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CARBON ISOTOPE COMPOSITION OF PLANTS ALONG ALTITUDINAL GRADIENT AND ITS RELATIONSHIP TO ENVIRONMENTAL FACTORS ON THE QINGHAI-TIBET PLATEAU

ABSTRACT: Distribution pattern of $\delta^{13}C$ values of plateau plants and their responses to environment along altitudinal gradients were investigated. In the growing season of 2003 (June–August), stable carbon isotope ratios ($\delta^{13}C$) of 174 plant samples belonging to 89 species of 20 families and 58 genera along the gradient 2800–4400 m (above sea level) was studied in six sites on the east edge of Qinghai-Tibet Plateau. The results indicated that the range of $\delta^{13}C$ values of plants is narrow from –30.2‰ to –25.2‰, which means that none of the species examined belonged to C_4 photosynthetic pathway and all of these species performed C_3 photosynthetic pathway. The average $\delta^{13}C$ values of plants at 6 sites were positively correlated to altitude ($r = 0.974$, $P < 0.01$). The results revealed that site-averaged $\delta^{13}C$ values were negatively correlated with temperature ($r = 0.907$, $P < 0.05$) as well as CO_2 partial pressure ($r = 0.940$, $P < 0.01$). The combination of these two factors account for 80% of the variation of $\delta^{13}C$ values ($r^2 = 0.859$, $P < 0.01$). Varying precipitation with increasing altitude does not affect the plant $\delta^{13}C$ values ($r = 0.469$, $P > 0.05$) as well as the sunlight duration($r = 0.630$, $P > 0.05$).

KEY WORDS: $\delta^{13}C$ value; plateau plants; environmental factors; Qinghai-Tibet Plateau

1. INTRODUCTION

Carbon isotope composition ($\delta^{13}C$) is an important tool in research on plant ecology and global change (McCarroll and Pawellek 2001). It reflects the relationship between photosynthetic demand and diffusive (stomatal) supply of CO_2 (Hamerlynck *et al.* 2004). The stable isotope ratio of plant organic matter contains an integrated record of environmental conditions during plant growth. Interpreting that record requires an understanding of how the isotope ratios of plant organic matter respond to changes in climate. In a number of studies the stable isotope ratios in either laboratory conditions or in the field were investigated. They have revealed the empirical relationships between carbon isotope ratios and a variety of environmental factors (Farquhar *et al.* 1982, Stuiver and Braziunas 1987, Damesin *et al.* 1997, Guillemette and Stephen 2001). For example, humidity and temperature were found to explain latitudinal variation of $\delta^{13}C$ values in deciduous and coniferous trees in North America (Stuiver and Braziunas 1987). Other authors have proposed light level as the dominant factor controlling plant stable isotopes (Ehleringer *et al.* 1986). It was also found that $\delta^{13}C$ correlates with precipitation (Damesin *et al.* 1997). Guillemette and Stephen (2001) considered the carbon isotopes as the climatic indicators.

The ecosystem of alpine meadow, prevailing over Qinghai-Tibet plateau, "the third pole of the world", is the ideal place for the research on structure and functioning of alpine meadow ecosystem in relation to climate changes. However, only few studies were performed in this area (Li *et al.* 1999). Due to the high-altitude climate, the ecosystem is here very fragile and sensitive to climate change. From low to high altitudes there are striking variations in temperature, precipitation, CO_2 partial pressure *etc.*

In this study we investigated the carbon isotope composition of 89 alpine plant species from 20 families and 58 genera grown at 6 different altitudes in the Qinghai-Tibet Plateau. The study aim is to estimate the spatial distribution of $\delta^{13}C$ values of plateau plants and their responses to environment along altitudinal gradient.

