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## Variations of foliar carbon isotope discrimination and nutrient concentrations in *Artemisia ordosica* and *Caragana korshinskii* at the southeastern margin of China's Tengger Desert

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**Abstract** Seasonal variations in foliar stable carbon isotope discrimination ( $\Delta$ ) of *Artemisia ordosica* and *Caragana korshinskii* and correlations of foliar  $\Delta$  with N, P, and K concentrations were studied under different planting regimes at the southeastern margin of China's Tengger Desert. Foliar  $\Delta$ , N, P, and K concentrations and the correlations of  $\Delta$  with N, P, and K differed between the species and planting regimes. Foliar  $\Delta$ , P and K concentrations in *A. ordosica* were markedly higher than in *C. korshinskii*, while foliar N concentrations in *C. korshinskii* was significantly higher than in *A. ordosica*. There were no significant differences in N, P, and K concentrations in *C. korshinskii* between planting regimes, but foliar  $\Delta$  was significantly increased after June in mixed-species planting. In *A. ordosica* foliar N concentrations in

mixed-species planting and foliar  $\Delta$  in single-species planting were significantly higher than those of corresponding planting regimes. According to water-use efficiency (WUE) calculated based on foliar  $\Delta$ , and on N, P, and K concentrations, *C. korshinskii*'s survival may profit from its higher WUE, whereas *A. ordosica* can avoid drought damage by its higher P and K concentrations in leaves in arid or semi-arid environments. The complex correlations of foliar  $\Delta$  with foliar N, P and K suggested that water in *C. korshinskii* and water and P nutrition in *A. ordosica* were the key factors limiting their growth.

**Keywords** Stable carbon isotope discrimination ( $\Delta$ ) · Nutrient concentrations · *A. ordosica* · *C. korshinskii*

### Introduction

N, P, and K are main nutrient elements in plant growth. Plants must absorb enough N, P, and K to maintain their growth and development. Many researches reported that photosynthetic capacity is highly correlated with relative and absolute nitrogen (N) contents in  $C_3$  plants (Diaz et al. 1996; Evans 1989; Reich et al. 1995, 1998; Tognetti 2003; Zhao et al. 2003). Phosphorus (P) also plays an important role in photosynthesis, and it can enhance the drought resistance of plant tissues due to its influence on osmotic adjustment and water reten-

tion (Beijing Agricultural University 1994).  $K^+$  also is a major plant macronutrient that plays important roles related to stomatal behavior, osmoregulation, and cell expansion. Plants must absorb the bulk of  $K^+$  from the soil to maintain normal growth and development (Elumalai et al. 2002). Large  $K^+$  concentrations are also closely related to drought resistance (Wang et al. 2004). Except the plant species, environmental conditions such as soil water, nutrient and planting regimes can affect those element concentrations in plant tissue.

Leaf  $\delta^{13}C$  is related to the ratio of photosynthetic capacity ( $A$ ) and stomatal conductance ( $g_s$ ), in such a

way that it can be used to indicate the long-term water use efficiency (WUE) (Farquhar et al. 1989a). Foliar  $\Delta$  values calculated by  $\delta^{13}\text{C}$  have been used as an integrated measure of the response of photosynthetic gas exchange to environmental variables such as water availability (Monneveux et al. 2005; Shaheen et al. 2005), water status (Korol et al. 1999) and nutrient (Choi et al. 2005; Iqbal et al. 2005). The use of stable isotopes provides fundamental insights into the interactions between plant nutrition and eco-physiological processes. Previous studies have found positive correlations between  $\Delta$  and indices of water availability such as rainfall, soil water potential, and soil water availability for woody species (McNulty and Swank 1995; Damesin et al. 1997; Laundré 1999; Miller et al. 2001). Increases in  $\Delta$  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), coffee (DaMatta et al. 2002) and wheat (Monneveux et al. 2005; Shaheen et al. 2005).

Among various environmental factors, nutrient (particularly nitrogen) deficiencies can result in more negative  $\delta^{13}\text{C}$  (higher  $\Delta$ ) by reducing photosynthetic assimilation of intercellular  $\text{CO}_2$  in leaf (Sparks and Ehleringer 1997). The robust negative correlation between foliar  $\Delta$  and N concentrations implied that high leaf N concentrations corresponded to increased photosynthetic capacities and decreased internal leaf  $\text{CO}_2$  concentrations (Sparks and Ehleringer 1997). And no significant relationship between foliar  $\Delta$  and N concentrations can indicate that N deficiency was not a factor limiting tree growth (Choi et al. 2005). However, few have attempted to examine the correlations between foliar  $\Delta$  and K, P concentrations.

In arid and semi-arid regions of China, water availability is a key limiting factor and determines plant performance, abundance, and distribution, especially in regions such as China's Tengger Desert. The Tengger Desert is the fourth-largest desert in the central part of western China, and is characterized by shifting sand dunes. The Baotou-Lanzhou railway crosses this desert, and to ensure safe operation of the railway, the Chinese Academy of Sciences and related institutions began establishing protective systems to provide sand fixation (Zhao 1998). Stabilized in the past by means of straw barriers in a checkerboard pattern and by artificial shrub forests, the mobile dunes have been changed into stabilized sands in the transition zone between desert and arid grassland (Xiao et al. 2003). Among the desert plants used to fix the sand, xerophytes (*C. korshinskii*) and succulent xerophytes (*A. ordosica*) played important roles in stabilizing shifting sands due to their great ability to adapt to desert climates. *C. korshinskii* is Leguminosae Papilionaceae, and *A. ordosica* is Compositae, Trip Ant-

hemideae (Lin and Lin 1991). They belong to desert and semi-desert biome (Walter and Breckle 1985) and have strong capability to fight a drought (Wang et al. 2002). However, the health of these species has varied as a function of planting regime and microhabitat (Tang et al. 2001). Here, this study was conducted to compare foliar stable carbon isotope discrimination ( $\Delta$ ) and the foliar N, P, and K concentrations, as well as the relationship between  $\Delta$  and these parameters, in *A. ordosica* and *C. korshinskii* in single-species and mixed-species plantings near the Tengger Desert. The goal of this paper was to investigate the effects of planting regime on foliar  $\Delta$  and foliar N, P, and K concentrations in a desert environment, and to discuss the potential mechanisms used by *A. ordosica* and *C. korshinskii* to adapt to desert conditions and the main limited factors that affected the *A. ordosica* and *C. korshinskii* growth.

