Regular research paper

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FOLIAR STABLE CARBON ISOTOPE DISCRIMINATION AND NUTRIENTS CONTENTS IN TWO DESERT PLANT SPECIES

ABSTRACT: Variation of foliar stable Carbon Isotope Discrimination (CID Δ‰) and nutrient contents of *Artemisia ordosica* (Krasch) (semi-shrub species) and *Caragana korshinskii* (Kom.) (shrub species) were studied at the southeastern margin of the Tengger Desert, China. Foliar CID Δ, total phosphorus content (TP) and potassium content (K) in *A. ordosica* were markedly higher than in *C. korshinskii* while foliar total nitrogen content (TN) and water-use efficiency (WUE) (calculated from foliar CID Δ) in *C. korshinskii* were significantly higher than those in *A. ordosica*. There were significant and positive relationships between foliar CID Δ, TN and TP contents ($P < 0.001$) in *C. korshinskii*, while in *A. ordosica* a strong and significant positive correlation existed between CID Δ and K content ($P < 0.001$). Based on WUE, TN, TP, and K contents, as well as their relationships, we may conclude that in arid environments, the survival of *C. korshinskii* profits from its higher WUE, while the survival of *A. ordosica* from its higher TP and K contents in leaves. In addition, the correlations of foliar CID Δ values with TN and TP contents in *C. korshinski* and with K content in *A. ordosica* revealed that the water was one of the main factors limiting the absorption capacity for N and P in *C. korshinskii*, and for K in *A. ordosica*. While nutrient conditions were not the factors affecting the growth of *C. korshinskii* and *A. ordosica* in the study areas.

KEY WORDS: carbon isotope discrimination (CID Δ), nutrient contents, *Artemisia ordosica*, *Caragana korshinski*, arid regions

1. INTRODUCTION

Foliar carbon isotope discrimination (CID Δ‰) values calculated by $\delta^{13}C$ have been used as an integrated measure of the response of photosynthetic gas exchange to environmental variables such as water availability (Shaheen and Rebecca 2005) and humidity (Winter *et al.* 1982). Leaf $\delta^{13}C$ being related to the ratio of photosynthetic capacity (*A*) and stomatal conductance (*g*s) can be used to indicate the long-term water use efficiency (WUE) (Farquhar *et al.* 1989). Previous studies of woody species have found positive correlation between CID Δ and indices of water availability such as rainfall, soil water potential, and soil water availability (Laundré 1999, Miller *et al.* 2001). Increases in CID Δ values of plants with a favorable water status have been observed for different plant species, such as conifers (Korol *et al.* 1999, Warren *et al.* 2001, Choi *et al.* 2005) and cultivated plants (DaMatta *et al.* 2002, Shaheen and Rebecca 2005).

The use of stable isotopes also provides fundamental insight into the interactions between plant nutrition and eco-physiological processes. Nutrient (particularly nitrogen) deficiencies can result in more negative $\delta^{13}C$ (higher Δ values) by reducing photosynthetic assimilation of intercellular CO_2 in leaves (Sparks and Ehleringer 1997). The robust negative correlation between foliar Δ values and N contents implied that high leaf N content corresponds to increased photosynthetic capacity and decreased internal leaf CO_2 concentration (Sparks and Ehleringer 1997). Lack of significant relationship between foliar Δ and N contents can indicate that N deficiency is not a factor limiting tree growth (Choi *et al.* 2005). Potassium is considered as closely related to Δ values because of its role in plant water economy *via* regulation of stomatal function (Rascio *et al.* 2001). A positive correlation between Δ values and K content was found (Tsialtas *et al.* 2002). Previously, contradictory results were reported regarding the relationship between Δ values and K content. Masle *et al.* (1992) reported a positive correlation in leaves of grasses, but Merah (2001) did not find any relation between leaf CID Δ and K content in wheat. However, there are only few attempts to examine the correlation between foliar CID Δ values and P content.

