

# Relationships between foliar carbon isotope discrimination with potassium concentration and ash content of the riparian plants in the extreme arid region of China

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## Abstract

Carbon isotope discrimination ( $\Delta$ ) has been proposed as an indirect estimation criterion for water use efficiency in  $C_3$  plants. Because of the higher cost for  $\Delta$  analysis, ash content or K concentration has been proposed as an alternative criterion for  $\Delta$  in many species. In five typical habitats of the extreme arid Ejina desert oasis in northwest of China, the seasonal variations of foliar  $\Delta$ , ash content, and potassium (K) concentration were researched in two constructive desert riparian plants (*Populus euphratica* Olivier, *Tamarix ramosissima* Ledeb.). The correlations of foliar  $\Delta$  with ash content and K concentration in both species were also examined to evaluate the feasibility of the foliar ash content and K concentration as surrogates of  $\Delta$  in *P. euphratica* and *T. ramosissima*. Results showed that there were significant effects of plant species, habitats and growth season on foliar  $\Delta$ , ash content, and K concentration. Foliar  $\Delta$  and K concentration in *P. euphratica* were significantly higher than those in *T. ramosissima*, whereas, the ash content was reverse. Among habitats, the trends of  $\Delta$  signatures in both *P. euphratica* and *T. ramosissima* were similar,  $\Delta$  values and ash content in both species were the lowest in the dune. Both in the Gobi and dune sites, K concentration in *P. euphratica* and *T. ramosissima* was different. In the whole growth period, foliar  $\Delta$  values and ash content in both species were gradually increased, but K concentration was decreased. Ash content was significantly and positively related to  $\Delta$  in both *P. euphratica* and *T. ramosissima*. However, significantly negative correlations between foliar  $\Delta$  and K concentration as well as between ash content and K in *P. euphratica* were found. In *T. ramosissima*, the relationship was positive but very weak.

*Additional key words:* ash; carbon isotope discrimination; desert riparian forest; extreme arid area; *Populus euphratica* Olivier; potassium concentration; *Tamarix ramosissima* Ledeb.

## Introduction

In ecological studies, the number of measurements of stable isotopes naturally occurring in biological materials have increased in recent years (Ehleringer 1993, Warren *et al.* 2001, Su *et al.* 2005, Xu *et al.* 2007, Tsialtas *et al.* 2008).  $\Delta$  (the  $^{13}\text{C}/^{12}\text{C}$  ratio in plant tissues compared to the air), determined mainly in leaves, has proved a powerful tool for studying plant ecophysiology under field conditions (Dawson *et al.* 2002).  $\Delta$  is associated with the ratio of  $\text{CO}_2$  concentration in the leaf inter-

cellular spaces to that one in the atmosphere ( $C_i/C_a$ ) (Farquhar *et al.* 1982). More positive  $\Delta$  indicates higher  $C_i/C_a$  ratio, resulting from either lower chloroplast demand for  $\text{CO}_2$  or greater stomatal conductance affecting the supply rate of  $\text{CO}_2$  and transpiration (Farquhar *et al.* 1982, 1989). Theoretical and empirical studies have demonstrated that  $\Delta$  is highly and negatively correlated with the plants long-term water use efficiency (WUE, the ratio of the biomass produced to the water consumed

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Abbreviations:  $C_i/C_a$  – ratio of  $\text{CO}_2$  concentration in the leaf intercellular spaces to that one in the atmosphere; DM – dry mass; K – potassium; MMT – mean maximum temperature; MT – mean temperature; P – precipitation; PAR – mean monthly photosynthetically active radiation; RH – mean relative humidity; ST – mean soil temperature; WUE – water use efficiency; WV – mean wind velocity;  $\Delta$  – carbon isotope discrimination;  $\delta^{13}\text{C}$  – carbon isotope composition.

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to produce it or the ratio of net photosynthesis to stomatal conductance over a period of seconds or minutes) in C<sub>3</sub> species (Farquhar *et al.* 1982, 1989, Farquhar and Richards 1984, Condon *et al.* 1990, Ehleringer 1993, Warren *et al.* 2001, Tsialtas *et al.* 2002). Furthermore, recent studies have verified that  $\Delta$  could be used as a surrogate to select for improving WUE in crops and trees (Farquhar *et al.* 1989, Yan *et al.*, 1998, Merah *et al.* 1999, 2001a, Impa *et al.* 2005, Tambussi *et al.* 2007, Tsialtas *et al.* 2008). WUE and  $\Delta$  also depend on the plant type (Yan *et al.* 1998, Zheng *et al.* 2007), growth season differences (Smedley *et al.* 1991, Ehleringer 1992, Leffler 1999, Zhao *et al.* 2006, 2007), and environmental factors (Farquhar 1989, Merah 1999, Dawson 2002, Zheng *et al.* 2007), among which the strongest correlation between  $\Delta$  and soil water availability in single environmental factor in many results has been documented (Wright *et al.* 1994, Warren *et al.* 2001, Monneveux *et al.* 2005). The  $\Delta$  signature of plant tissue may be an information-rich signal that provides useful insights into plant performance in the context of ecosystem functions (Warren *et al.* 2001) and integrates physiological and environmental properties that influence the interaction among all aspects of plant carbon and water relations over the period of growth (Smedley *et al.* 1991).