## Materials and methods

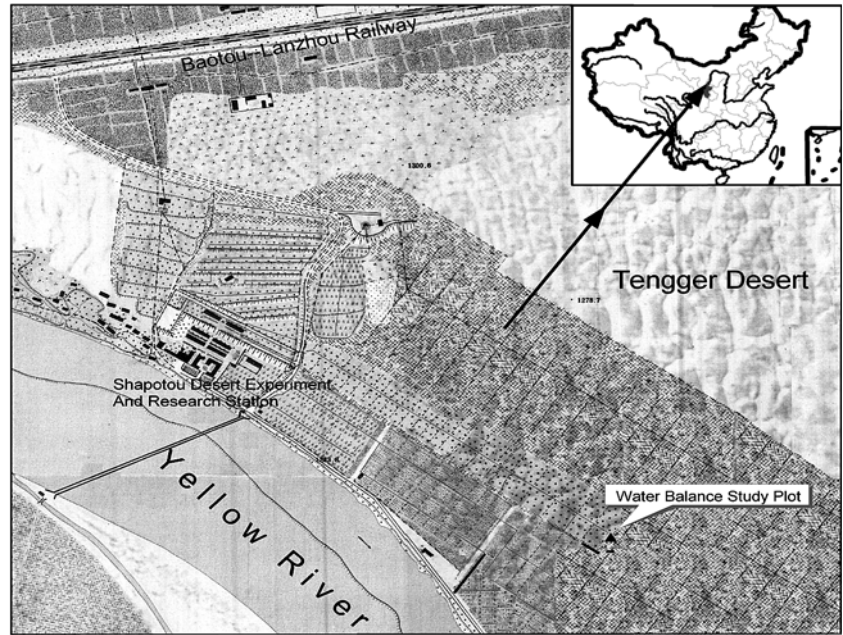
### The study area

The study was conducted in the water balance study plot at the Shapotou Desert Experimental Research Station (37°27.55'N, 105°00.64'E), which borders on the Tengger Desert (Fig. 1). The area is located 1,300 m above sea level, and has abundant sunshine and low relative humidity (Wang et al. 2002). Average annual precipitation is 180.2 mm per year, with 80% of the rainfall occurring between May and September. Annual mean temperature is 10.0°C, with a mean January temperature of -6.9°C and a mean July temperature of 24.3°C (Li et al. 2004). 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 150–180 days per year. The soil is an aeolian sandy soil (Xun and Li 1987).

### Planting regime and conditions at the sample site

At the study site, 4-year-old seedlings of *A. ordosica* and *C. korshinskii* were planted under eight planting regimes on April 1990 in a rain-fed area, with no irrigation provided after planting (Wang et al. 2002). In the present study, only three of these planting regimes were studied (Table 1). By 2004, the soil properties in the study field had improved to the values shown in Table 2 as a result of the planting of sand-fixing plants such as *A. ordosica* and *C. korshinskii* (Table 2).

**Fig. 1** The study region and sampling site of Shapotou Desert Research and Experimental Station of Chinese Academy Sciences



### Plant sampling

Sampled leaves of *A. ordosica* and *C. korshinskii* were collected on 13 and 28 May, 30 June, 28 July, 28 August, and 23 September 2004 in sites 1, 2, and 3. Meteorological data for the corresponding growing season are presented in Table 3. At each sampling time, the leaves were taken between 8 and 10 a.m., and about 20 leaves from each of 5 trees were taken as a sample from each species growing in each of the three planting regimes. Every sample was repeated two times. The samples were dried at 70°C for 24 h before analysis of N, P, and K concentrations and carbon isotope ratio ( $\delta^{13}\text{C}$ ).

### Determination of leaf N, P, K concentrations

The dried samples were ground in a stainless steel mill, and wet-digested in concentrated  $\text{H}_2\text{SO}_4$  for determina-

tion of total N and in a di-acid mixture ( $\text{HNO}_3$  and  $\text{HClO}_4$  mixed in a 4:1 ratio) for determination of total P. The N content was determined by means of semi-micro Kjeldahl analysis (Bremner and Mulvaney 1982); P according to the method of Dickman and Bray and Woods and Mellon (described by Jackson 1982); and the potassium (K) content of leaves was determined by means of flame spectrophotometry (Allen et al. 1989). Pooled samples were analyzed (the combination of the two replicates collected for each sample) and were measured twice.

### Analysis of $\delta^{13}\text{C}$

The carbon isotope ratio ( $^{13}\text{C}/^{12}\text{C}$ ) was determined by mass spectrometry (MAT 252 spectrometer, Thermo Electron Corporation, Waltham, MA, USA) (Liu et al. 2003). The precision of the analysis was better than

**Table 1** Sample sites and planting regimes for *Artemisia ordosica* and *Caragana korshinskii*

Plant species	Microhabitat	Spacing (m)	Planting regime
Water balance study field			
<i>A. ordosica</i>	Site 1: AOM	1×1	Mixed-species planting: two lines of <i>A. ordosica</i> (1×1 m) followed by two lines <i>C. korshinskii</i> (1×1 m), then followed by a 2-m gap
	Site 2: AOS	1×1	<i>A. ordosica</i> single-species planting
<i>C. korshinskii</i>	Site 1: CKM	1×1	Mixed-species planting: two lines of <i>A. ordosica</i> (1×1 m) followed by two lines <i>C. korshinskii</i> (1×1 m), then followed by a 2-m gap
	Site 3: CKS	2×2	<i>C. korshinskii</i> single-species planting

AOM and AOS indicate *A. ordosica* mixed and single plantings, respectively; CKM and CKS indicate *C. korshinskii* mixed and single plantings, respectively

**Table 2** Physical and chemical properties of the soil in the study area

Soil depth (cm)	Organic matter (g kg <sup>-1</sup> )	Total nutrient content (g kg <sup>-1</sup> )			Available nutrient content (g kg <sup>-1</sup> )			pH
		N	P	K	N	P	K	
0–5	1.16	0.09	0.32	20.0	12.8	3.7	140	8.22
>5	0.74	0.05	0.29	20.0	2.5	2.8	100	8.49

0.10‰. The  $\delta^{13}\text{C}$  ( $\delta p$ , relative to Pee Dee Belemnite, the international standard) was expressed as:

$$\delta^{13}\text{C}(\text{‰}) = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1,000 \quad (1)$$

where  $R$  is the  $^{13}\text{C}/^{12}\text{C}$  ratio. The analysis of leaf  $\delta^{13}\text{C}$  used pooled samples and every measurement was replicated two times.

