Characterization of photosynthetic pathway of plant species growing in the eastern Tibetan plateau using stable carbon isotope composition

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Abstract

The photosynthetic pathway of plant species collected at Menyuan, Henan, and Maduo sites, east of Tibetan Plateau, China, during the growing season were studied using stable carbon isotopes in leaves. The 232 samples leaves analyzed belonged to 161 species, 30 families, and 94 genera. The $\delta^{13}C$ values (from –24.6 to –29.2 ‰) indicated that all the considered species had a photosynthetic C_3 pathway. The absence of plant species with C_4 photosynthetic pathway might be due to the extremely low air temperature characterizing the Tibetan Plateau. The average $\delta^{13}C$ value was significantly (p<0.05) different between annuals and perennials at the three considered study sites. Hence the longer-lived species had greater water-use efficiency (WUE) than shorter-lived species, that is, longer-lived species are better adapted to the extreme environmental conditions of the Tibetan Plateau.

Additional key words: adaptation to environment; alpine meadow; species differences; water use efficiency; $\delta^{13}C$ values.

Introduction

Photosynthetic pathway of plant species and their relationship to climatic conditions has received much attention by scientists (Hattersley 1983, Li 1993a,b, Redmann *et al.* 1995, Yin and Wang 1997, Tang *et al.* 1999a,b, Qu *et al.* 2001, Wang 2002a,b, 2003). Stable carbon isotope technique is a useful method to investigate C_3 and C_4 photosynthetic pathways. The isotope distribution can reveal information about physical, chemical, and metabolic processes involved in carbon transformations. Bender (1971) and Smith and Epstein (1971) showed that plants utilizing the C_4 pathway had $\delta^{13}C$ value ($^{13}C/^{12}C$) in the range from –6 to –19 ‰, while those utilizing the C_3 pathway from –22 to –34 ‰. These variations have been related to differences in heavy carbon isotope (^{13}C) discrimination by the primary carboxylases. Phospho*enol*pyruvate carboxylase has high affinity and low discrimination to ^{13}C and is associated with C_4 photosynthesis. Ribulose-1,5-bisphosphate carboxylase has lower affinity and higher discrimination to ^{13}C; it is associated with C_3 photosynthesis.

The environmental conditions of the Tibetan Plateau have influenced the distribution of plant species (Du *et al.* 1995, Wang 1997, Du *et al.* 2003, Hirota *et al.* 2004). There are few reports on the $\delta^{13}C$ values and photosynthetic pathways of plant species on the Tibetan Plateau (Li *et al.* 1999, Wang 2003). The purpose of the present study was to analyze the photosynthetic pathways based on stable carbon isotope compositions of plant species at three different altitudinal sites in the eastern Tibetan Plateau, Qinghai province, China, where alpine meadow ecosystems are de-paupered.

Materials and methods

Study area: This study was conducted in three counties of Qinghai province, in the eastern Tibetan Plateau. The average altitudes of the considered counties were 3 150, 3 560, and 4 210 m for Menyuan, Henan, and Maduo, respectively (Table 1). The considered counties were dominated by alpine meadow, but there are also few

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semi-desert plants and cushion species. The growing period of plant species was from June to August.The climate of the considered counties was dominated by the southeast monsoon and the high-pressure system of Siberia. The continental monsoon type climate had severe and long winters and short cool summers. The considered counties were characterized by a warm season from May to August, and a long cold season from November to April. At Menyuan, Henan, and Maduo, the annual average air temperatures were –0.1, –0.6, and –3.8 °C, mean maximum air temperatures 26.6, 26.2, and 22.4 °C, and mean minimum air temperatures –35.1, –37.2, and –48.1 °C, respectively (data from the Qinghai Meteorological Office).

Table 1. Stational and climatic characteristics of the studied counties.

Sites	Altitude [m]	Latitude [ºN]	Longitude [ºE]	Annu. min. temp. [°C]	Annu. max. temp. [°C]	Annu. mean temp. [°C]	Annu. prec. [mm]	Annu. evap. [mm]	Sunlight duration [h]
Menyuan	3 150	37°26'	101°29'	–35.1	26.6	–0.1	512.0	1 106.6	2 460.6
Henan	3 560	34°50'	101°36'	–37.2	26.2	–0.6	554.9	1 235.3	2 459.3
Maduo	4 210	34°55'	98°13'	–48.1	22.4	–3.8	321.6	1 322.5	2 838.3

Collection and stable carbon isotope analysis: 161 plant species of 30 families and 90 genera were examined (Table 2). Leaf samples for isotope analysis were collected during the growing season (July–August 2003). Each sample consisted of 15–20 leaves from ten plants per species. Leaves were oven dried to constant mass at 75 °C, ground finely, and then sub-sampled for isotopic analysis. Carbon isotope ratios ($\delta^{13}C$) were determined by *Finnigan MAT DELTA^{PLUS}XL* isotope ratio mass spectrometer and calculated by equation of Craig (1957):

$$\delta^{13}C = [(^{13}C/^{12}C)_s/(^{13}C/^{12}C)_{sta} - 1] \times 1\,000$$

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

Table 2. Carbon isotope ($\delta^{13}C$) values and photosynthetic pathways of plant species grown in the eastern Tibetan plateau, Qinghai, China: A = annual, P = perennial, D = dicotyledon, M = monocotyledon, F = forb, S = sedge, G = grass, Sh = shrub.