Meanwhile, the use of carbon isotope discrimination in screening of high WUE plants has its advantages over the conventional techniques.  $\Delta$  is an integrated value over plant life and only small sample of dry matter is required. The measurement is precise with a coefficient variation of 0.2‰ and  $\delta^{13}\text{C}$  can be measured at any stage of the plant. However, the expensive equipment and high cost of analysis as well as the precise technical skills required for carbon isotope analysis have seriously restricted  $\Delta$  use (Araus *et al.* 1998, Tsialtas *et al.* 2002). So, reliable surrogates need to be found so as to substitute for  $\Delta$  determination (Voltas *et al.* 1998, Tsialtas *et al.* 2002, 2006, 2008). Many researches have documented that ash content or K concentration could be a cheap and easy way to determine surrogates of  $\Delta$  (Araus *et al.* 1998, Merah *et al.* 1999, 2001b, Misra *et al.* 2006, Zhao *et al.* 2007, Tsialtas *et al.* 2002, 2008). Moreover, K is a major plant macronutrient that plays important roles related to stomatal behavior, osmoregulation, enzyme activity, cell expansion, neutralization of nondiffusible negatively charged ions, and membrane polarization (Epstein 1972, Clarkson and Hanson 1980, Marschner 1995, Elumalai *et al.* 2002). Plants must absorb the bulk of K<sup>+</sup> from the soil to maintain normal growth and development (Kochian and Lucas 1988, Maathuis and Sanders 1996). Thus, relationships between  $\Delta$  and K concentration will continue to be an interesting spot in plant physiological aspects for further research.

However, there were different correlations with foliar  $\Delta$  and ash content or K concentration. For example, positive association between leaf  $\Delta$  and ash content, and a negative relationship between grain  $\Delta$  and grain ash

content were found in several cereals (Masle *et al.* 1992, Voltas *et al.* 1998, Merah *et al.* 1999, 2001b, Xu *et al.* 2007). The positive correlations between  $\Delta$  and K concentration were found in grassland species (Masle *et al.* 1992, Tsialtas *et al.* 2002), *Artemisia ordosica* and *Hedysarum scoparium* (Zhao *et al.* 2006, 2007). But there was a significant negative relationship between foliar K concentration and  $\Delta$  in *Caragana korshinskii* (Zhao *et al.* 2007). Those variable relationships between foliar  $\Delta$  and ash content or K concentration indicated that it was essential that a relationship between  $\Delta$  and its surrogates in different species should be firstly established under field conditions before this technique could be reliably applied.

Shortage of water is often a critical limiting factor for vegetation establishment and growth in arid and semiarid lands. Water deficit is becoming a serious problem for the desert riparian forest in the extreme arid region. The Ejina oasis is a typical hyperarid desert oasis at the downstream end of the Heihe River basin in northwest China. It is also a natural ecological screen to protect the Hexi Corridor region, or even to northwest China and north China (Fig. 1). In recent decades, as a result of the combined effects of a number of factors, such as a continuous decrease of discharge of the Heihe River, human and animal population growth, socioeconomic activity increase, and climatic warming, the eco-environment of the oasis has markedly deteriorated, thus resulting in a series of eco-environmental problems: salinization, degeneration of natural vegetation, and desertification, etc. This widespread degradation is changing the lower regions of the Heihe River, converting it to one of China's 'sandstorm origin'. *P. euphratica* and *T. ramosissima*, as constructive species in the Ejina desert riparian ecosystem, have substantially decreased. *P. euphratica* area consists mainly of over-matured forest, *T. ramosissima* shrubs become sparsely distributed and dwarf communities (Si *et al.* 2005a,b). Decay of *P. euphratica* and *T. ramosissima* has seriously affected the survival of the Ejina desert riparian oasis. More and more researches deal with photosynthetic (Wang *et al.* 1997, Deng *et al.* 2003, Chen *et al.* 2006), water-use (Si *et al.* 2005a,b; 2007), ecophysiological, and biochemical response to water stress (Devitt *et al.* 1998, Horton *et al.* 2001, Chen *et al.* 2003a, Wang *et al.* 2007) and to the salt one (Ma *et al.* 1997, 2002, Shin *et al.* 2000, Chen *et al.* 2004) as well as to both of them (Zhuang *et al.* 2007). Some results are greatly useful to preserve and restore the desert riparian vegetation. However, to make reasonable use of water resources, one important aspect that is lacking is long-term WUE by means of the new methods of carbon isotope from the desert riparian forest in the Heihe River basin. Moreover, because high WUE is considered to be a trait contributing to successful growth and production of species in arid and semiarid environments (Ehleringer 1993), it is very significant to study the physiological properties,

especially in long-term water-use efficiency by foliar  $\Delta$ . Due to the effects of species, growing conditions and seasons on  $\Delta$ , this study selected two constructive species and five typically habitats surviving them in Ejina desert riparian forest in China during the growing season of 2008 to find out WUE difference in two species and to understand the effect of habitat and season on their  $\Delta$  and WUE. To facilitate large scale or regional survey of plant water use characteristics in this arid ecosystem, this study chose commonly used ash content and K concentration to evaluate and determine the feasibility of leaf ash content and K concentration as surrogates of  $\Delta$  of those species through research on the correlations between  $\Delta$  with ash content and K concentration.

## Materials and methods

**Sketch of the experimental region:** The experiment was conducted at the *P. euphratica* reserve ( $41^{\circ}57'35.3''N$   $101^{\circ}01'36.5''E$  –  $42^{\circ}1'40.86''N$   $101^{\circ}3'45.12''E$ ) in the Ejina oasis in the lower reaches of the Heihe River, northwestern China (Fig. 1). The dominant woody species at the study site are *P. euphratica* and *T. ramosissima*. *P. euphratica*, one of the deciduous arbor belonging to the Salicaceae and genus *Populus* family (Wang *et al.* 1995), is the dominant native woody species, capable of forming an imposing canopy ( $>20$  m high) in some areas. *T. ramosissima*, an important multi-purpose tree species of arid region serving as fodder, fuel, timber, and shelterbelt (Devitt *et al.* 1997), is a weedy, invasive xerophytic shrub species, which can form monospecific stands at a height varying between 2 and 3 m.

The region of study is one of the extremely arid regions in China. The annual precipitation in the region is less than 50 mm, of which 84% occurs during the rainy season (May–September); evaporation is greater than 3,500 mm. The average yearly air temperature is approximately  $8.2^{\circ}C$ . Prevailing wind directions are northwest in winter and spring, and southwest to south in summer and autumn. The yearly average wind speed is approx.  $3.4$ – $4.0$  m s $^{-1}$ . Monthly climatic variables during the growing season in 2008 are presented in Table 1.