### Definitions and basic equations

The  $\Delta^{13}\text{C}$  was calculated by Eq. 2:

$$\Delta^{13}\text{C} = \frac{\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}}}{1 - \frac{\delta^{13}\text{C}_{\text{plant}}}{1,000}} \quad (2)$$

where  $\Delta^{13}\text{C}$  is the carbon isotope discrimination by the plant:

$$\Delta^{13}\text{C} = a + (b - a) \times \frac{C_i}{C_a} \quad (3)$$

where  $a$  is the fractionation 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  $\text{CO}_2$  concentration, and  $C_a$  represents the atmospheric  $\text{CO}_2$  concentration (in this paper,  $C_a$  was  $375.5 \mu\text{mol mol}^{-1} \text{CO}_2$ , which represents the monthly average from January to December 2003 in Waliguan Atmospheric Background Station of China Meteorological Administration).

$$\frac{C_i}{C_a} = \frac{\delta^{13}\text{C}_{\text{plant}} - \delta^{13}\text{C}_{\text{air}} + a}{a - b} \quad (4)$$

$$\text{WUE} = C_a \times \frac{1 - (C_i/C_a)}{1.6} \quad (5)$$

where WUE represents the water-use efficiency. Statistical analysis was carried out using ANOVA and SPSS software (10.0).

## Results

### Seasonal variations in foliar $\Delta$ and water use efficiency

There were significant differences in carbon isotope discriminations ( $\Delta$ ) in the leaves of *C. korshinskii* only from July to September (lower in the single-species planting than in the mixed-species planting) (Fig. 2d). However, the leaf  $\Delta$  values for *A. ordosica* in the single-species planting were significantly higher than those in the mixed-species planting ( $P < 0.001$ ) throughout the growing season (Fig. 2h). The seasonal patterns for *C. korshinskii* in the single-species planting and for *A. ordosica* in the two planting regimes were similar (Fig. 2d, h). Foliar  $\Delta$  of *A. ordosica* in single-species planting and in mixed-species planting were significantly higher than those of *C. korshinskii* in mixed-species planting ( $P = 0.002$ ) and single-species planting ( $P = 0.038$ ), respectively.

In *C. korshinskii*, WUE through  $\delta^{13}\text{C}$  analysis was higher in the single-species planting than in the mixed-

**Table 3** Meteorological data from the Shapotou station during the 2004 growing season

	1 April–12 May	13–27 May	28 May–29 June	30 June–27 July	28 July–27 August	28 August–22 September
MT (°C)	16.0	19.3	22.0	24.7	22.0	19.0
MMT (°C)	23.2	26.7	28.9	31.1	27.7	25.6
MLT (°C)	8.7	11.9	15.0	18.3	16.3	12.3
MST (°C)	19.7	24.7	26.8	28.7	26.1	23.0
P (mm)	1.5	2.9	25.5	26.4	48.7	2.1
RH (%)	24.2	28.9	41.0	44.3	64.0	46.7
WV (m s <sup>-1</sup> )	4.1	4.2	3.8	3.4	2.9	2.5

MT, MMT, MLT, and MST represent the mean temperature, mean maximum temperature, mean lowest temperature, and mean surface temperature for each period, respectively. P, RH, and WV indicate precipitation, mean relative humidity, and mean wind velocity for each period, respectively. From 1 April to 22 September the precipitation is 107.1 mm

species planting, whereas in *A. ordosica*, the WUE was lower in the single-species planting than in the mixed-species planting. Differences in WUE between *A. ordosica* ( $99.10 \pm 10.20 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ ) and *C. korshinskii* ( $111.37 \pm 7.68 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ ) were very significant ( $P < 0.001$ ) (Table 4).

#### Seasonal variations in foliar nutrient concentrations

Foliar N concentrations in *C. korshinskii* did not differ between planting regimes and the mean foliar N concentrations for the whole season were similar (Fig. 2a). In contrast, foliar N concentrations in *A. ordosica* were significantly higher in the mixed-species planting ( $P < 0.001$ ). The difference between the two species was strongly significant ( $P = 0.007$ ), with mean foliar N concentrations 17.84% higher in *C. korshinskii* than in *A. ordosica* for both planting regimes combined. There was a significant effect of date for both species, with N concentrations trending upward over the course of the season in both planting regimes (Fig. 2a, e).

There were no significant differences in mean P concentrations over the course of the season between planting regimes for either species (Fig. 2b, f). However, the P concentration in *A. ordosica* in the mixed-species planting was significantly greater from 28 May to the end of the season ( $P = 0.037$ ; Fig. 2f). Seasonal variations in mean P concentration were only significant in *C. korshinskii*. The mean foliar P concentration in *A. ordosica* was significantly greater than that in *C. korshinskii* (2.25 times).

The mean foliar K concentrations also differed significantly between the species ( $P < 0.001$ ; Fig. 2c, g). Mean foliar K concentrations in *A. ordosica* were 1.40 times the values in *C. korshinskii*. However, mean K concentrations were not significantly different between planting regimes for either species, though individual K concentrations were significantly higher in both species in the single-species planting at several points in the season (Fig. 2c, g). Mean foliar K concentrations showed no significant seasonal variation in either species or planting regime, though individual concentrations in *A. ordosica* tended to be significantly higher in the single-species planting (Fig. 2g). Except for N concentration in *A. ordosica* ( $P < 0.001$ ), there were no significant month  $\times$  planting regime interactions for any other parameters.