2. STUDY AREA

Six study sites covered with meadow plants were selected along the altitudinal gradient from 2800 to 4400 m a.s.l. at the east part of the Qinghai-Tibet Plateau. Samples were collected from these sites ranging from Heiquan where altitude is the lowest (2800 m a.s.l.) to Changshitou where altitude is nearly 4400 m (Table 1). Except Maduo where few semi-desert plants and cushion species have been found in recent years, other studied sites were mainly covered by alpine meadow vegetation. The growing period of plant species lasts from June to August. The climate of the considered areas was dominated by the southeast monsoon and the high-pressure system of Siberia. Severe and long winters and short cool summers are characteristic for the continental monsoon type climate. Because the stable carbon isotope values of plants were controlled by environmental factors during the growing season, the climatic data from June to August were analyzed. The climatic data are represented by 29 yearly averages, from 1975 to 2003. The most important climatic data for each site were summarized in Table 1.

Table 1. Climatic description of the 6 sampling sites in Qinghai-Tibet Plateau. The altitude, vegetation, temperature, precipitation, CO_2 partial pressure, relative humidity and light correspond to mean bimonthly values during growing season (June–August) and annual mean values. The climatic data represent 29 years averages from 1975 to 2003.

Name of site	Vegetation type	Altitude (m a.s.l.)	Annual mean temp. (°C)	Temp. (Jul–Aug) (°C)	Annual precipitation (mm)	Precipitation (Jul–Aug) (mm)	Annual sunlight duration (h)	Sunlight duration (Jul–Aug) (h)	CO_2 partial pressure (ppm)
1 Heiquan	Alpine meadow	2800	2.3	11.3	565.4	330.0	2386.1	209.2	371.8
2 Haibei	Alpine meadow	3250	−0.6	9.9	526.0	230.6	2406.6	210.1	360.0
3 Henan	Alpine meadow	3620	−0.8	9.8	564.9	354.5	2459.3	215.4	343.7
4 Wenquan	Alpine meadow	4000	−2.8	7.5	537.8	278.0	2399.9	210.2	322.1
5 Maduo	Alpine meadow, semi-desert	4210	−3.8	6.3	321.6	193.5	2838.3	236.5	312.9
6 Changshitou	Alpine meadow	4400	−4.6	5.8	469.1	238.8	2418.6	223.6	308.5

3. MATERIAL AND METHODS

Carbon isotope fractionation during photosynthesis is commonly presented with the following equation:

$$\delta^{13}C_{plant} = \delta\,^{13}C_{air} - a - (b-a)\;Pi/Pa \qquad (1)$$

Where:

$\delta^{13}C_{plant}$ is the carbon isotope ratio of the plant, $\delta^{13}C_{air}$ is the carbon isotope ratio of CO_2 in the atmosphere, *Pi, Pa* are the intercellular and atmospheric partial pressures of CO_2, respectively, *a* is the discrimination factor which results from the different diffusion of ^{12}C and ^{13}C and *b* is the net fractionation induced by carboxylation by Rubisco (Farquhar *et al.* 1982). The values of *a* is about 4.4‰ and *b* is close to 27‰ (Farquhar *et al.* 1982).

One important part of the total diffusional resistance to CO_2 uptake is the stomatal conductance (*g*). Another factor that regulated CO_2 uptake is the assimilation rate (*A*). The link between the ratio *Pi/Pa* and the two physiological parameters may be expressed by the following equation (Francey and Farquhar 1982).

$$Pi = Pa - A/g \qquad (2)$$

A number of different environmental factors may affect the *A*, *g* and the ratio *Pi/Pa* and thus influence on carbon isotopic values.

174 leaf samples belonging to 89 plant species from 20 families and 58 genera were collected from the 6 altitude sites (Appendix I). These species are dominantly or commonly distributed on the plateau. At each study site, leaves of dominant and common species in relation to 10^3 m^2 were collected. Leaf samples were collected in the middle of August during the growing season 2003. Each sample consisted of 15–20 leaves from ten individual plants per one species. Leaves were oven dried to constant mass at 75°C, ground finely, and then sub-samples were taken for isotopic analysis. Carbon isotope ratios ($\delta^{13}C$) were determined by *finnigan MAT DELTAPLUSXL* isotope ratio mass spectrometer and calculated by equation of Craig (1957):

$$\delta^{13}C = [(^{13}C\,/\,^{12}C)_s\,/\,(^{13}C\,/\,^{12}C)_{sta} - 1] \times 1000 \qquad (3)$$

where:

$(^{13}C/^{12}C)_s$ and $(^{13}C/^{12}C)_{sta}$ are the carbon isotopic ratio of sample and standard, respectively. The overall analytical precision is ± 0.2‰.