**Meteorology and soil moisture:** During the study, climatic data was measured in an open field at the site. Solar radiation, net radiation, air temperature, air humidity, wind direction, and wind speed were measured every 5 min and data stored in a data logger as mean values of 30-min period. The global short-wave radiation was measured in the open field with a pyranometer (*Kipp and Zonen CM5*, Delft, The Netherlands), whereas air temperature and humidity (*DTR500*, *Vaisala*, Vantaa, Finland), and wind speed were measured at a height of 3 m using a *Rotronic* sensor (*RS2*; *Rotronic AG*, Bassersdrof, Switzerland). An automatic weather station (*EnviroStation TM*, *ICT*, Armidale, Australia), data logger (*ZENO-3200*, *Coastal Environmental Systems*,

This study was directed at: (1) studying the variations of foliar  $\Delta$ , ash content, and K concentration in *P. euphratica* and *T. ramosissima* in different growth period and under different habitats; (2) evaluating the feasibility of leaf ash content and K concentration as surrogates of the foliar  $\Delta$  of *P. euphratica* and *T. ramosissima* in the extreme arid region. These results could have important implications to solute rational ecological required water of hyperarid riparian vegetation, scientifically allocated regional water resources for restoration ecology in extreme arid inland basin and further study of long-term water-use efficiency in larger scope and scale.

*Inc.*, Seattle, USA) and *HPVR (SF-300, Greenspan Technology Pty Ltd.*, Maitland, Australia) were used to synchronously record various parameters and meteorological factors.

Soil moisture content was measured twice a week from the surface to a depth of 2.0 m using a time domain reflectory (*TDR*; *IMKO*, Ettlingen, Germany). The ranges of measured depths were 0–20, 20–40, 40–60, 60–80, 80–100, 100–120, 120–140, 140–160, 160–180, and 180–200 cm. In the present study, the whole unit of the soil water content is expressed as volumetric water content.

**Sampling process:** Sampled leaves of *P. euphratica* and *T. ramosissima* were collected on 18 May, 21 June, 23 July, 20 August, and 20 September 2008 in *P. euphratica* reserve. To objectively assess WUE and nutrient status of *P. euphratica* and *T. ramosissima*, we selected five typical sampling plots with the area of  $50 \times 50$  m in April, which represented widespread habitats of their growth at present, such as dune, Gobi, riparian sandpile, riparian lowland, typical *P. euphratica* flatland (Table 2). Due to the restrictions of the *P. euphratica* protection law, this study could not determine specific ages of species by growth cone. There were selected and tagged five individuals of each species as sampling trees in every plot, which had similar diameter at breast height (DBH) and coverage. At each sampling time, we repeatedly collected the mature leaves and the assimilating new twigs from the same sampling trees for *P. euphratica* and *T. ramosissima*, respectively. The mature leaves/twigs from the light-facing side and the same heights at the same sampling trees were taken between 8 and 10 h, and about 20 leaves/twigs from each sampling tree were pooled as a sample from each species in every habitat. Plant samples were first ultrasonically washed with distilled water and air-dried, then oven-dried at  $70^{\circ}C$  for at least 48 h to a constant mass and ground with a plant-sample mill (*1093 Sample Mill*, *Tecator AB*, Hoganas, Sweden) into uniformly fine powder, and finally sieved with a 0.25-mm-mesh screen.

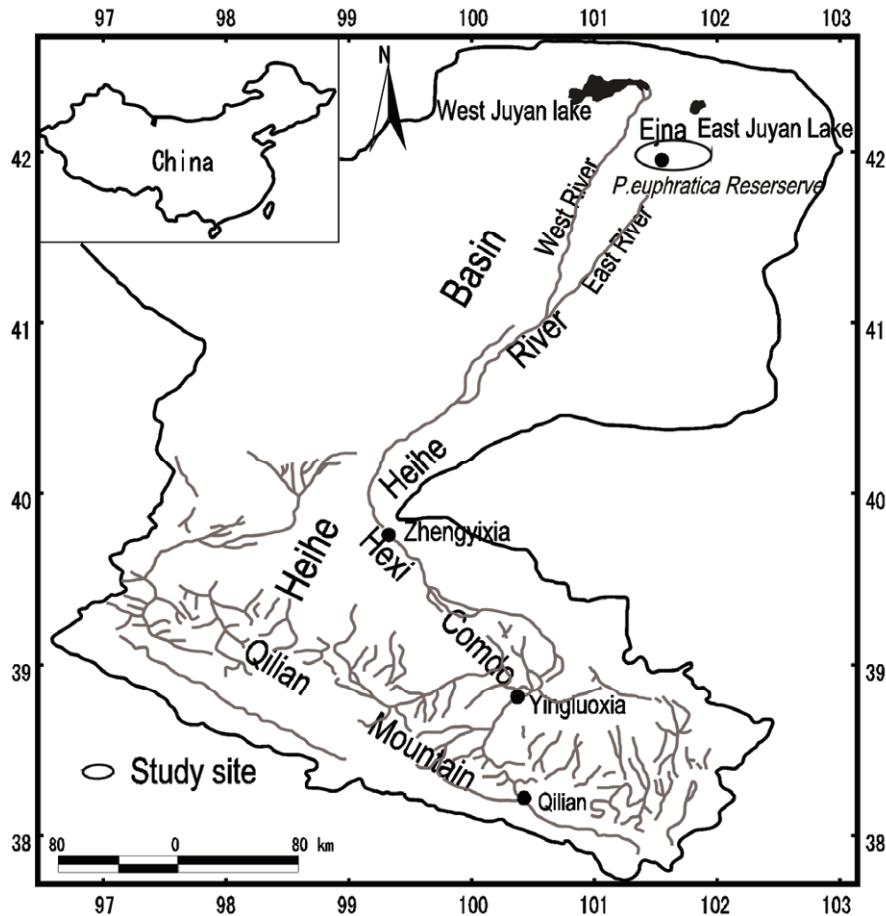


Fig.1. The sketch of the Heihe River and study site. X-axis – longitude, y-axis – latitude.