In arid and semi-arid regions, the water availability is a key limiting factor and determines plant performance, abundance, and distribution, especially in regions such as the Tengger Desert, China. Previous study reported that arid land plants that can utilize more water often acquire more nitrogen, which is usually allocated to photosynthetic capacity (Reich et al. 1998). The Tengger Desert is the fourth-largest desert in the central part of western China, and is characterized by shifting sand dunes. In order to protect the railway crossing the desert, the measures to provide sand fixation were introduced (Zhao 1998). As the result of applying straw barriers and artificial shrub forests, in the transition zone between desert and arid grassland the mobile sand dunes have been changed into the stabilized areas (Xiao *et al.* 2003). Among the desert plants used to fix the sand, xerophytes (*Caragana korshinskii* Kom.) and succulent xerophytes

(*Artemisia ordosica* Krasch.) played the important roles in stabilizing the shifting sands due to their ability to adapt to desert conditions. We present the results of a study on the foliar stable carbon isotope discrimination (CID Δ‰) and the foliar TN, TP, and K contents, as well as the relationships between CID Δ values and these elements, in *A. ordosica* and *C. korshinskii* under different site conditions of the Tengger Desert. Our goal was to consider the potential mechanism used by *A. ordosica* and *C. korshinskii* to adapt to desert conditions, and to find out the main limiting factors that affect the growth of those species.

2. THE STUDY AREA

The study took place at the Shapotou Desert Experiment Research Station (37°27.55'N, 105°00.64'E), which is located at the southeast margin of the Tengger Desert. The area is 1300 m above sea level with high insolation and low relative humidity. Average annual precipitation is 180.2 mm and 80% of the rainfall occurs between May and September. Annual mean temperature is 10.0°C, with mean January temperature –6.9°C and mean July temperature 24.3°C. However, the maximum temperature at the surface of the sand may reach 74°C (Chen *et al.* 1991). The depth to the water table is more than 80 m, thus rainfall is usually the only source of water for plant growth. The frost-free period spans from 150 to 180 days per year. An aeolian sandy soil dominates in the area (Xun and Li 1987).

The study was carried out at two plots (Table 1). In plot A (rain-fed area), 4-year-old seedlings of *A. ordosica* and *C. korshinskii* were planted in lines at distance 1m × 1m on April 1990, with no irrigation provided after planting (Wang *et al.* 2002). In plot B (irrigated area), the seedlings of *A. ordosica* and *C. korshinskii* were planted singly in 1980, and at the time of study the coverage of plants varied from 30 to 80%. The irrigation was applied once a month in April, May, September, October and November with the quantity of about 360 mm each time, and twice a month in June, July and August with the same amount. Meteorological data for the study areas at growing season in 2004

was showed in Table 2. The soil characteristics were similar in plot A and B. In 2004, the soil properties in two plots have been improved to the values shown in Table 3 as a result of the planting of desert plants, namely *A. ordosica* and *C. korshinskii* (Table 3).

Table 1. Study plots of desert, sand fixing plants *Artemisia ordosica* and *Caragana korshinskii*.

Plot	Area (ha)	Plant distribution
A (rain-fed)	1.0	Regular planting in lines at distance 1 m × 1 m
B (irrigated)	30.0*	Plants growing densely – Coverage from 30 to 80 %

*Acc. to Li *et al.* (2005).

Table 2. Meteorological data (mean values) for the study plots at the Shapotou Station at growing season in 2004.*

Parameter	1 April–12 May	13–27 May	28 May–29 June	30 June–27 July	28 July–27 August	28 August– 22 Sept.
Mean air temperature (°C)	16.0	19.3	22.0	24.7	22.0	19.0
Mean maximum temperature (°C)	23.2	26.7	28.9	31.1	27.7	25.6
Mean lowest temperature (°C)	8.7	11.9	15.0	18.3	16.3	12.3
Mean ground surface temperature (°C)	19.7	24.7	26.8	28.7	26.1	23.0
Precipitation (mm)	1.5	2.9	25.5	26.4	48.7	2.1
Mean relative humidity (%)	24.2	28.9	41.0	44.3	64.0	46.7
Mean wind velocity (m s^{-1})	4.1	4.2	3.8	3.4	2.9	2.5

* from 1 April to 22 September the precipitation is equal to 107.1 mm.

Table 3. Physical and chemical properties of soil in plot A and plot B (see Table 1) after 15 and 24 years of the introduction of the sand fixing plants, Tengger Desert.