4. RESULTS

We investigated the stable carbon isotope ratios of 174 leaf samples belonging to 89 plant species. The results indicated that the variation of $\delta^{13}C$ values for plants is narrow and range from –30.2‰ to –25.2‰, with an average of –27.4‰ (Appendix I).

The relationships between stable carbon isotope ratios of plant species collected from each site and altitude were shown in Fig. 1. In general, the $\delta^{13}C$ values of plants increased with the altitudinal gradient from 2800 to 4400 m a.s.l. Average $\delta^{13}C$ values at each site were significantly correlated with altitude ($r = 0.974$, $P < 0.01$) and $\delta^{13}C$ values of all plants showed significant variation from –25.2‰ to –30.2‰ along the altitude gradient (Fig. 1, Table 2). The rate of change of $\delta^{13}C$ value (+1.1‰ km^{-1}) was slightly lower than the global trend of increasing $\delta^{13}C$ (+1.2‰ km^{-1}) with altitude (Körner *et al.* 1988). It, however, indicates that variation in altitude produced a similar effect on $\delta^{13}C$ values of plants.

Variation range of $\delta^{13}C$ values tended to be narrower at the higher altitude sites compared with low altitude areas (Fig. 2). At the Heiquan (2800 m a.s.l.), $\delta^{13}C$ values ranged from –30.1‰ to –26.4‰, while at Changshitou area (4400 m a.s.l.) from –27.9‰ to –25.2‰ (Table 2). The frequency of isotope ratio values tends to increase with the altitudes. At the 2800 m site, the value about –28‰ occurs with maximum frequency (44%), however, at the 4400 m it is the value –26‰ (50%). In summary, $\delta^{13}C$ tended to be more positive along the increasing altitudinal gradient (Table 2, Fig. 2).

5. DISCUSSION

The $\delta^{13}C$ values of C_3 plant species ranged from –32‰ to 20‰, with a mean of

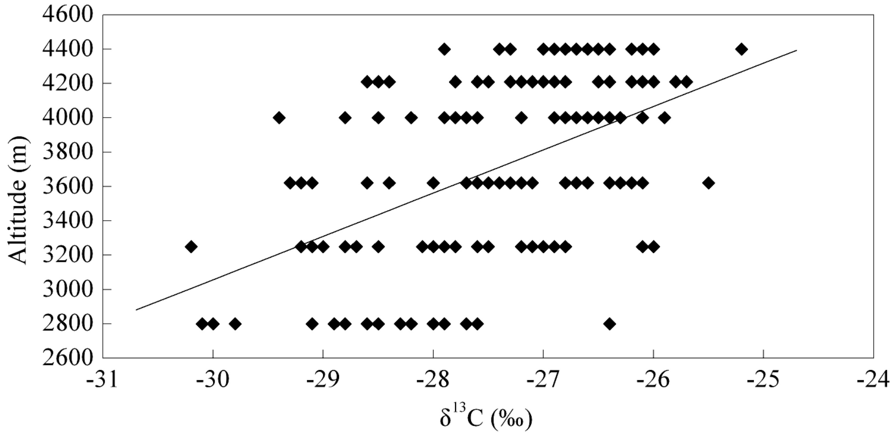

Fig. 1. The relationship between stable carbon isotope ratios in leaves of studied plants (Appendix I) and altitude. Each point represents $\delta^{13}C$ ratio of one sample.