Table 1. Meteorological condition of the experimental site in Ejina desert oasis from the microclimate station during the growing season in 2008. MT, MMT and ST – mean temperature, mean maximum temperature and mean soil temperature for each period, respectively. P, PAR, RH, and WV – precipitation, mean monthly photosynthetically active radiation, mean relative humidity, and mean wind velocity for each month, respectively.

Month	P [mm]	RH [%]	MT [°C]	MMT [°C]	ST [°C]	WV [m s <sup>-1</sup> ]	PAR [MJ m <sup>-2</sup> ]
April	1.21	22.41	14.61	18.57	12.33	3.67	300.97
May	2.73	28.56	21.54	28.21	18.45	2.46	365.46
June	10.9	30.25	27.28	34.20	22.67	2.40	410.58
July	7.30	40.14	30.80	36.50	26.89	2.02	365.79
August	6.80	36.24	25.50	31.80	22.06	2.25	340.15
September	2.30	48.50	19.76	25.00	17.43	2.20	174.28

**Determination of  $\delta^{13}\text{C}$ , ash content, and  $\text{K}^+$  concentration:** From the same sample, dried powder was weighed into small tin cups for stable carbon analysis (0.06–0.09 mg of carbon). Samples for carbon analysis were combusted with an elemental analyzer (IRMS, *DELTA<sup>plus</sup> Finnigan MAT*, Bremen, Germany). The isotopic signature was obtained *via* the connected continuous flow mass spectrometer (IRMS, *DELTA<sup>plus</sup> Finnigan MAT*, Bremen, Germany). The isotopic signature is expressed in the  $\delta$  notation:

$$\delta^{13}\text{C} [\text{\textperthousand}] = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000 \quad (1)$$

where  $\delta^{13}\text{C}$  is the carbon isotope ratio in part per mille [‰], respectively;  $R = ^{13}\text{C}/^{12}\text{C}$  in samples ( $R_{\text{sample}}$ ) and in the international standard [ $R_{\text{standard}}$ : PDB (PeeDee Belemnite)] for carbon. The overall, long-term sample preparation and analysis error between repeated analyses of the same ground tissue was less than 0.1‰ for  $\delta^{13}\text{C}$ .

Every measurement was replicated two times.

Table 2. The condition of five typical sites.

Site	Latitude and longitude	Altitude [m]	Soil type	Organic matter [g kg <sup>-1</sup> ]	Organic carbon [g kg <sup>-1</sup> ]	Total nitrogen [g kg <sup>-1</sup> ]	C/N	Available K [mg kg <sup>-1</sup> ]
Gobi (G)	41°57'35.3"N, 101°01'36.5"E	970	coarse sand	0.63	0.37	0.07	5.29	87.61
Riparian sandpile (S)	41°59'00.0"N, 101°07'30.7"E	975	fine sand	1.09	0.63	0.11	5.73	99.94
Riparian lowland (O)	41°58'11.8"N, 101°05'00.9"E	986	fine sand	1.18	0.68	0.13	5.23	153.26
Typical <i>P. euphratica</i> flatland (N)	41°57'20.5"N, 101°04'44.6"E	995	clay loam	4.99	2.89	0.41	7.05	170.61
Dune (D)	42° 1'40.86"N, 101° 3'45.12"E	990	fine sand	0.89	0.52	0.08	6.50	80.16

$\Delta$  was calculated by Eq. 2 (Farquhar *et al.* 1982):

$$\Delta [\text{‰}] = \frac{\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}}}{1 - \frac{\delta^{13}\text{C}_{\text{plant}}}{1000}} \quad (2)$$

where  $\delta^{13}\text{C}_{\text{air}}$  (-8‰) and  $\delta^{13}\text{C}_{\text{plant}}$  is carbon isotope composition of air and plant tissue, respectively.

Ash content and K concentration were determined according to the methods by Tsialtas *et al.* (2008). Briefly, ash content was determined by combustion method in a muffle furnace. K concentration was measured by means of flame spectrophotometry. The

measurement was replicated two times. The K concentration [%] and ash content [%] were expressed as  $10^4 \text{ mg kg}^{-1}$  (sample dry mass, DM).

**Statistical analyses:** Analyses of variance (ANOVA) for variables from measurements were used for testing the species and treatment differences. Comparisons of interest were made using Tukey's honest significant difference (HSD). Correlations between  $\Delta$  and ash content or K concentration were examined using the regression (REG) procedure in SPSS 13.0. All statistical analyses were performed with SPSS 13.0 for Windows statistical software package (SPSS Inc., Chicago, USA).

## Results

**Effect of species and habitat on foliar  $\Delta$ , ash content and K concentration:** The three traits measured, including  $\Delta$ , ash content and K concentration, were affected by species and habitats (Fig. 2). There was an apparent difference in  $\Delta$  signatures between *P. euphratica* and *T. ramosissima*. The values of  $\Delta$  signatures in *P. euphratica* were generally larger than those of *T. ramosissima* in each site. Mean of foliar  $\Delta$  in *P. euphratica* ( $20.30 \pm 0.14\text{‰}$ , the result was presented as a mean  $\pm$  SE, where  $n = 50$ ). The following data represented the same) was significantly higher than that of *T. ramosissima* ( $19.20 \pm 0.15\text{‰}$ ). Among different habitats, the trends of  $\Delta$  signatures in both *P. euphratica* and *T. ramosissima* were similar, where the  $\Delta$  signature in dune was the lowest and the next lowest value was in Gobi. Foliar  $\Delta$  values of each species in the other three habitats were not significantly different. The ash content in *T. ramosissima* ( $14.14 \pm 0.48\%$ ) was significantly higher than that of *P. euphratica* ( $8.21 \pm 0.48\%$ ). It was 1.72 times higher than that of *P. euphratica*. The values of ash content in *T. ramosissima* were significantly higher than those of *P. euphratica* among different

habitats ( $p < 0.05$ ). Among habitats, the lowest ash content was found in both species in the dune. The trend of ash content in both species among different habitats was similar. But the ash content in *P. euphratica* among different sites was not strikingly different. Those of *T. ramosissima* were reverse, and there was a distinct difference in ash content among habitats ( $p < 0.05$ ), excluding in the riparian lowland and typical *P. euphratica* flatland.