Plot	Soil depth	O.M. (g kg^{-1})	pH	Total nutrient content (g kg^{-1})			Available nutrient content (mg kg^{-1})		
				N	P	K	N	P	K
Plot A	0–5 cm	1.16	8.22	0.09	0.32	20	12.8	0.37	14
	>5 cm	0.74	8.49	0.05	0.29	20	2.5	0.28	10
Plot B	0–20 cm	1.22	8.05	0.11	0.41	20	13.6	0.39	14

3. METHODS

We sampled leaves from several sites of the plot A and plot B. Leaves of *A. ordosica* and *C. korshinskii* were collected on 13 and 28 May, 30 June, 28 July, 28 August, and 23 September 2004. At each sampling time, the samples were collected between 8:00 a.m. and 10:00 a.m. We collected about 20 leaves from each of 5 shrubs as a sample (in two replicates) from each species growing in every site. The samples were dried at 70°C for 24 h before analysis of N, P, and K contents and carbon isotope ratio (δ^{13}C).

The dried samples were grinded in a stainless steel mill, and wet-digested in concentrated H_2SO_4 for determination of total N (TN) content and in a di-acid mixture (HNO_3 and $HClO_4$ mixed in a 4:1 ratio) for determination of total P (TP) content. The TN content was determined by means of semi-micro Kjeldahl analysis (Bremner and Mulvaney 1982); TP content – according to the method of Dickman and Bray and Woods and Mellon (described by Jackson 1982), and K content by means of flame spectrophotometry (Allen 1989). The pooled samples (two replicates collected for each sample) were used for the analysis which was repeated twice.

Mass spectrometry (MAT 252 spectrometer) was used to determine the carbon isotope ratios (^{13}C/^{12}C) (Liu *et al.* 2003). The precision of the analysis was higher than 0.10‰. The leaf δ^{13}C (δp, relative to Pee Dee Belemnite, the international standard) was expressed as:

$$\delta^{13}C \text{ (‰)} = [(R_{sample} / R_{standard}) - 1] \times 1000 \qquad (1)$$

where R is the ^{13}C/^{12}C ratio. The analysis of leaf δ^{13}C (leaf carbon isotope ratio) was done in pooled samples and the measurement was replicated two times.

Foliar Δ (‰) is the carbon isotope discrimination (CID) by the plant and it was calculated as follow:

$$\Delta \text{ (‰)} = (\delta^{13}C_{air} - \delta^{13}C_{plant}) / (1 - \delta^{13}C_{plant} / 1000)$$

$$(2)$$

$$\Delta \text{ (‰)} = a + (b - a) \times C_i / C_a \qquad (3)$$

Where *a* is the fraction that occurs due to the diffusion of air through stomata (4.4%), and *b* is the net fractionation caused by carboxylation (mainly by RuBP carboxylase, approximately 27%). C_i represents the internal CO_2 concentration, and C_a represents the atmospheric CO_2 concentration (in our study, C_a was equal to 375.5 umol mol^{-1} CO_2; it represents the monthly average from January to December 2003 in Waliguan Atmospheric Background Station of China Meteorological Administration).

$$C_i = C_a \times (\delta^{13}C_{plant} - \delta^{13}C_{air} + a) / (a - b)$$

$$(4)$$

$$WUE = C_a \times (1 - 1.6 \times C_i / C_a) \qquad (5)$$

where the *WUE* (μmol CO_2·mol^{-1} H_2O) represents the water-use efficiency. Statistical analysis was carried out using SPSS software (10.0) and DPS software (3.01).

4. RESULTS

There were significant differences in water use efficiency (WUE) (based on δ^{13}C analysis), foliar CID values (Δ‰) and nutrient contents between *A. ordosica* and *C. korshinskii* under different plots (Table 4). Both in *A. ordosica* and *C. korshinskii*, the effects of species, plot and species × plot interactions on foliar CID Δ, WUE and K content were significant. In *A. ordosica*, the effects of plots on TN and K contents were significant, while these effects on TP were not significant. However, the effects of plots on foliar TN, TP and K contents in *C. korshinskii* were also not significant (Table 4). The WUE of *C. korshinskii* was 14% higher than that of *A. ordosica*. Except foliar TN in *C. korshinskii* which was similar to that of *A. ord*osica, foliar CID Δ, TP and K contents in *A. ordosica* were significantly higher than that of *C. korshinskii*. Mean foliar TP and K contents in *A. ordosica* were 2.4 times and 2.2 times higher than the values for *C. korshinskii* respectively, and mean of foliar CID Δ was 7% higher than that of *C. korshinskii*.

