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BRIEF COMMUNICATION

Photosynthetic pathway of dominant plant species in the Qaidam Basin: evidence from foliar stable carbon isotope measurement

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Abstract

Foliar $\delta^{13}C$ values of *Calligogum kozlovi* and *Haloxylon ammodendron* ranged from –13.13 to –15.11 ‰, while those of the rest 11 species were in the range of –22.22 to –27.73 ‰. This indicates that two of 13 dominant plant species in the Qaidam Basin possess a C_4 photosynthetic pathway. Significant differences were observed for the average foliar $\delta^{13}C$ values between C_3 or C_4 plant communities, between grass and shrub communities, even between the same species derived from different sites. Precipitation accounted for the major part of the differences.

Additional key words: C_3 plants; C_4 plants; desert vegetation; precipitation.

Foliar $\delta^{13}C$ values of C_4 plants vary between –6 and –19 ‰ with a mean value of –12.5 ‰ whereas those of C_3 plants range from –22 to –34 ‰ with a mean value of –27 ‰ (Bender 1971, Smith and Epstein 1971). As a result, foliar $\delta^{13}C$ values have been developed as an effective approach to identify plant photosynthetic types (Sternberg *et al*. 1984). Up to date, a growing body of studies has identified photosynthetic pathways in a variety of ecosystems using foliar $\delta^{13}C$ values over the world (Waller and Lewis 1979, Ziegler *et al*. 1981, Ehleringer *et al*. 1987, Lin *et al*. 1988, Yin and Wang 1997, Tang *et al*. 1999). Although a few studies have compared photosynthetic pathways using the foliar $\delta^{13}C$ values in the Qinghai-Tibet Plateau (Wang 2003, Yi *et al*. 2003, Wang *et al*. 2004, Li *et al*. 2006), only some of them have been conducted in the Qaidam Basin.

Qaidam Basin is located in the northeast of the Qinghai-Tibet plateau (95º02′–99º00′E, 36º24′–37º38′N, 2 500–3 600 m a.s.l.). It is characterized by a typical desert climate. Annual precipitation varies from 200 to 320 mm in the east and from 40 to 90 mm in the west. The aridity increases gradually from 1.0 in the east to 8.5 in the west. Over the whole area, the wind-eroded terra, sand hills, deserts, salt lakes, and salt soil plains appear alternatively. On a horizontal level, it is occupied by alpine meadows, desert-grassland, and typical desert vegetation (mainly desert shrubs and semi-shrubs) from the southeast to the northwest (Wu *et al*. 1985, Zhou *et al*. 1987). This provides a unique transect for exploring photosynthetic pathway of dominant plant species and their adaptation to arid environments.

Leaves of all the dominant species were collected during the growing season (July–August 2005). In total, 90 foliar samples (or assimilation branches) including 13 plant species of 6 families from 18 sites were measured. Each sample was from an individual plant and three individuals were selected at each site. Leaves were dried to constant mass at 75 °C in an oven, and aliquots of plant

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material (2 mg) were weighed into tins for isotopic analysis. Carbon isotope ratios were determined by gas isotope ratio mass spectrometry (*Finnigan MAT 253*, Bremen, Germany). Stable isotope abundances are reported as (Craig 1957):

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

where R is the ratio of $^{13}C/^{12}C$ of either the sample or reference standard. The standard deviation of repeated measurements of laboratory standards is ±0.2 ‰ for $\delta^{13}C$.

Meteorological data were collected from meteorological observation data in years 1960–1990 with *PRISM* interpolation. Soluble full-salt in the soil was obtained with electric conductance (Liu *et al.* 1996). One-way ANOVA was used to test the effects of precipitation or plant types on foliar $\delta^{13}C$ values, using a *SPSS 11.5* statistical software package. All results were considered significant at the $p<0.05$ level.

Among the studied 13 plant species, the foliar $\delta^{13}C$ values of *C. kozlovi* and *H. ammodendron* ranged from –13.13 to –15.11 ‰ (Table 1), which fell within the scope of C_4 plants. These values were similar to those observed by Su *et al.* (2004, 2005) in a desert of Hexi Corridor, Gansu Province. Wang (2003) suggested that C_4 plants derived from Chenopodiaceae can colonize those regions of more than 3 000 m a.s.l., while in this study *C. kozlovi* belongs to Chenopodiaceae which occupy about 2 800 m a.s.l. in the Qaidam Basin. The foliar $\delta^{13}C$ values of the other 11 plant species were in the range of –22.22 and –27.73 ‰, characterizing a C_3 photosynthetic pathway.