#### Correlations between foliar $\Delta$ and N, P, and K concentrations

In *C. korshinskii*, with data pooled across planting regimes,  $\Delta$  was significantly and positively correlated with foliar N and P concentrations ( $P < 0.001$ ) but was not

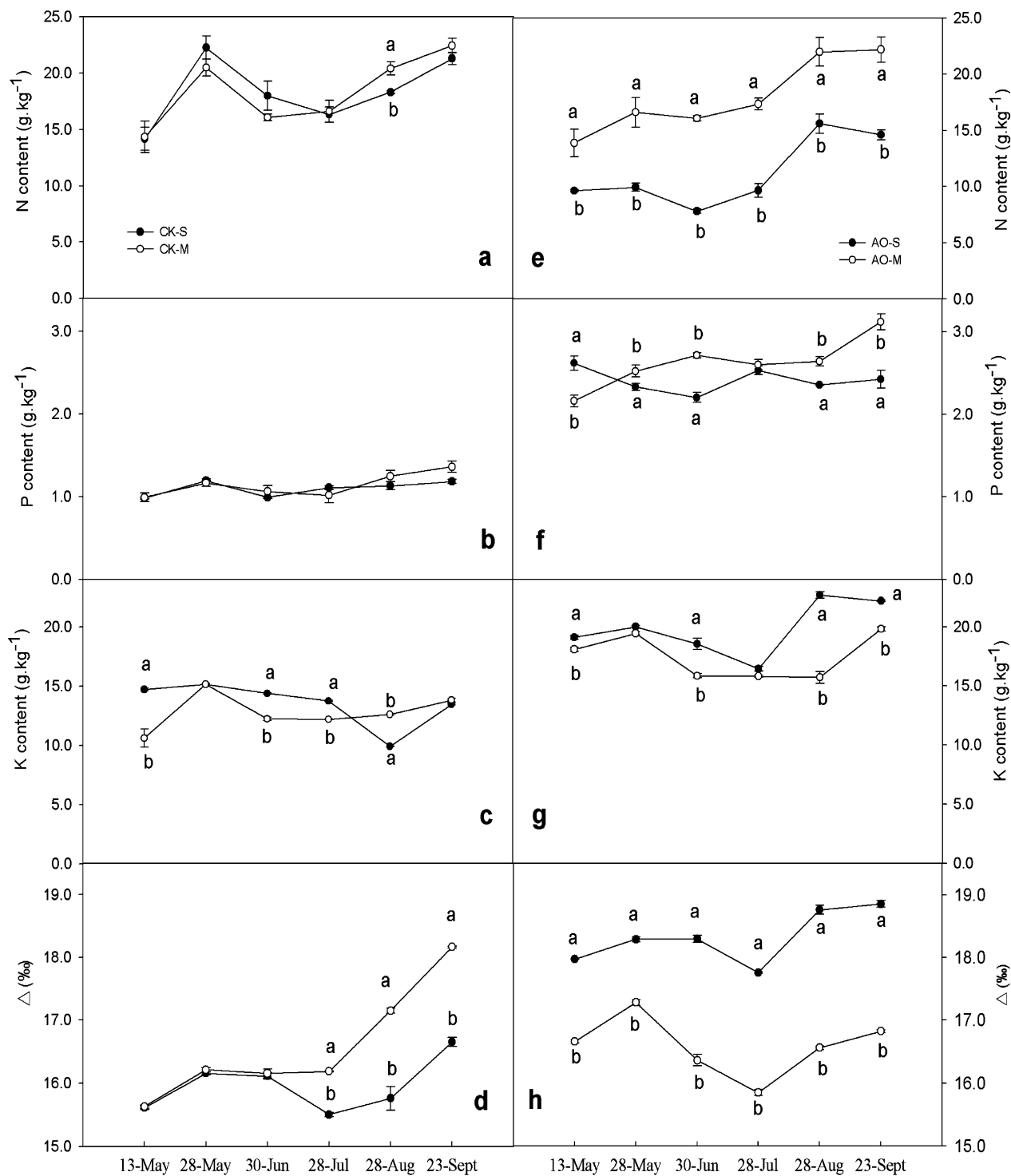
significantly correlated with foliar K concentration (Fig. 3). Furthermore, these relationships differed among planting regimes. For example, the relationships between foliar  $\Delta$  and N concentrations were positive with single-species planting ( $P = 0.004$ ) and mixed-species planting ( $P < 0.001$ ), and the  $a$  regression coefficients, which represent the rate of increase per unit increase (1‰) in foliar  $\Delta$ , clearly differed (values of 2.77 in the pooled data, 5.448 in the single-species data, and 2.926 in the mixed-species data; Fig. 3a). The relationship between foliar  $\Delta$  and P was significantly positive in the mixed-species planting ( $P < 0.001$ ), but not in the single-species planting ( $P = 0.130$ ; Fig. 3b).

In *A. ordosica* pooled across both planting regimes, a strong and significant positive correlation existed between  $\Delta$  and K ( $P < 0.001$ ; Fig. 4c). In contrast, strong and weak negative relationships existed between  $\Delta$  and foliar P and N concentrations ( $P = 0.032$  and  $0.056$ , respectively; Fig. 4a, b). In addition, the relationships between  $\Delta$  and foliar K concentration were significantly positive in both planting regimes (Fig. 4c). For the other regressions, there was only a significant (positive) relationship between  $\Delta$  and N concentration in the single-species planting ( $P = 0.001$ ).