In different plots, there were significant differences of foliar CID Δ, TP and K contents between *A. ordosica* and *C. korshin-*

Table 4. Variation of stable carbon isotope discrimination (CID Δ) (equations 1, 2, 3) and nutrient contents of *Artemisia ordosica* and *Caragana korshinskii* growing on different plot A and B (Table 1). Mean values for growing season (±SD).
Lowercase letters indicate a comparison of plot means within the same species; capital letters indicate a comparison of means for the plot A between two species; bold capital letters indicate a comparison of means for the plot B between two species. * – *P* <0.05, ** – *P* <0.01, *** – *P* <0.001.

Species	Plot	Foliar CID Δ (‰)	WUE[1] (μmol CO_2·mol^{-1} H_2O)	Foliar nutrient contents (g kg^{-1}) TN	TP	TK
Artemisia ordosica	A	16.80 ± 0.94aA	105.92 ± 9.80aB	15.30 ± 4.92bA	2.63 ± 0.33aA	18.45 ± 2.49bA
	B	18.94 ± 0.47b**A**	83.70 ± 4.91b**B**	20.38 ± 0.79a**A**	2.80 ± 0.07a**A**	24.80 ± 1.32a**A**
Caragana korshinskii	A	15.50 ± 0.63bB	119.47 ± 6.56aA	18.09 ± 2.84aA	1.11 ± 0.12aB	10.70 ± 3.20aB
	B	17.79 ± 0.56a**B**	95.66 ± 5.87b**A**	19.65 ± 1.75a**A**	1.16 ± 0.13a**B**	9.32 ± 2.91a**B**
Significance:						
Species		***	***	ns	***	***
Plot		***	***	*	ns	*
Species × Plot		***	***	ns	**	**

[1] see equations (4) and (5)

skii. In plot A, the foliar CID Δ, TP and K contents of *A. ordosica* were 8, 137 and 72% higher than those of *C. korshinskii*, respectively. In plot B, those differences were 7, 141 and 166%, respectively. However, WUE of *C. korshinskii* was significantly higher (13 and 14% in plot A and B, respectively) than those of *A. ordosica*. In addition, except foliar TN, TP and K contents in *C. korshinskii* and TP content in *A. ordosica* which were similar in two plots, there were significant differences of WUE, foliar CID Δ, TN and K contents in both plants (Table 4).

In *C. korshinskii*, foliar CID Δ values were significantly and positively correlated with foliar TN and TP contents (*P* <0.001; r = 0.571 and 0.556, respectively) but were not significantly correlated with foliar K content (Fig. 1). The *a* regression coefficients, which represent the rate of increase per unit of increase (1‰) in foliar CID Δ, were 1.59 and 0.07 in TN and TP contents, respectively. In *A. ordosica*, a strong and significant positive correlation existed between CID Δ and K

content (*P* <0.001; r = 0.734) with the *a* being 2.04. In contrast, weak negative relationships existed between CID Δ and foliar TN and TP contents (Fig. 2).