One-way ANOVA analysis showed that there were significant differences in foliar $\delta^{13}C$ values between C_3 or C_4 plants as well as between shrub and grass communities with the C_3 photosynthetic pathway (Table 2). Concretely, *Phragmites communis*, *Achnatherum splendens*, and *Kobresia* sp. had the lowest $\delta^{13}C$ values. In contrast, *Ceratoides latens*, *Sympegma regelii*, *Kalidium gracile*, and the other desert species had relatively higher $\delta^{13}C$ values, similar to foliar $\delta^{13}C$ values of grasses. *Ephedra sinica* was a type of desert C_3 plants with the highest $\delta^{13}C$ value, and was significantly different from the other grasses and desert shrubs. Of C_4 plants, foliar $\delta^{13}C$ value of *C. kozlovi* was significantly higher than that of *H. ammodendron* (Table 1).

C_3 plants in the Qaidam Basin were concentrated in those areas with annual precipitation of 22 to 423 mm (averaging 155 mm) and annual temperature of below 5 °C (mean temperature being 0.04 °C). Normally, the lowest temperature during growing seasons ranged from –3.5 to 4.1 °C (averaging 0.8 °C), and the aridity degree from 1.0 to 12.6 (averaging 5.5). In contrast, C_4 plants such as *H. ammodendron* and *C. kozlovi* lived in an environment where annual precipitation was 38.3 to 85.2 mm (averaging 52 mm) and the aridity degree ranged from 4.5 to 12.9 (averaging 8.3). 80 % of C_4 plant samples belonged to the area of 10 % lowest precipitation and highest aridity degree (including C_3 and C_4). The highest temperatures varied from 11.4 to 17.2 °C while the lowest temperatures ranged from –0.4 to 4.1 °C, with the mean temperature ranging from 8.5 to 14.7 °C during the growing season. This indicates that C_4 plants in the Qaidam Basin grow in relatively dry and warm environments.

The $\delta^{13}C$ values of C_3 plants correlated positive with altitude, soil moisture, mean annual precipitation, and mean precipitation as well as aridity degree during the growing season, but not with the temperature. By comparison, those of C_4 plants exhibited a negative correlation with precipitation and lowest temperature as well as aridity degree during the growing season whereas they showed a positive correlation with mean annual temperature and the highest temperature. These results are consistent with the conclusion drawn by Tang *et al.* (1999) that the frequency of C_4 plants' occurrences is in positive correlation with the temperature and in negative correlation with the precipitation. Correlations between $\delta^{13}C$ values and environmental factors showed that the main factor influencing the distribution of C_3 plants is precipitation.

Plants possess a number of mechanisms to adapt themselves to arid environments including physiological adaptation, morphological adaptation, *etc.* (Monson and Smith 1982, Wu *et al.* 1985, Kalapos 1994). In the Qaidam Basin, leaves of *E. sinica*, *H. ammodendron*, and *C. kozlovi* have been aborted to assimilated branches. However, *H. ammodendron* and *C. kozlovi* showed a C_4 photosynthetic pathway while *E. sinica* possessed a C_3 photosynthetic pathway. It has been suggested that temperature controls the distribution of C_4 plants (Long 1983, Li *et al*. 2006). However, low annual mean temperature (8.5 °C) and the lowest temperature (3.4 °C) during the growing season for *H. ammodendron* and *C. kozlovi* indicate that temperature does not limit the colony of C_4 plants in the Qaidam Basin. Possible explanation is that very high irradiance and very long duration of sunlight in the Qaidam desert offset the effects caused by lower temperature in the Qinghai-Tibet Plateau. Besides, soluble salt concentration (3 451.42 μS cm^{-1}) of the soil occupied by *H. ammodendron* and *C. kozlovi* was far higher than that of the soil grown by *E. sinica* (536.69 μS cm^{-1}). This implies that C_4 plants have greater advantages than the C_3 ones under stress conditions in the Qaidam Basin. This means that the distribution of C_4 plants in the Tibet Plateau might be controlled by multiple factors, not only by temperature.

The mean foliar $\delta^{13}C$ values in the Qaidam Basin and the northern Namaqualand desert in South Africa are higher than those in Arizona State in the U.S.A. and Fukang in China (Ziegler *et al*. 1981, Ehleringer and Cooper 1988, Rundel *et al*. 1999, Chen *et al*. 2002). The

Table 1. Stable carbon isotope values and photosynthetic pathways of dominant species in the Qaidam Basin. Vegetation type: Sh = shrub, G = grass. SE = standard error.