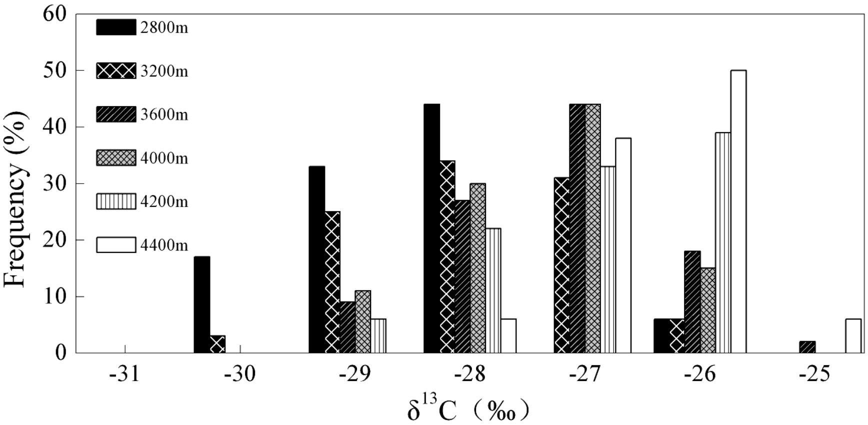

Fig. 2. The distribution of frequencies of $\delta^{13}C$ values in leaves of studied plant (Appendix I) at different altitudes.

−27‰. In contrast, $\delta^{13}C$ of C_4 plant species ranged from −17‰ to −9‰, with a mean of −13‰ (Bender 1971, Smith and Epstein 1971). The $\delta^{13}C$ values monitored in this study indicate that all the considered plant species belong to C_3 photosynthetic pathway and there are no C_4 species found at the 6 study sites in the eastern Tibetan Plateau. It may be due to the long-term adaptation of this vegetation to the typical environmental factors, especially under the severe low temperatures at the Qinghai-Xizang (Tibet) Plateau alpine ecosystems; the low temperature may be the limiting factor for C_4 plant species (Li *et al.* 1999).

Results in this study indicate that the $\delta^{13}C$ values of plants show marked variation with the increasing of altitude. The increase in $\delta^{13}C$ values might result from plastic response of these plants to environmental changes with different altitudes.

Effects of temperature may operate via anatomical and physiological routes (Eq. 1). An effect of temperature on plant carbon isotope fractionation is that it can affect the stomatal conductance (*g*), then the ratio *Pi/Pa*. Another effect is the variation in the activities of enzymes during photosynthesis. Most laboratory studies suggest an increase of $\delta^{13}C$ as temperature decreases (O'Leary 1988; Morecroft *et al.* 1990, Edwards *et al.* 2000, Feng *et al.* 2003), while some field studies show the opposite trends (Stuiver and Braziunas 1987, Robertson *et al.* 1997). In some field studies it may be difficult to separate the effect of temperature

Table 2. The variation ranges of $\delta^{13}C$ values in leaves of plant species (see Appendix I) grown at the 6 sites at different altitude.

Name of site	Altitude (m a.s.l.)	Sample (number)	$\delta^{13}C$(‰) (mean±SD)	Range (‰)
1 Heiquan	2800	18	−28.6(±1)	−30.1/−26.4
2 Menyuan	3250	32	−27.8(±1)	−30.2/−26.0
3 Henan	3620	45	−27.3(±0.8)	−29.3/−25.5
4 Wenquan	4000	27	−27.2(±0.9)	−29.4/−25.9
5 Maduo	4210	36	−27.0(±0.8)	−28.4/−25.8
6 Changshitou	4400	16	−26.6(±0.6)	−27.9/−25.2

from other environmental factors. In this study, the results indicate that the site-averaged $\delta^{13}C$ values of plants increased with the decrease of temperature from lower altitude to higher altitude($r = 0.907$, $P < 0.05$) (Fig. 3A). Temperature seems to be the dominant environmental factor to affect the variation of $\delta^{13}C$ values. Low temperature at higher altitude reduces the stomatal conductance and then decreases the ratio, therefore, the discrimination for ^{13}C is relatively reduced (Körner *et al.* 1988). The increase of $\delta^{13}C$ may be associated with an increase in palisade layer thickness affected by low temperature (Körner *et al.* 1988). Decreasing activities of leaf enzymes during the process of photosynthesis at high elevation caused by low temperature is another important reason for increase of plant $\delta^{13}C$ values (Guillemette and Stephen 2001).