## Discussion

### Variations of foliar $\Delta$ and WUE

In arid and semi-arid regions, the growth of plants depends strongly on soil and atmospheric water. Previous studies have found positive correlations between  $\Delta$  and indices of water availability (Laundré 1999; Miller et al. 2001; Wang et al. 2001). The carbon isotope discrimination model suggested that decreased  $\Delta$  by drought was due to increased WUE through decreased stomatal and/or mesophyll conductance. In the study, the foliar  $\Delta$  of both species differed between the two planting regimes, and the foliar  $\Delta$  of *A. ordosica* was higher in the single-species planting, suggesting more severe water stress in the mixed-species planting. This hypothesis is supported by field investigation: in the single-species planting, few young seedlings appeared, whereas in the mixed-species planting plot, a few grown trees died during a drought in May and June, suggesting that the single-species planting was more favorable for growth and regeneration of *A. ordosica*. However, markedly higher  $\Delta$  was found in the leaves of *C. korshinskii* in the mixed-species planting after June. These results showed that single-species planting is favorable for the growth of *A. ordosica*, but mixed-species planting is more favorable for *C. korshinskii*. These results support those of Tang et al. (2001), who found that the niche fitness of *A. ordosica* was higher in single-species plantings whereas that of *C. korshinskii* was lower in single-species plantings.



**Fig. 2** Foliar nitrogen (N), phosphorus (P), potassium (K) concentrations ( $\text{g kg}^{-1}$ ), carbon isotope discrimination ( $\Delta$ , ‰) in *Artemisia ordosica* and *Caragana korshinskii* leaves collected monthly from May to September 2004. Figure 2a, b, c, and d for

*C. korshinskii*; Fig. 2e, f, g and h are for *A. ordosica*. Points within a graph for a given data that are followed by different letters differed significantly between two planting regimes during the same month ( $P < 0.05$ )

Plant productivity is constrained by the availability of soil water, and higher WUE is a key feature of plants that are able to survive in arid and semi-arid regions (Thumma et al. 1998). Farquhar et al. (1989b) suggested that foliar  $\Delta$  can be used to indicate the long-term WUE of a species (Farquhar and Richards 1984). Much of this work focuses on the relationship between  $\Delta$  and WUE, and results have typically shown that this relationship is negative (Yan et al. 1998). In this study, long term monitoring of tree WUE through  $\delta^{13}\text{C}$  analysis (as described by Cowan and Farquhar 1977) revealed significantly ( $P < 0.001$ ) higher WUE in *C. korshinskii* than in *A. ordosica* (Table 4). The investigations of Smith and Nowak (1990) suggest 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 accordance 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). Furthermore, the WUE values of *C. korshinskii* and *A. ordosica* differed significantly as a function of planting regime, suggesting that plant WUE was influenced by planting regime. In mixed planting conditions, the WUE of *A. ordosica* was higher than in single-planting condition, one of main reason may be that *A. ordosica* and *C. korshinskii* have different root system, and *C. korshinskii* has strong competitive capacity for limited water resources (Li et al. 2001). The WUE of *C. korshinskii* in single-planting conditions was higher than in mixed-planting conditions. This may be correlated with that there was less soil evaporation due to good canopy closure of *A. ordosica* (Wang et al. 2002).

#### Variations of foliar N, P and K concentrations

Significantly higher foliar N concentrations in *C. korshinskii* showed that *C. korshinskii* is a leguminous shrub and can fix nitrogen (Cadisch et al. 1994; Ledgard and Steele 1992). Differences in foliar N concentration between mixed-species and single-species plantings were not significant in *C. korshinskii*, suggesting that planting

regime had no effect on the foliar N concentration of the species. However, in *A. ordosica*, the mean foliar N concentration was 60.89% higher in the mixed-species planting. One of main reason was that growing together with *C. korshinskii*, *A. ordosica* can absorb more N nutrient which is fixed by *C. korshinskii* (Shearer and Kohl 1986; Niu and Jiang 2004). In a previous study, foliar P and K significantly increased the osmotic adjustment capacity and cell membrane stability of plant (Turner 1986; Gnansiri and Hirohumi 1990), and under drought conditions, P and K played a primary control role in the accumulation of osmotic components (Xu et al. 2002; Yang et al. 2003; Wang et al. 2004). In this study, the mean foliar P and K concentrations in *A. ordosica* were 2.25 and 1.40 times those of *C. korshinskii*, respectively (Fig. 1b, f). In addition, soluble sugar contents in *A. ordosica* were significantly higher (2.21 times) than those of *C. korshinskii* under different water conditions (Table 5) (Shapotou Desert Research and Experiment Station 1991). Those results suggested that *A. ordosica* had stronger osmotic adjustment capacity than that of *C. korshinskii*. Furthermore, there were no significant differences in foliar P and K concentrations between single- and mixed-species plantings in *C. korshinskii*. In contrast, the foliar P concentration in the mixed-species planting of *A. ordosica* was higher than in the single-species planting except on 13 May and 28 July. This showed that under drought conditions, *A. ordosica* is likely to absorb more P and thereby improve its drought resistance, while the foliar K concentrations in *A. ordosica* were significantly higher in the single-species planting than in the mixed-species planting, suggesting that the effect of planting regime on K and P concentration was significant.