5. DISCUSSION

In arid and semi-arid regions, the growth of plants depends strongly on soil and atmospheric water. Previous studies have found positive correlations between carbon isotope discrimination (CID Δ) and indices of water availability (Laundré 1999, Miller *et al.* 2001, Wang *et al.* 2001). The carbon isotope discrimination model suggested that the decrease of CID Δ by drought was due to increase of water use efficiency (WUE i.e., dry matter produced per kg of water consumed in its production) through decrease of stomatal and/or mesophyll conductance. In our study, the foliar CID Δ of *A. ordosica* was significantly higher than that of *C. korshinskii*. The foliar CID Δ of *C. korshinskii* and *A. ordosica* in the irrigated plot were significantly
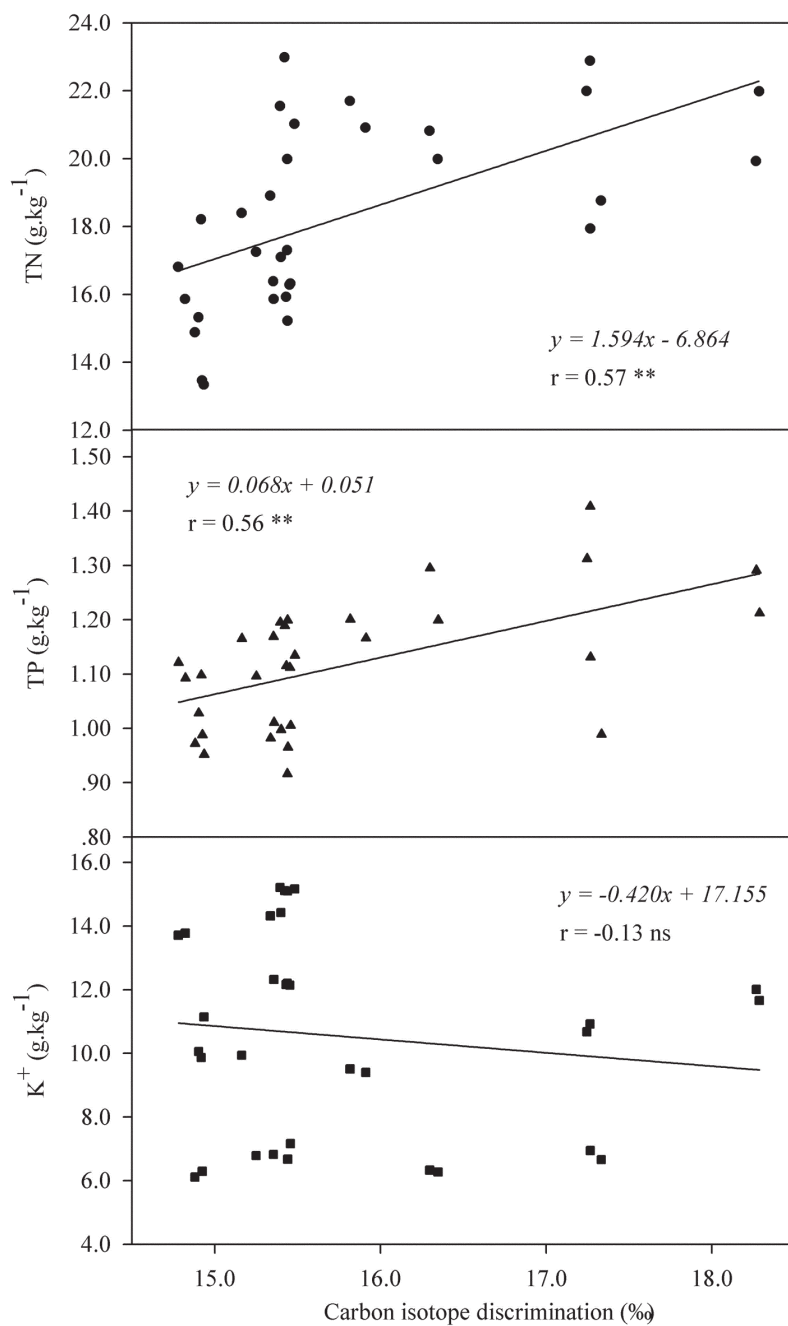
Fig. 1. Correlations between foliar carbon isotope discrimination (CID Δ‰) and foliar TN, TP and K contents (g·kg⁻¹) in *Caragana korshinskii*. The corresponding linear regression equations *(y = ax + b)* were showed. Significance of the regression: ns – not significant; * – significant at *P* <0.05; ** – significant at *P* <0.01.
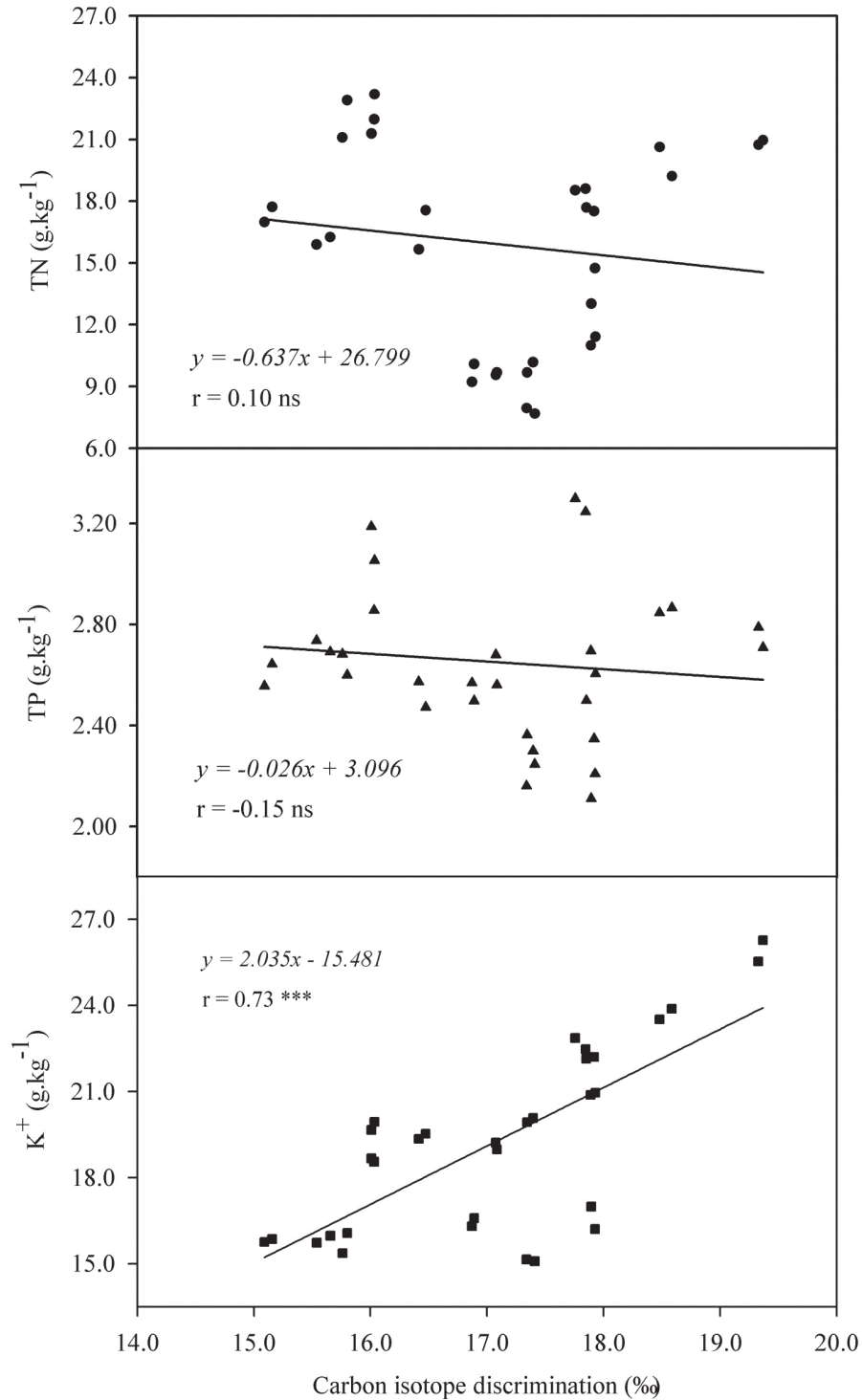
Fig. 2. Correlations between foliar carbon isotope discrimination (CID Δ‰) and foliar TN, TP and K contents (g·kg^{-1}) in *Artemisia ordosica*. The corresponding linear regression equations *(y = ax + b)* were showed. Significance of the regression: ns – not significant; * – significant at *P* <0.05; ** – significant at *P* <0.01, *** – significant at *P* <0.001.