The mean of K concentration in *P. euphratica* ( $1.17 \pm 0.07\%$ ) was remarkably higher than that of *T. ramosissima* ( $0.76 \pm 0.04\%$ ). There were only significant differences in K concentration between *P. euphratica* and *T. ramosissima* in the Gobi and dune sites.

In terms of variability of  $\Delta$ , ash content and K concentration among different sites,  $\Delta$  and ash content had similar trends in both *P. euphratica* and *T. ramosissima*. In other words, there was uniformity in ascending and descending between  $\Delta$  and ash content. But as for K concentration, variability of K concentration did not follow with  $\Delta$  and ash content under different habitats (Fig. 2).

**Seasonal variations of foliar  $\Delta$ , ash content, and K concentration:** Foliar  $\Delta$ , ash content, and K concentration were significantly changed with species in the growth period (Table 3). Foliar  $\Delta$  values and K concentration in *P. euphratica* were significantly higher than those of *T. ramosissima* during the whole growing season. The ash content of *T. ramosissima* was remarkably higher than that in *P. euphratica*. Foliar  $\Delta$  values in *P. euphratica* during the growing season increased gradually. They were the highest at the end of July and the lowest at the end of May. Meanwhile, this parameter showed similar trends in *T. ramosissima*, except that the highest one appeared at the end of August. There were similar variable trends of foliar ash content in *P. euphratica* and *T. ramosissima*. The highest ash content in both species was by the end of the season. Foliar K concentration decreased gradually in *P. euphratica* and *T. ramosissima*, except that K concentration in *T. ramosissima* was increased at the end of September. The highest K concentration in both *P. euphratica* and *T. ramosissima* appeared at the beginning of season.

**Correlations of foliar  $\Delta$  with foliar ash content and K concentration:** As Figs. 3 and 4 show, with data pooled from all habitats across the growing season, correlations of foliar  $\Delta$  with ash content and K concentration varied significantly with species. Foliar  $\Delta$  values were significantly and positively related to the ash content in *P. euphratica* ( $R^2 = 0.63, p < 0.0001$ ) and *T. ramosissima* ( $R^2 = 0.76, p < 0.0001$ ). The correlations of foliar  $\Delta$  with K concentration were significantly negative in *P. euphratica* ( $R^2 = 0.60, p < 0.0001$ ), while the weak positive relationship between foliar  $\Delta$  and K concentration was found in *T. ramosissima* ( $R^2 = 0.18, p = 0.002$ ). Meanwhile, there were significantly different correlations of K concentration and ash content in *P. euphratica* and *T. ramosissima* when data were pooled. A negative relationship between K concentration and the ash content in *P. euphratica* was found ( $R^2 = 0.40, p < 0.0001$ ) but there was a positive relationship in *T. ramosissima* ( $R^2 = 0.30, p < 0.0001$ ).

## Discussion

The means of foliar  $\Delta$  in *P. euphratica* were significantly higher than those of *T. ramosissima*, suggesting that WUE of *T. ramosissima* was significantly higher than that of *P. euphratica* inferred from the negative correlations between  $\Delta$  and WUE for many C<sub>3</sub> species (Farquhar *et al.* 1982, 1989, Farquhar and Richards 1984, Condon *et al.* 1990, Ehleringer 1993, Wright *et al.* 1994, Turner 1997). Moreover,  $\Delta$  values can be used to assess the drought tolerance of different species (Ehleringer *et al.* 1992). The higher  $\Delta$  signatures in *P. euphratica* under all habitats indicated that *P. euphratica* has weaker drought tolerance than *T. ramosissima*, which achieved this through the lower transpiration by the tiny assimilating