#### Correlations between $\Delta$ with foliar N, P and K concentrations

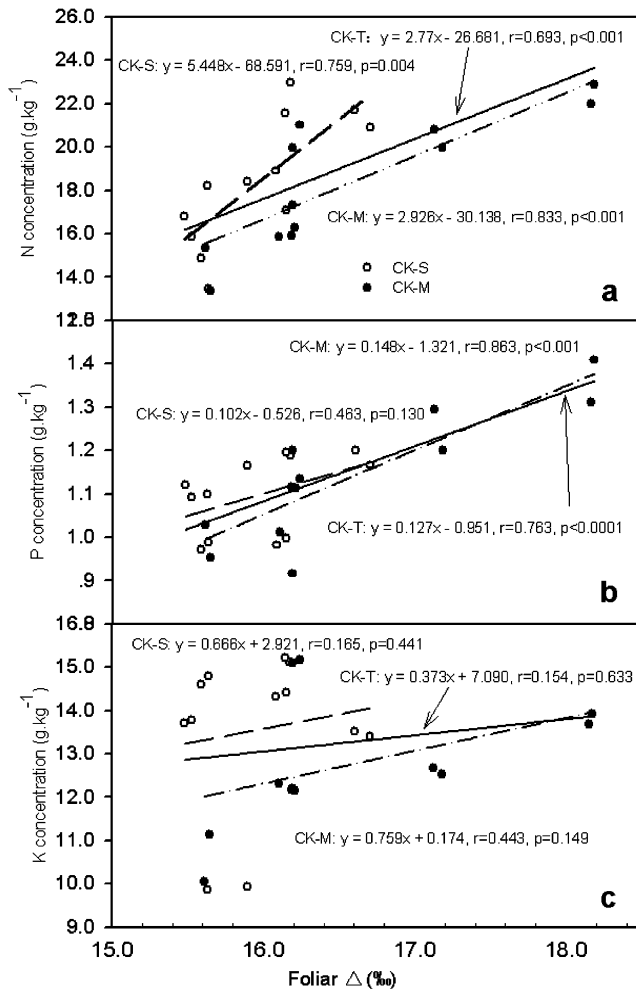
Among various environmental factors, nutrient (particularly nitrogen) deficiencies (Sparks and Ehleringer 1997) can result in more negative  $\delta^{13}\text{C}$  (higher  $\Delta$ ) by reducing photosynthetic assimilation of intercellular  $\text{CO}_2$  in leaves. Thus the negative relationship between

**Table 4** The water-use efficiency (WUE) of *C. korshinskii* and *A. ordosica* calculated based on their foliar  $\Delta$

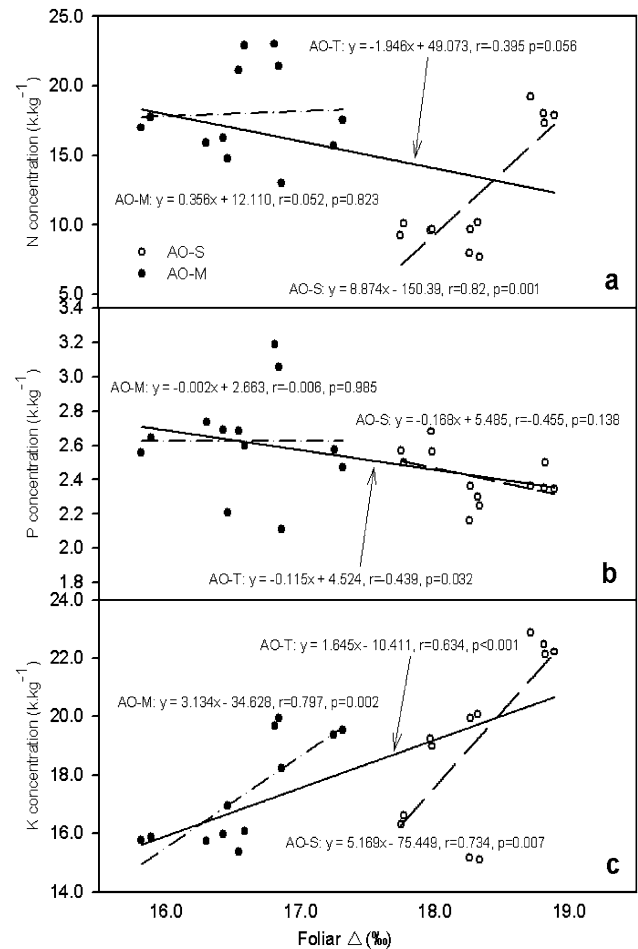
<i>C. korshinskii</i>	WUE ( $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ )		<i>A. ordosica</i>	WUE ( $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ )	
	Mean	SD		Mean	SD
Pooled across both planting regimes	111.37A	7.68	Pooled across both planting regimes	99.10B	10.20
Single-species planting	114.57a	4.28	Single-species planting	90.11b	4.26
Mixed-species planting	108.17b	9.09	Mixed-species planting	108.09a	4.81

foliar nutrient concentration and  $\Delta$  can be found. However, in the study, there were positive relationships between foliar  $\Delta$  and foliar N, P and K concentrations in *C. korshinskii* in single- and mixed-species plantings, and when both datasets were pooled. This result suggests that absorption capacity of this species for nutrient elements increased as water became more available due to the positive relationship between water availability (McNulty and Swank 1995; Damesin et al. 1997; Laundré 1999; Miller et al. 2001), and indicated that water conditions was one of a main factors that limited the nutrient absorption capacity and the growth of

*C. korshinskii*, while nutrient deficiencies was not a main factor (Choi et al. 2005). However, in *A. ordosica*, those correlations were complex due to planting regimes. The correlations between foliar K concentration and  $\Delta$  in *A. ordosica* were all positive and significant in the single- and mixed-species plantings, as well as in the pooled data for both planting regimes (Fig. 4c), suggesting that the capacity to absorb K increases with improved water conditions. However, there were no consistent correlations between foliar  $\Delta$  and N concentrations. But there was significant negative relationship between foliar  $\Delta$  and P concentration when both datasets were pooled,



**Fig. 3** Correlations between  $\Delta$  and foliar N, P, and K concentrations in *C. korshinskii*, and the corresponding linear regression equations. *CK-T*, *CK-S*, and *CK-M* indicate the total (pooled) data for both planting regimes, and the data for the single-species and mixed-species plantings, respectively. The *a* regression coefficient represents the slope of the linear regression, and thus represents the change in N, P, and K concentrations per unit (1‰) increase in foliar  $\Delta$ ; *r* represents the correlation coefficient. The *solid*, *long-dash*, and *dash-dot* lines correspond to the regressions for *CK-T*, *CK-S*, and *CK-M*, respectively



**Fig. 4** Correlations between  $\Delta$  and foliar N, P, and K concentrations in *A. ordosica*, and the corresponding linear regression equations. *AO-T*, *AO-S*, and *AO-M* indicate the total (pooled) data for both planting regimes, and the data for the single-species and mixed-species plantings, respectively. The *regression coefficient* represents the slope of the linear regression, and thus represents the change in N, P, and K concentrations per unit (1‰) increase in foliar  $\Delta$ ; *r* represents the correlation coefficient. The *solid*, *long-dash*, and *dash-dot* lines correspond to the regressions for *AO-T*, *AO-S*, and *AO-M*, respectively