higher than those of the rain-fed plot, indicating that the CID Δ values increased with the improvement of water conditions.

High water use efficiency (WUE) is considered to be a trait contributing to the successful growth and production of species in arid and semi-arid environments, where plant productivity is mainly constrained by soil water availability (Thumma *et al.* 1998). Farquhar and Richards (1984) suggested that the foliar CID Δ can be used to indicate the long-term WUE of a species. Much of this work focuses on the relationship between CID Δ and WUE, and the results have typically shown that this relationship is negative (Yan *et al.* 1998). In our study, long term monitoring of tree WUE through $\delta^{13}C$ analysis revealed significantly (P <0.001) higher WUE in *C. korshinskii* than in *A. ordosica* (Table 4). The investigations of Smith and Nowak (1990) suggested that high WUE is associated with increased drought tolerance and is thus found in trees that grow in dry areas; this suggests that *C. korshinskii* has greater drought tolerance than *A. ordosica.* This result also agrees with the previous report that the resistance to drought, high temperatures, and dehydration of *C. korshinskii* was greater than that of *A. ordosica* (Shapotou Desert Research and Experiment Station, 1991). In addition, in *C. korshinskii*, catalase (CAT) activity and the ratios of bound water content to free water content were significantly higher, and leaf water potential were significantly lower than those of *A. ordosica* under different water conditions (Jiang and Dai 1988). Those references also suggested that drought tolerance of *C. korshinskii* was stronger than that of *A. ordosica*.