The elevation of altitude induces a decrease of CO_2 partial pressure. Based on Eq. 1, variation will lead to changes in $\delta^{13}C$ values. Lowering CO_2 partial press will tend to increase stomatal conductance as the diffusion of molecules is higher at low pressures (Gale 1973). The low atmospheric pressure can also induce greater stomata densities in various plants. Experiments under controlled atmospheric conditions show that $\delta^{13}C$ values increase when *Pa* decreases (Polley *et al.* 1995). Guillemette and Stephen (2001) had quantified the $\delta^{13}C$ values response to changing *Pa*, with an average +0.8‰ km^{-1} in a field study. In this study, significantly negative correlation between *Pa* and averaged $\delta^{13}C$ values ($r = 0.940$, $P < 0.01$) was also found (Fig. 3B). Therefore the variation of CO_2 pressure is another important environmental factor that affects the $\delta^{13}C$ values along the altitude gradients.

Precipitation is a critical factor in plant growth. The effect of decreased average precipitation should induce the decrease of stomatal conductance (*g*), a reduction of *Pi/Pa*, thus a general increase of $\delta^{13}C$ values (Stuiver and Braziunas 1987). Field and laboratory studies show that carbon isotope discrimination declines as precipitation increase (Rice and Giles 1996, Ma *et al.* 2005). On the Qinghai-Tibet Plateau precipitation is an important environmental factor for plant growth. However, there is no relationship with $\delta^{13}C$ values ($P > 0.05$). Therefore, the precipitation may show weak or no influence on the variation of plant $\delta^{13}C$ value which means that on the Qinghai-Tibet Plateau precipitation is not limiting factor for plant growth. The climate of the considered sites was