**Table 5** Soluble sugar content (percentage of dry matter) of *C. korshinskii* and *A. ordosica* under different water conditions

	Percent of field water content (%)				
	20–40	40–60	60–80	80–100	Average
<i>C. korshinskii</i>	3.2	3.0	2.6	2.5	2.8 ± 0.33a
<i>A. ordosica</i>	7.8	6.8	6.7	3.5	6.2 ± 1.87b

Cited from Shapotou Desert Research and Experiment Station of Lanzhou (1991). The different letter indicates significant difference between two species plants (\* $P < 0.05$ )

suggesting that except the water conditions, the P nutrition was another limited factor that affected the growth of *A. ordosica* (Choi et al. 2005). In addition, foliar N and K concentrations can be foliar  $\Delta$  indicators of *C. korshinskii* and *A. ordosica*, respectively.

In summary, the WUE (calculated from foliar  $\Delta$ ) of *C. korshinskii* was significantly higher than that of

*A. ordosica*. In *A. ordosica*, the P, K and soluble sugar concentrations were significantly higher than that of *C. korshinskii*, this results implied that *A. ordosica* with a higher capacity for osmotic adjustment than that of *C. korshinskii*. Therefore, those results suggested that *A. ordosica* and *C. korshinskii* were desirable species for stabilizing sand dunes and for the afforestation of degraded arid lands due to their different mechanism to adapt dried conditions. The relationships between foliar  $\Delta$  and N, P and K concentrations implied that water was a key factor limiting the growth of *A. ordosica* and *C. korshinskii*. In addition, except water conditions, P nutrition was also a limited factor that affected the growth of *A. ordosica*.

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## References

- Allen SE (1989) Analysis of vegetation and other organic materials. In: SE Allen (ed) Chemical analysis of ecological materials, 2nd edn. Blackwell, Britain, pp 46–61
- Beijing Agricultural University (1994) Agricultural chemistry (pandect) (in Chinese). Agricultural Press, Beijing
- Bremner JM, Mulvaney CS (1982) Nitrogen-total. In: Page AL, Mille RH, Keeney DR (eds) Methods of soil analysis, part 2. Agronomy, vol 9, 2nd edn. Soil Sci Soc Am, Madison, WI, pp 595–624
- Cadisch GR, Schunke M, Giller KZ (1994) Nitrogen cycle in monoculture grassland and legume-grass mixture in Brazil red soil. *Trop Grasslands* 28:43–52
- Chen H, Kang Y, Feng J (1991) Preliminary study on the plant growth and water balance in Shapotou area, Tengger Desert (in Chinese). *J Desert Res* 11:1–10
- Choi WJ, Chang SX, Allen HL, Kelting DL, Ro HM (2005) Irrigation and fertilization effects on foliar and soil carbon and nitrogen isotope ratios in a loblolly pine stand. *For Ecol Manage* 213:90–101
- Cowan IR, Farquhar GD (1977) Stomatal function in relation to metabolism and environment. In: Jennings DH (eds) Integration of activity in the higher plant (Society for experimental biology symposia, no 31). Cambridge University Press, Cambridge, pp 471–505
- DaMatta FM, Loos RA, Silva EA, Loureiro ME, Ducatti C (2002) Effects of soil water deficit and nitrogen nutrition on water relations and photosynthesis of pot-grown *Coffea canephora* Pierre. *Trees* 16:555–558
- Damesin C, Rambal S, Joffre R (1997) Between-tree variations in leaf  $\delta^{13}\text{C}$  of *Quercus pubescens* and *Quercus ilex* among Mediterranean habitats with different water availability. *Oecologia* 111:26–35
- Díaz M, Haag-Kerwer A, Wingfield R, Ball E, Olivares E, Grams TEE, Ziegler H, Lüttge U (1996) Relationships between carbon and hydrogen isotope ratios and nitrogen levels of *Clusia* species and two other Clusiaceae genera at various sites and different altitudes in Venezuela. *Tree* 10:351–358
- Elumalai RP, Nagpal P, Reed JW (2002) A mutation in the Arabidopsis KT2/KUP2 potassium transporter gene affects shoot cell expansion. *Plant Cell* 14:119–131
- Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of  $\text{C}_3$  plants. *Oecologia* 78:9–19
- Farquhar GD, Hubick KT, Condon AG et al (1989a) Carbon isotope fractionation and plant water use efficiency [A] stable isotopes in ecological research [C]. Springer, Berlin Heidelberg New York, pp 21–40
- Farquhar GD, Ehleringer JR, Hubick KT (1989b) Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 40:503–537
- Farquhar GD, Richards RA (1984) Isotopic composition of plant carbon correlates with water use efficiency of wheat genotypes. *Aust J Plant Physiol* 11:539–552
- Gnansiri S, Hirohumi S (1990) Cell membrane stability and leaf water relation as affected by phosphorus nutrition under water stress in maize. *Soil Sci Plant Nutr* 36(4):661–666
- Iqbal MM, Akhter J, Mohammad W, Shah SM, Nawaz H, Mahmood K (2005) Effect of tillage and fertilizer levels on wheat yield, nitrogen uptake and their correlation with carbon isotope discrimination under rainfed conditions in north-west Pakistan. *Soil Tillage Res* 80:47–57
- Jackson ML (1982) Análisis químicos de suelos. Ediciones Omega SA, Barcelona, pp 203–205
- Korol RL, Kirschbaum MUF, Farquhar GD, Jeffreys M (1999) Effects of water status and soil fertility on the C-isotope signature in *Pinus radiata*. *Tree Physiol* 19:551–562
- Laundré JW (1999) Relationships between water availability, carbon isotope discrimination and plant productivity in two semi-arid grass and shrub species. *J Arid Environ* 41(1):49–60
- Ledgard SF, Steele KW (1992) Biological nitrogen fixation in mixed legume/grass pastures. *Plant Soil* 141:137–153