Sampling site code	Family	Species	Vegetation type	Mean ± SE [‰]	Photosynthetic pathway
724CJC	Gramineae	*Achnatherum splendens*	G	–27.22±0.28	C_3
725CTR	Chenopodiaceae	*Ceratoides latens*	Sh	–25.54±0.30	C_3
	Chenopodiaceae	*Kalidium gracile*	Sh	–25.74±0.89	C_3
	Chenopodiaceae	*Salsola abrotanoides*	Sh	–24.41±0.75	C_3
725CYZ	Chenopodiaceae	*Salsola abrotanoides*	Sh	–23.81±1.09	C_3
728CHT	Chenopodiaceae	*Sympegma regelii*	Sh	–25.45±0.45	C_3
728CTH	Chenopodiaceae	*Ceratoides latens*	Sh	–24.67±0.47	C_3
	Chenopodiaceae	*Salsola abrotanoides*	Sh	–23.21±0.19	C_3
	Tamaricaceae	*Reaumuria soongorica*	Sh	–24.60±0.37	C_3
728CTL	Chenopodiaceae	*Ceratoides latens*	Sh	–24.92±0.34	C_3
	Chenopodiaceae	*Salsola abrotanoides*	Sh	–23.50±0.58	C_3
	Chenopodiaceae	*Sympegma regelii*	Sh	–23.65±0.53	C_3
729CLW	Gramineae	*Phragmites communis*	G	–26.72±0.05	C_3
729CMH	Chenopodiaceae	*Sympegma regelii*	Sh	–23.24±0.59	C_3
	Ephedraceae	*Ephedra sinica*	Sh	–22.22±0.32	C_3
731CTR	Chenopodiaceae	*Ceratoides latens*	Sh	–24.75±0.13	C_3
	Chenopodiaceae	*Salsola abrotanoides*	Sh	–24.76±0.55	C_3
801CCL	Polygonaceae	*Calligogum kozlovi*	Sh	–13.13±0.30	C_3
	Tamaricaceae	*Tamarix chinensis*	Sh	–26.26±0.79	C_3
801CSS	Chenopodiaceae	*Haloxylon ammodendron*	Sh	–15.11±0.16	C_4
	Chenopodiaceae	*Sympegma regelii*	Sh	–23.74±0.73	C_3
801CSZ	Polygonaceae	*Calligogum kozlovi*	Sh	–13.95±0.18	C_4
802CJC	Gramineae	*Achnatherum splendens*	G	–26.89±0.13	C_3
802CJJC	Gramineae	*Achnatherum splendens*	G	–27.07±0.12	C_3
802CZM	Chenopodiaceae	*Salsola abrotanoides*	Sh	–27.43±0.47	C_3
	Tamaricaceae	*Reaumuria soongorica*	Sh	–27.54±0.28	C_3
803CJC	Gramineae	*Achnatherum splendens*	G	–27.07±0.11	C_3
803CSC	Cyperaceae	*Kobresia* sp.	G	–26.74±0.14	C_3
803CTR	Chenopodiaceae	*Ceratoides compacta*	Sh	–25.82±0.37	C_3
	Chenopodiaceae	*Salsola abrotanoides*	Sh	–25.73±0.29	C_3

Table 2. Significance analysis of stable carbon isotope value differences between C_3 and C_4 plant communities as well as between grass and shrub communities.

Plant types	Sum of squares	df	Mean square	F	Significance of overall groups
C_3 plants	164.56	16	10.29	12.76	<0.01
C_4 plants	5.94	2	2.97	20.09	<0.01
shrubs and grasses	175.07	1	175.07	14.44	<0.01

disparity is related to precipitation features in the climate zone of different deserts.

Compared to the mean $\delta^{13}C$ value (–28.74 ‰) obtained from the investigation on the global scale, the mean value in the Qaitam Basin (–24.98 ‰) is far higher. This indicates that foliar $\delta^{13}C$ values of desert plants can reveal their adaptation to arid environments by enhancing water use efficiency.

The main conclusions of this study are as follows: (*1*) Among the 13 dominant plant species, *C. kozlovi* and *H. ammodendron* have a C_4 photosynthetic pathway while the other plant species possess a C_3 photosynthetic pathway. (*2*) Desert plants can adapt dry environment by increasing water use efficiency. (*3*) Compared to C_3 plants, C_4 plants in the Qaidam Basin grow in relatively warmer and drier environment and can adapt better to depressed conditions. (*4*) The $\delta^{13}C$ values of desert shrub communities in the Qaidam Basin are higher than those of grass communities, showing that desert shrubs are more adaptable to dry environments than grasses.

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