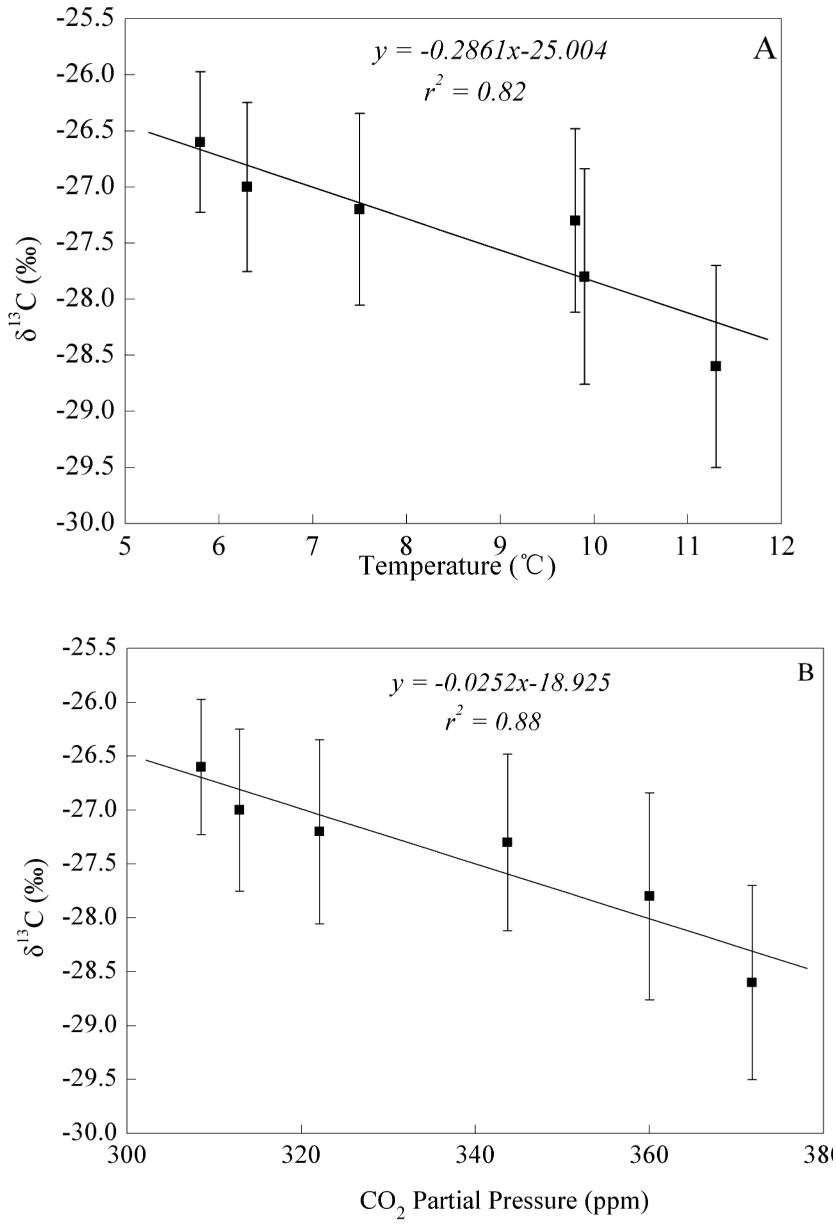

Fig. 3. Relationships between average values of stable carbon isotope values in leaves of plants collected from different altitude and temperatures (A), and CO_2 partial pressure(B). Vertical bars represent ± SD.

dominated by the southeast monsoon and the high-pressure system of Siberia. The severe and long winters and short cool summers are characteristic for the continental monsoon type climate (Hirota *et al.* 2004). In addition, 80% of average annual precipitation falls in the short summer growing season from May to September, especially July–August. Therefore, low temperature on the Qinghai-Tibet plateau may be more dominant factor for plant development and growth than precipitation during short growing season.

The physiological effect associated with an increasing light intensity or light duration is an increase of assimilation rate, a decrease of *Pi/Pa* ratio, and an increase of plant $\delta^{13}C$. The relationship between light duration and $\delta^{13}C$ values in laboratory studies of vascular plants was approximately 2‰

for a five-fold increase in light intensity or duration (Körner *et al.* 1988). But studies on the actual impact of changes in light regimes under field environment didn't agree with controlled studies (Farquhar and Wong 1984). In this study, the results indicated no significant relationship between the variation in light intensity and site-averaged $\delta^{13}C$ values ($P > 0.05$). The changes of light duration along the altitudinal gradients are probably too small to induce the significant variation in $\delta^{13}C$ values of studied plants. In this case, light duration might be not a main factor affecting $\delta^{13}C$ values of plants.

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APPENDIX

Carbon isotope ($\delta^{13}C$) values in leaves and detailed information of the studied plants from different altitudes (2800–4400 m a.s.l.). A = annual, P = perennial, D = dicotyledon, M = monocotyledon, F = forb, S = sedge, G = grass, Sh = shrub.