- Li ZZ, Shi WL, Tang HP, Wang XP (2001) Studies on numerical simulation of moisture niche-fitness procedure of arid plants (in Chinese with English abstract). *J Desert Res* 21(3):281–285
- Li XR, Zhang ZS, Zhang JG, Wang XP, Jia XH (2004) Association between vegetation patterns and soil properties in the Southeastern Tengger Desert, China. *Arid Land Res Manage* 18:1–15
- Lin R, Lin YR (1991) *Flora Reipublicae Popularis Sinicae* [M]. Science Press, Beijing 76(2):195
- Liu XH, Qin DH, Shao XM, Chen T, Ren JW (2003) Climatic significance of stable carbon isotope in tree rings of *Abies spectabilis* in southeastern Tibet. *Chin Sci Bull* 48(18):2000–2004
- McNulty SG, Swank WT (1995) Wood  $\delta^{13}\text{C}$  as a measure of annual basal area growth and soil water stress in a *Pinus strobes* forest. *Ecology* 76:1581–1586
- Miller JM, Williams RJ Farquhar GD (2001) Carbon isotope discrimination by a sequence of *Eucalyptus* species along a subcontinental rainfall gradient in Australia. *Funct Ecol* 15:222–232
- Monneveux P, Reynolds MP, Trethowan R, González-Santoyo H, Peña RJ, Zapata F (2005) Relationship between grain yield and carbon isotope discrimination in bread wheat under four water regimes. *Europ J Agron* 22:231–242
- Niu SL, Jiang GM (2004) The importance of legume in China grassland ecosystem and the advances in physiology and ecology studies. *Chin Bull Bot* 21(1):9–18
- Reich PB, Kloeppel BD, Ellsworth DS, Walters MB (1995) Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* 104:24–30
- Reich PB, Ellsworth DS, Walters MB (1998) Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. *Funct Ecol* 12:948–958
- Shaheen R, Hood-Nowotny RC (2005) Effect of drought and salinity on carbon isotope discrimination in wheat cultivars. *Plant Sci* 168:901–909
- Shapotou Desert Research and Experiment Station of Lanzhou (1991) The principle and measure of quicksand bandage in Shapotou of railroad from Baotou to Lanzhou [M]. Ninxia People's Press, Yinchuan, 58–65, 217–218 pp
- Shearer G, Kohl DH (1986)  $\text{N}_2$ -fixation in field setting: estimations based on natural  $^{15}\text{N}$  abundance. *Aust J Plant Physiol* 13:699–756
- Smith SD, Nowak RS (1990) Physiology of plants in the inter-mountain lowlands. In: Osmond CB, Pitelka LF, Hidy GM (eds) *Plant biology of the basin and range*, vol 80. Ecological studies, pp 179–241
- Sparks JP, Ehleringer JR (1997) Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transects. *Oecologia* 109:362–367
- Tang HP, Shi PJ, Li ZZ (2001) Variation in growth characteristics among different planting patterns of *Artemisia ordosica* and *Caragana korshinskii* under varying water availability regimes. *Acta Phytocol Sin* 25(1):6–10
- Thumma BR, Naidu BP, Cameron DF, Bahnisch LM (1998) Transpiration efficiency and its relationship with carbon isotope discrimination under well-watered and water-stressed conditions in *Stylosanthes scabra*. *Aust J Agric Res* 49:1039–1045
- Tognetti R, Peñuelas J, (2003) Nitrogen and carbon concentrations, and stable isotope ratios in Mediterranean shrubs growing in the proximity of a  $\text{CO}_2$  spring. *Biol Plant* 46(3):411–418
- Turner NC (1986) Adaptation to water deficits: a changing perspective. *Aust J Plant Physiol* 13:175–190
- Walter HS, Breckle (1985) *Ecological systems of the geobiosphere*. Springer, Berlin Heidelberg New York
- Wang GA, Han JM (2001)  $\delta^{13}\text{C}$  variations of  $\text{C}_3$  plants in dry and rainy seasons (in Chinese). *Mar Geol Quaternary Biol* 21(4):43–47
- Wang SM, Wan CG, Wang YR et al (2004) The characteristics of  $\text{Na}^+$ ,  $\text{K}^+$  and free proline distribution in several drought-resistant plants of the Alxa Desert, China. *J Arid Environ* 56:525–539
- Wang XP, Li XR, Kang ES, Li JG, Zhang JG, Liu LC (2002) Experiment on evapotranspiration of xerophyte communities in a revegetated desert zone (in Chinese). *J Desert Res* 22(4):363–367
- Warren CR, McGrath JF, Adams MA (2001) Water availability and carbon isotope discrimination in conifers. *Oecologia* 127:476–486
- Xiao HL, Li XR, Duan ZH, Li T, Li SZ (2003) Impact of evolution of plant-soil system on the water environment during the mobile dunes stabilization. *Acta Pedologica Sin* 40(6):809–814
- Xu SJ, An LZ, Feng HY (2002) The seasonal effects of water stress on *Ammopiptanthus mongolicus* in a desert environment. *J Arid Environ* 51:437–447
- Xun Y, Li QK (1987) *Soil in China* (in Chinese). 2nd edn. Science Press, Beijing
- Yan CR, Han XG, Chen LZ, Huang JH, Su B (1998) Foliar  $\delta^{13}\text{C}$  within temperate deciduous forest: its spatial change and interspecies variation. *Acta Bot Sin* 40(9):853–859
- Yang JX, Zhang T, Wu DX (2003) Study on effect of phosphorus nutrition on drought resistance of plant (in Chinese). *Guang Dong Wei Liang Yuan Su Ke Xue* 10(12):13–19
- Zhao LJ, Liu XH, Xiao HL, Guo TW (2003) The effect of soil nutrients on crop organism  $\delta^{13}\text{C}$  and biomass (in Chinese). *Acta Geosci Sin* 24(6):519–524
- Zhao XL (1998) A study on the control of shifting sand dunes of Shapotou regions in the edge of southeastern Tengger Desert. Ninxia People's Press, Yinchuan, p 5