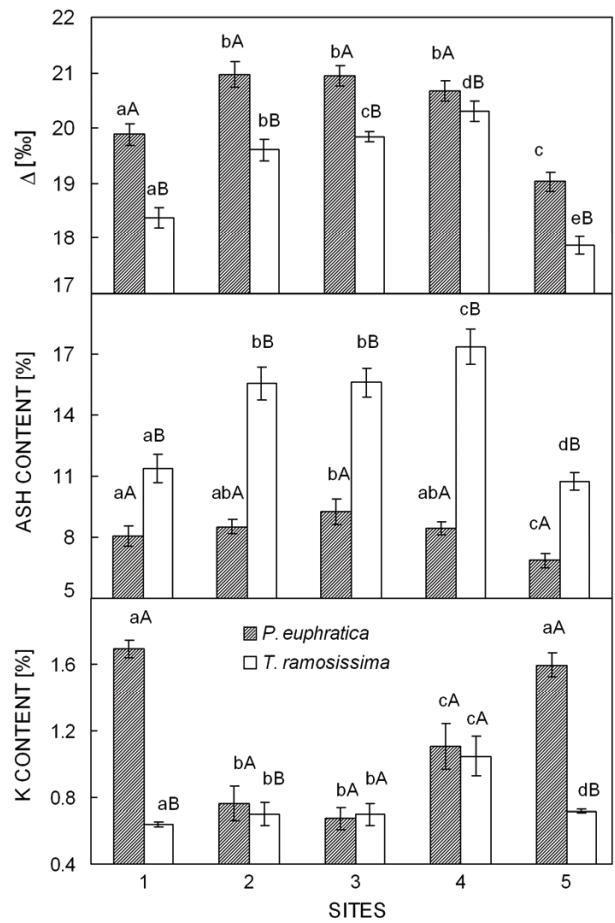


Fig. 2. Seasonal means of carbon isotope discrimination ( $\Delta$ ), ash and K content for different micro habitats (1: Gobi; 2: riparian lowland; 3: typical *P. euphratica* flatland; 4: riparian sandpile; 5: dune) for *P. euphratica* and *T. ramosissima* in 2008. Results are means estimated from May to September in every plot, the error bars mean SE ( $n = 10$ ). Capital letters indicate a comparison of means for the same treatment among the different species. Lowercase letters indicate a comparison of treatment means within the same species. Bars with the same letter do not differ at  $p < 0.05$  by Duncan's multiple range tests.

twigs of *T. ramosissima*. This reference was supported by the study of stem sap flow by means of heat pulse techniques reported by Zhang *et al.* (2003). Their drought tolerance also agreed with their field distribution. According to the reports by He *et al.* (2006), the riparian community dominated by *P. euphratica* is generally distributed within 500 m of the river. In contrast, *T. ramosissima* is the most prevalent riparian in communities located between 500 and 1,500 m from the river. And they exist in numerous different sized 'sandbags' fixed by *T. ramosissima* in the lower reaches of Heihe River.

The significant differences of foliar ash content between *P. euphratica* and *T. ramosissima* showed that

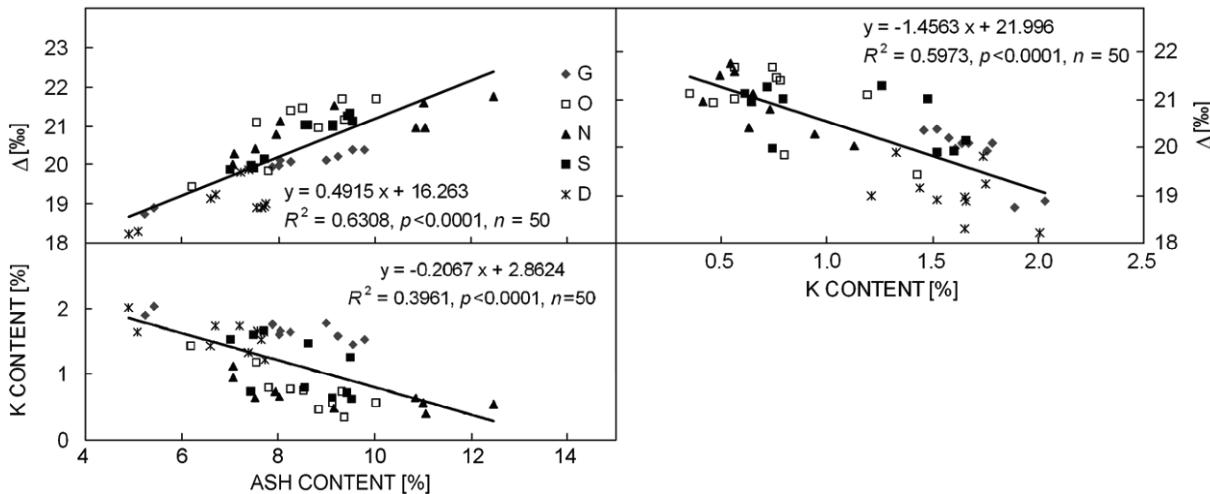


Fig. 3. Correlations of foliar  $\Delta$  with ash and K content [%] in *P. euphratica*. The corresponding linear regression equations are shown in the figures. The 'a' represents the slope of the linear regression, and thus represents the change in foliar  $\Delta$  [%] in per unit ash and K content increase or the change in foliar K [%] in per unit ash content.  $R$  represents the correlation coefficient. G, O, N, S, D represent the five plots of Gobi, riparian lowland, typical *P. euphratica* flatland, riparian sandpile and dune, respectively.