Family	Species		$\delta^{13}C$ values(‰)					
			2800	3250	3620	4000	4210	4400
Boraginaceae	*Microula pseudotrichocarpa* W.T. Wang	D,F,A				−26.3		−26.0
	M. sikkimensis (Clarke) Hemsl	D,F,A	−28.9	−28.8			−27.6	
	M. tibetica Benth.	D,F,A						−26.2
	Trigonotis peduncularis (Trev.) Benth.ex Barker et Moore	D,F,P		−26.8				
Caprifoliaceae	*Lonicera minuta* Batal.	Sh,F,P	−27.7			−26.5		
Caryophyllaceae	*Arenaria bryophylla* Fevnald	D,F,P					−26.1	
	Stellaria uda Williams	D,F,P			−26.4			
Chenopodiaceae	*Atriplex centralasiatica*	D,F,A		−28.0			−26.5	
	A. fera (L.) Bge.	D,F,A		−27.1				
	Ceratoides compacta (Losinsk.) Tsien et C.G. Ma	D,F,A					−27.2	−26.1
Compositae	*Ajania tenuifolia* (Jacq.) Tzvel	D,F,P		−29.0	−27.6		−27.8	−27.9
	Anaphalis lacteal Maxim.	D,F,P		−30.2	−29.3		−28.5	
	Artemisia hedinii Ostenf. et Pauls.	D,F,P	−30.0	−29.0		−28.5		
	A. sieversiara Ehrhart ex Willd	D,F,A					−27.3	−27.0
	Aster flaccidus Bunge	D,F,P	−28.5	−27.5	−27.1		−27.0	
	Cirsium setosum (Wild.)MB.	D,F,P			−26.6	−26.6		
	Echinops gmelini Turcz.	D,F,P				−26.4		−26.7
	Heteropappus altaicus (Willd.) Novopokr	D,F,P			−26.3			
	H. gouldii (C.E.Fisch) Griers.	D,F,P			−27.3			
	Leontopodium nanum Hook. f. et Thans	D,F,P		−27.0				−26.4
	Ligularia virgaurea (Maxim.) Mattf.	D,F,P			−26.8			
	Saussurea arenaria Maxim.	D,F,P		−27.2		−26.7		
	S. eopygmaea Hand.-Mazz.	D,F,P			−28.0	−27.6	−27.1	
	S. salsa (Pall.) Spreng.	D,F,P			−27.1		−26.5	

Family	Species		δ					
			2800	3250	3620	4000	4210	4400
	S. stella Maxim.	D,F,P					–26.0	
	S. superba Anth.	D,F,P						–26.9
	Taraxacum mongolicum Hand.-Mazz.	D,F,P	–28.6	–26.0	–27.4			
Cruciferae	*Capsella bursa-pastoris* (L.) Medic.	D,F,A				–26.8		
	Descurainia Sophia (L.) Webb. Ex Prantl	D,F,A				–27.8		
	Neotorularia humilis (C.A.Mey) Hedgeet	D,F,P		–29.1	–27.5		–27.8	
Cyperaceae	*Carex atro-fusca* Schkuhr subsp.	M,S,P		–28.7		–28.2		–26.6
	C. moorcroftii Falc. Ex Boott	M,S,P			–28.4		–27.1	–26.5
	C. orbicularis Boott	M,S,P			–27.6			
	Kobresia bellardii (All.) egl.	M,S,P		–28.5			–28.6	
	K. capillifolia (Decne.) C.B. Clarke	M,S,P		–28.5				–27.4
	K. humulis (C.A.Mey. ex Trautv) Sergn	M,S,P		–27.2			–26.4	
	K. pygmaea C.B.Clake	M,S,P	–30.1		–27.2	–26.8		
	K. schoenoides (C.A.Mey.) Stend.	M,S,P		–26.9				
	K. tibetica Maxim.	M,S,P		–27.8	–27.6		–27.6	
	Scirpus distigmaticus (Kükenth.) Tang et Wang	M,S,P			–27.2		–26.2	–25.2
Gentianaceae	*Gentiana farreri* (f. Balf.) T.N. Ho	D,F,P				–26.9		
	G. straminea Maxim.	D,F,P			–26.2	–27.2		
	G. tricolor Dielset Gilg	D,F,A			–26.7	–26.6		
	Gentianopsis paludosa (Hook.f.) Ma	D,F,A	–28				–27.2	
	Lomatogonium rotatum (L.) Fries ex Nym.	D,F,A				–27.9		–27.3
	Swertia bifolia Betal.	D,F,P			–29.2	–28.8		
Gramineae	*Agrostis perlaxa* Pilger	M,G,P		–28.0	–27.6			
	Aneurolepidium dasystachys (Georgi) Tzvel.	M,G,P	–27.9			–27.6	–27.5	
	Elymus nutans Griseb.	M,G,P		–27.1			–26.8	