No difference in foliar TN content between *C. korshinskii* and *A. ordosica* was found in this study. Foliar TP and K significantly increased the osmotic adjustment capacity and cell membrane stability of plant (Turner 1986, Gnansiri and Hirohumi 1990). Under drought conditions, P and K played the primary control role in the accumulation of osmotic components (Xu *et al.* 2002, Yang *et al.* 2003). In this study, foliar TP and K contents in *A. ordosica* were significantly higher than those of *C. korshinskii* (Table 4). This suggests that enrichment of

P and K was characteristic for *A. ordosica*, and thus its osmotic adjustment capacity was superior to that of *C. korshinskii*. In addition, soluble sugars content in *A. ordosica* was significantly higher (2.2 times) than that of *C. korshinskii* under different water conditions (Jiang and Dai 1988). These results also showed that *A. ordosica* had stronger osmotic adjustment capacity than *C. korshinskii*.

Among various environmental factors, nutrient (particularly nitrogen) deficiencies (Sparks and Ehleringer 1997) can result in more negative $\delta^{13}C$ values (higher CID Δ values) by reducing photosynthetic assimilation of intercellular CO_2 in leaves. Thus the negative relationship between foliar N content and CID Δ can be found. A negative relationship between foliar N content and CID Δ values was attributed to a lower stomatal conductance caused by the higher leaf N content (Tsialtas et al. 2002). However, in our study, there were significantly positive relationships between foliar CID Δ and foliar TN, TP contents in *C. korshinskii*. This result suggests that absorption capacity of this species for N and P elements increased as water became more available due to the positive relationship between water availability and CID Δ of plant tissues (Laundré 1999, Miller *et al.* 2001). It indicated that water conditions were one of the main factors that limited the N and P absorption capacity and the growth of *C. korshinskii*, while nutrient deficiencies were not (Choi *et al.* 2005). The *a* values (the rate of increase per unit of increase – 1.0 ‰ – of foliar CID Δ) imply that the effect of water conditions on N absorption capacity of *C. korshinskii* was significantly stronger than that of P (Fig. 1). Thus, in agreement with our results (Fig. 1), the negative correlation between foliar TN and CID Δ values is not always evident.

Potassium was selected to be evaluated as a surrogate of CID Δ because of its role in plant water economy *via* regulation of stomatal function (Masle *et al.* 1992, Rascio *et al.* 2001). The strong and positive correlation between foliar K content and CID Δ in *A. ordosica* was found in our study (Fig. 2). This result also suggests that the capacity to absorb K increases with improved water conditions. The *a* values,

which were $2.04 g \cdot kg^{-1}$ ‰$^{-1}$ in foliar K of *A. ordosica*, and 1.59 and $0.07 g\ kg^{-1}$ ‰$^{-1}$ in foliar TN and TP of *C. korshinskii*, implied that the effects of water conditions on the above parameters varied due to differences of species and elements. In addition, the significant relationships between foliar CID Δ and nutrient contents revealed that foliar TN and TP contents in *C. korshinskii* and K content in *A. ordosica* can be indicated by their foliar CID Δ, respectively.

In summary, by comparing WUE (calculated by foliar CID Δ values) of *A. ordosica* and *C. korshinskii*, we concluded that the WUE of *C. korshinskii* was significantly higher than that of *A ordosica*. In *A. ordosica*, the TP, K and soluble sugars content were significantly higher than that of *C. korshinskii*. Those results implied that *A. ordosica* has a higher capacity for osmotic adjustment than *C. korshinskii*.

We may conclude that *A. ordosica* and *C. korshinskii* were the desirable species for stabilizing sand dunes and for the afforestation of degraded arid lands due to their different mechanism to adapt to dry conditions. The relationships between foliar CID Δ and TN, TP and K contents implied that water was a key factor limiting the growth and the absorption capacity for N and P in *C. korshinskii*, and for K in *A. ordosica*.

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