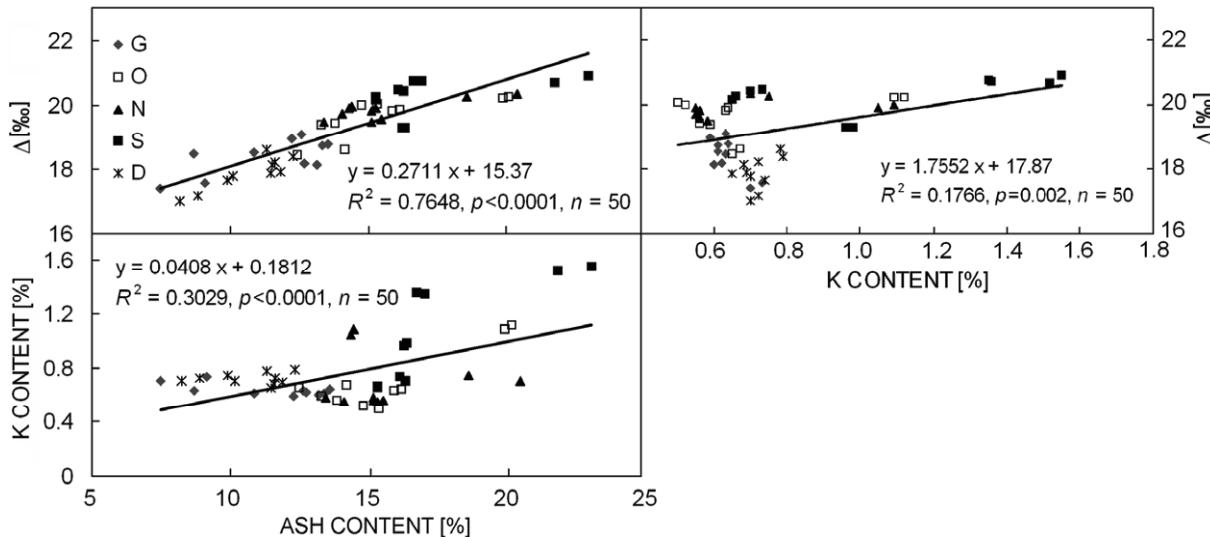


Fig. 4. Correlations of foliar  $\Delta$  with ash and K content [%] in *T. ramosissima*. The corresponding linear regression equations are shown in the figures. The 'a' represents the slope of the linear regression, and thus represents the change in foliar  $\Delta$  [%] in per unit ash and K content increase or the change in foliar K [%] in per unit ash content.  $R$  represents the correlation coefficient. G, O, N, S, D represent the five plots of Gobi, riparian lowland, typical *P. euphratica* flatland, riparian sandpile and dune, respectively.

the capabilities of absorbing minerals were different in the two species. Higher foliar K concentration in *P. euphratica* suggested that *P. euphratica* has stronger stomatal behavior, osmoregulation, and cell expansion than *T. ramosissima* (Elumalai *et al.* 2002).

Except for foliar K concentration in *P. euphratica*, which was higher than that of typical *P. euphratica* flatland, riparian lowland and riparian sandpile, foliar  $\Delta$  and ash content of *P. euphratica* and *T. ramosissima* were the lowest in the dune, and were the second lowest at the Gobi site. Those results suggested that the physiological activities such as carbon isotope discrimination

and mineral absorbing capacities of *P. euphratica* and *T. ramosissima* depended on the soil water availability. There were significant positive correlations between mean  $\Delta$  and mean monthly soil water content in both *P. euphratica* ( $R^2 = 0.54$ ,  $p < 0.0001$ ,  $n = 25$ ) and *T. ramosissima* ( $R^2 = 0.44$ ,  $p = 0.0003$ ,  $n = 25$ ) (Fig. not shown). This result also accorded with the previous reports, which have found positive correlations between  $\Delta$  and indices of water availability such as rainfall, soil water potential, and soil water availability for different species (Damesin *et al.* 1997, Lefler and Evans 1999, DaMatta *et al.* 2002, Monneveux *et al.* 2005). The

Table 3. One-way ANOVA table showing the seasonal variations of foliar carbon isotope discrimination ( $\Delta$ ), ash and K content in *P. euphratica* and *T. ramosissima*. Data are means of different regions and  $n = 10$ . Lowercase letters indicate a comparison of growth season means within the same species. Bold capital letters, capital letters and italic capital letters indicate a comparison of means for foliar  $\Delta$ , ash and K content among the different species, respectively. Numbers with the same letter do not differ at  $p < 0.05$  by Duncan's multiple range tests.

Time	<i>P. euphratica</i>			<i>T. ramosissima</i>		
	$\Delta$ [%](SE)	Ash [%](SE)	K [%](SE)	$\Delta$ [%](SE)	Ash [%](SE)	K [%](SE)
18 May	19.51(0.30) <sup>a</sup>	6.37(0.36) <sup>a</sup>	1.55(0.12) <sup>a</sup>	18.47(0.36) <sup>a</sup>	12.16(1.08) <sup>a</sup>	0.83(0.05) <sup>a</sup>
21 June	20.18(0.25) <sup>b</sup>	8.06(0.43) <sup>b</sup>	1.16(0.16) <sup>b</sup>	19.24(0.34) <sup>b</sup>	14.94(1.37) <sup>b</sup>	0.81(0.12) <sup>b</sup>
23 July	20.70(0.22) <sup>c</sup>	8.61(0.46) <sup>bc</sup>	1.12(0.16) <sup>b</sup>	19.31(0.32) <sup>bd</sup>	13.77(0.88) <sup>c</sup>	0.64(0.02) <sup>c</sup>
20 Aug.	20.51(0.31) <sup>bc</sup>	8.72(0.33) <sup>bc</sup>	1.07(0.15) <sup>bc</sup>	19.61(0.24) <sup>c</sup>	14.81(0.92) <sup>b</sup>	0.66(0.03) <sup>cd</sup>
20 Sept.	20.60(0.31) <sup>c</sup>	9.30(0.32) <sup>c</sup>	0.92(0.17) <sup>c</sup>	19.38(0.35) <sup>d</sup>	15.00(1.01) <sup>b</sup>	0.87(0.10) <sup>e</sup>
Mean	20.30(0.14) <sup>A</sup>	8.21(0.22) <sup>A</sup>	1.17(0.07) <sup>A</sup>	19.20(0.15) <sup>B</sup>	14.14(0.48) <sup>B</sup>	0.76(0.04) <sup>B</sup>

different water conditions induced significant differences in  $\Delta$  and ash content. A decrease in soil water availability led to a decrease in both  $\Delta$  and ash content in the leaves (Farquhar *et al.* 1989, Merah *et al.* 1999, 2001a,d; Misra *et al.* 2006), because water stress led to strong stomatal limitations, which decreased the  $C_i/C_a$  ratio and  $\Delta$  (Morgan *et al.* 1993). Meanwhile, this study indicated that water was the one key factor limiting the healthy vegetative growth in the riparian forestry system of the extreme arid desert. It also suggested that  $\Delta$  and ash content were positively affected among different habitats by stomatal conductance. The higher K concentration in *P. euphratica* at the Gobi and dune sites showed that *P. euphratica* might respond to water stress *via* regulation of stomatal function (Tsialtas *et al.* 2002) and osmotic adjustment (Clarkson 1980, Marschner 1995). On the contrary, the near values of K concentration in *T. ramosissima* at the five habitats just showed that K might not take part in the osmotic adjustment and stomatal regulation due to its lower content in the small assimilated twigs.