Family	Species		δ¹³C values(‰)					
			2800	3250	3620	4000	4210	4400
	Festuca ovina L.	M,G,P		–27.1				
	Helictotrichon tibeticum (Roshev.) Holwb	M,G,P	–28.5					
	Koeleria cristata (L.) Pers.	M,G,P	–28.2		–25.5			
	Poa annua L.	M,G,A			–27.7		–27.6	
	Stipa purpurea Griseb.	M,G,P	–26.4	–26.1			–25.7	
Labiatae	*Ajuga lupulina* Maxim.	D,F,P		–26.9	–26.6			
	Dracocephalum heterophyllum Benth.	M,F,P	–28.6		–26.1	–26.8		
	Lamiophlomis rotate (Benth.) Kudo	M,F,P		–27.5	–27.3			
	Mentha haplocalyx Briq.	D,F,P		–28.8				
Leguminosae	*Astragalus adsurgens* Pall.	D,F,P			–27.2		–25.8	
	A. licentianus Hand.-Mazz.	D,F,P	–28.8		–26.4	–27.7		
	A. mattam Tsai et Yü	D,F,P			–28.0		–26.9	
	Oxytropis caerulea (Pall.) DC.	D,F,P				–26.8		–26.8
	O. falcata Bunge	D,F,P			–28.6	–27.8	–27.5	
	O. ochrocephala Bunge	D,F,P	–28.2				–28.4	
Polygonaceae	*Polygonum alatum* Buch.-Ham.	D,F,A		–27.9				
	P. sibiricum Laxm.	D,F,P	–29.1		–27.7		–26.5	
	P. viviparum L.	D,F,P			–26.4			
Primulaceae	*Anarosace septentrionalis* L.	D,F,P		–27.1				
	Glaux maritima L.	D,F,P		–27.6	–27.7		–26.4	
Ranunculaceae	*Aconitum gymanandrum* Maxim.	D,F,A	–28.3		–26.7			
	A. pendulum Busch	D,F,P			–27.3			
	Halerpestes tricuspis (Maxim.) Hand.-Mazz.	D,F,P			–27.1		–26.1	
	Oxygraphis glaoiabs Bunge	D,F,P			–27.2			
	Ranunculus tanguticus (Maxim.) Ovcz.	D,F,P				–26.6		
	Trollius chinenses Bunge	D,F,P				–27.7		–26.5
Rosaceae	*Dasiphora fruticosa* L.	D,Sh,P	–27.6			–27.2		
	Potantilla anserina L.	D,F,P		–28.1			–27.2	
	P. nivea L.	D,F,P		–27.5	–26.7			

Family	Species		δ^{13}C values(‰)					
			2800	3250	3620	4000	4210	4400
	Sibiracea angustata (Rehd.) Hand.-Mazz.	D,Sh,P			–27.6		–27.1	
Rubiaceae	*Galium boreale* L.	D,F,P			–26.3	–25.9		
	G. verum L.	D,F,P			–27.3			
Salicaceae	*Salix oritrepha* Schneid.	D,P	–29.8			–29.4		
Scrophulariaceae	*Euphrasia tatarica* Ten.Fl.Jap.	D,F,A		–29.2	–27.2		–27.2	
	Pedicularis kansuensis Maxim.	D,F,A		–27.8	–29.1		–27.0	
	P. muscicola Maxim.	D,F,P			–27.1		–26.1	
	P. przewalskii Maxim.	D,F,P					–27.5	–26.7
	P. roylei Maxim.	D,F,P			–26.3			
Solanaceae	*Przewalskia tangutica* Maxim.	D,F,P					–26.0	
Umbelliferae	*Bupleurum condensatum* Shan et Y. Li	D,F,P				–26.1		