 5, 6). These results suggest that *H. aphyllum* maintains low transpiration rates over a wide range of soil moisture and salinity conditions. Our $\delta^{18}O_{stem}$ data indicate that *H. aphyllum* is able to access less saline water in the deeper soil layer (Fig. 2), in agreement with a previous report showing that *H. aphyllum* extends its roots 9–16 m deep (Gintzburger et al. 2003). Such a water-use strategy may enable *H.*

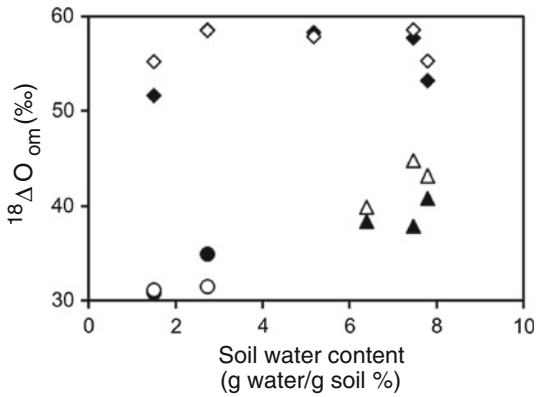

Fig. 5 Oxygen isotope enrichment in leaf organic matter above stem water ($\Delta^{18}O_{om}$) in *Artemisia diffusa* (*circles*), *Tamarix hispida* (*triangles*), and *Haloxylon aphyllum* (*diamonds*) plotted against the mean water content in the soil at 0–120 cm deep. *White* and *black symbols* refer to the 2007 and 2008 data, respectively. The *solid* and *dashed lines* are simple regression lines for *A. diffusa* during 2008 and *T. hispida* during 2007, respectively. *Error bars* represent the standard deviation of the mean

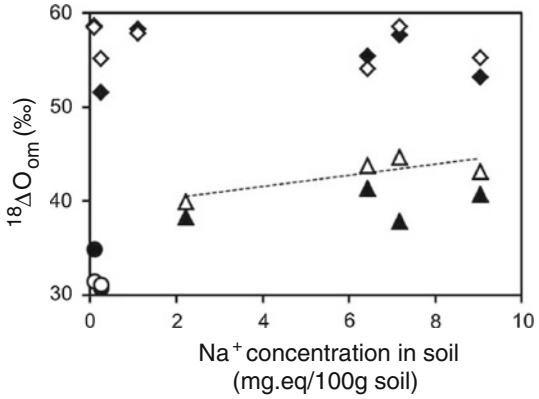

Fig. 6 Oxygen isotope enrichment in leaf organic matter above that of stem water ($\Delta^{18}O_{om}$) in *Artemisia diffusa* (*circles*), *Tamarix hispida* (*triangles*), and *Haloxylon aphyllum* (*diamonds*) plotted against the mean Na^+ concentration in the soil at 0–120 cm deep. *White* and *black symbols* refer to the 2007 and 2008 data, respectively. The *dashed line* is a simple regression line for *T. hispida* during 2007. *Error bars* represent the standard deviation of the mean

aphyllum to maintain a low transpiration rate under various salt conditions and reduce the damage caused by salinity.

In addition to the differences in source water and water-use efficiency estimated by the $\delta^{18}O_{sw}$ and $\delta^{13}C_{om}$, respectively, we found that the responses of transpiration to increasing soil salinity were different among the three species by investigating the $\Delta^{18}O_{om}$. Our findings indicate that the water-use strategy of desert plants in high-salinity environments can be assessed by the $\delta^{13}C$ and $\delta^{18}O$ of leaf organic matter and the $\delta^{18}O$ of stem water.

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