The significant seasonal variations of foliar  $\Delta$ , ash content, and K concentration and the similar seasonal patterns in *P. euphratica* and *T. ramosissima* (Table 3) suggested that they had the similar response to variations of environmental conditions during their growth season. The ascending trends of foliar  $\Delta$  values in both species during the growing season were in line with the previous reports by Garten *et al.* (1992), Yan *et al.* (1998), Damesin *et al.* (2003), and Su *et al.* (2005). The reason for it may be related to the foliar degree of maturity (Garten *et al.* 1992, Yan *et al.* 1998) and the more positive  $\delta^{13}\text{C}$  signature of storage-derived C (Damesin *et al.* 2003, Helle *et al.* 2004). The same pattern of rising ash content in both *P. euphratica* and *T. ramosissima* showed that most minerals were mainly transported passively through the xylem and accumulated in transpiring plant tissues, according to the results of seasonal variations of transpiration of *P. euphratica* and evapotranspiration of *T. ramosissima* reported by Si *et al.* (2005a,b; 2007, respectively). In this study, the lower K

content in leaves at the end of growth season than at incipient stage suggested that a quantity of K was removed out of leaves during late growth periods and recycled by the species (Zhu *et al.* 2008).

To reduce the high cost of  $\Delta$  analysis, many previous studies have suggested that foliar ash content and K concentration could be used as cheap, putative surrogates of  $\Delta$  (Febrero *et al.* 1994, Araus *et al.* 1998, Merah *et al.* 2001a, Misra *et al.* 2006, Tsialtas *et al.* 2002, 2008). In this study, the significantly positive relationships between  $\Delta$  and ash content in both *P. euphratica* and *T. ramosissima* were revealed. That was because higher  $\Delta$  was associated with higher stomatal conductance and thus higher transpiration, which passively accumulated minerals in leaves (Masle *et al.* 1992). This study accorded with the previous reports (Masle *et al.* 1992, Araus *et al.* 1998, Voltas *et al.* 1998, Merah *et al.* 1999, Tsialtas *et al.* 2008). Although this study did not measure transpiration of *P. euphratica* and *T. ramosissima*, the positive correlations between  $\Delta$  and ash content in both *P. euphratica* and *T. ramosissima* suggested that most minerals were passively accumulated in the vegetative parts through the xylem system by the transpiration stream in *P. euphratica* and *T. ramosissima*, based on increasing seasonal variations of transpiration of *P. euphratica* and evapotranspiration of *T. ramosissima* (Si *et al.* 2005a,b; 2007, respectively) and informed results in other species (Jones and Handreck 1965, Merah *et al.* 1999).

As far as the relationship between foliar  $\Delta$  and K concentration was concerned, there was a weak positive correlation between  $\Delta$  and K concentration in *T. ramosissima* (Fig. 4), which could result from the lower K concentration in the assimilating twigs of *T. ramosissima* and different soil K content among habitats. The similar positive correlations between  $\Delta$  and K concentration were also found in grassland species (Masle *et al.* 1992, Tsialtas *et al.* 2002) *A. ordosica* and *H. scoparium* (Zhao *et al.* 2006, 2007). Those and our results indicate that the accumulation of individual minerals in plant organs are, however, complex because these elements are actively

transported and can be redistributed to the most active cells of the plant. By contrast, foliar  $\Delta$  and K concentration in *P. euphratica* was significantly and negatively correlated within environments (Fig. 3). Grain in bread wheat and barley (Masle *et al.* 1992, Febrero *et al.* 1994) and in *C. korshinskii* (Zhao *et al.* 2007) as well as seed cotton (Tsialtas *et al.* 2008) were also found in the same negative correlation. Those show that a passive transport of K nutrients through the transpiration stream is not the only factor that determines mineral content in *P. euphratica*, and that K plays an important role in regulating stomatal functions as well as showing that K is an easily lapsed nutrient element. The detailed reason should be further studied. As a main osmotic solute in plant, foliar K plays key roles in regulating stomatal movement. Under drought conditions, higher foliar K concentration could cause higher stomatal sensitivity to water stress and smaller stomatal conductance (lower  $\Delta$ ). Moreover, foliar K is also in contact with photosynthesis. According to results obtained by Fu *et al.* (1996), the rice genotypes with high K use efficiency have higher photosynthetic capacity. Higher foliar K concentration associated with higher photosynthetic rates could cause lower  $C_i/C_a$  and lower  $\Delta$  value, which magnified the significantly negative correlation between foliar K concentration and  $\Delta$  values. So, the significantly negative correlation between foliar  $\Delta$  and K concentration and higher K concentration in *P. euphratica* also showed that *P. euphratica* might have higher stomatal sensitivity to water stress, stronger osmotic adjustment capacity and

photosynthetic rate than *T. ramosissima*. The higher photosynthetic rate in *P. euphratica* has been documented by Deng *et al.* (2003), but the other two aspects need to be further studied and determined in the near future. Overall, the opposite correlation of  $\Delta$ -K and ash-K in *P. euphratica* and *T. ramosissima* might be attributed to the different K concentration in both species leading to different roles of foliar K functions and reverse processes of the easily lapsed K and accumulated ash in growth season advancing.

**Conclusions:** There were different correlations between foliar  $\Delta$  values and ash content and K concentration in *P. euphratica* and *T. ramosissima*.  $\Delta$  was positively related with ash content, and a significantly negative relationship between  $\Delta$  and K concentration in *P. euphratica* was evident when data from the five typical habitats during the entire season were pooled. The positive correlations of foliar  $\Delta$  values with ash content and K concentration in *T. ramosissima* were found but the relationship to  $\Delta$ -K was extremely weak. Those results verified that foliar ash content and K concentration could serve as indirect and suitable surrogates of foliar  $\Delta$  values in *P. euphratica*. However, ash content only served as an indirect selection criteria of foliar  $\Delta$  values in *T. ramosissima*. This result also implied that the correlations of foliar  $\Delta$  with K concentration varied with species due to different physiological features between species.

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