Family	Species	Basic characteristics	$\delta^{13}C$ values Menyuan	Henan	Maduo	Photosynthetic pathways
Boraginaceae	*Microula pseudotrichocarpa*	D,F,A		–28.9		C_3
	M. sikkimensis	D,F,A	–28.8		–27.6	C_3
	M. tibetica	D,F,A		–26.6	–25.9	C_3
	Trigonotis peduncularis	D,F,P	–26.8			C_3
Caprifoliaceae	*Lonicera minuta*	Sh,F,P	–26.5		–26.2	C_3
Caryophyllaceae	*Arenaria bryophylla*	D,F,P			–26.1	C_3
	A. kansuensis	D,F,A			–26.5	C_3
	Stellaria uda	D,F,P		–26.4		C_3
Chenopodiaceae	*Ajania tenuifolia*	D,F,P	–27.9	–27.6	–26.4	C_3
	Anaphalis lacteal	D,F,P	–28.2	–27.6		C_3
	Atriplex centralasiatica	D,F,A	–28.0	–26.4	–26.6	C_3
	A. fera	D,F,A	–27.1			C_3
	Ceratoides compacta	D,F,A			–27.2	C_3
Compositae	*Artemisia hedinii*	D,F,P		–28.2	–26.2	C_3
	A. scoparia	D,F,P		–27.6		C_3
	A. sieversiara	D,F,A	–26.9		–27.3	C_3
	Aster flaccidus	D,F,P	–27.5		–27.0	C_3
	Cirsium setosum	D,F,P		–26.6		C_3
	Echinops gmelini	D,F,P		–27.3		C_3
	Heteropappus altaicus	D,F,P		–26.3		C_3
	H. gouldii	D,F,P		–27.3		C_3
	Leontopodium nanum	D,F,P	–27.0	–26.8	–27.3	C_3
	Ligularia purdomii	D,F,P	–26.5		–25.8	C_3
	L. sagitta	D,F,P	–26.6			C_3
	L. virgaurea	D,F,P		–26.9		C_3

Table 2 (continued)

Family	Species	Basic characteristics	$\delta^{13}C$ values Menyuan	Henan	Maduo	Photosynthetic pathways
Compositae (cont.)	*Saussurea amara*	D,F,P	–26.6		–26.1	C_3
	S. arenaria	D,F,P	–27.2	–26.8	–26.7	C_3
	S. eopygmaea	D,F,P			–27.1	C_3
	S. katochaete	D,F,P	–26.3			C_3
	S. kokonorensis	D,F,P	–25.1			C_3
	S. salsa	D,F,P			–26. 5	C_3
	S. stella	D,F,P			–26.0	C_3
	S. superba	D,F,P	–27.1	–26.0		C_3
	Taraxacum mongolicum	D,F,P	–26.0	–27.4	–26.1	C_3
Cruciferae	*Capsella bursa-pastoris*	D,F,A	–28.5			C_3
	Descurainia sophia	D,F,A	–27.1			C_3
	Draba oreades	D,F,A	–26.9			C_3
	Hedinia tibetica	D,F,P		–27.2	–25.5	C_3
	Neotorularia humilis	D,F,P		–27.5	–27.8	C_3
Cyperaceae	*Blysmus sinocompressus*	M,S,P	–27.0			C_3
	Carex atro-fusca	M,S,P		–27.2		C_3
	C. crebra	M,S,P	–26.5			C_3
	C. moorcroftii	M,S,P	–27.3		–27.1	C_3
	C. orbicularis	M,S,P			–25.1	C_3
	Kobresia capillifolia	M,S,P		–26.4		C_3
	K. filifolia	M,S,P	–27.3	–27.6		C_3
	K. humulis	M,S ,P	–27.2	–26.5	–26.4	C_3
	K. pygmaea	M,S,P	–26.2			C_3
	K. royleana	M,S,P		–26.3	–25.6	C_3
	K. schoenoides	M,S,P	–26.9			C_3
	K. tibetica	M,S,P			–27.6	C_3
	Scirpus distigmaticus	M,S,P	–27.3	–27.2	–26.2	C_3
Dipsacaceae	*Morina chinensis*	D,F,P		–24.6		C_3
Equisetaceae	*Equisetum arvense*	D,F,P	–25.5			C_3
Euphorbiaceae	*Euphorbia helioscopia*	D,F,P		–26.1		C_3
Gentianaceae	*Gentiana aristata*	D,F,P	–27.7	–28		C_3
	G. dahuica	D,F,P	–26.3		–26.7	C_3
	G. farreri	D,F,P			–26.4	C_3
	G. leucomelaena	D,F,P	–27.6			C_3
	G. siphonantha	D,F,P	–26.6	–27.5		C_3
	G. squarrosa	D,F,P	–26.8			C_3
	G. straminea	D,F,P	–27.0	–26.2	–25.2	C_3
	G. tricolor	D,F,A	–27.1			C_3
	G. zekuensis	D,F,P		–26.3		C_3
	Gentianopsis paludosa	D,F,A	–27.6		–27.2	C_3
	Lomatogonium rotatum	D,F,A	–28.5	–27.0		C_3
	Swertia bifolia	D,F,P	–28.1			C_3
	S. diluta	D,F,A	–27.7			C_3
	S. przewalskii	D,F,P	–27.6			C_3
	S. tetraptera	D,F,P	–26.8			C_3
Geraniaceae	*Geranium sibiricum*	D,F,P		–26.6		C_3
Gramineae	*Agrostis perlaxa*	M,G,P	–28.0	–27.6		C_3
	Aneurolepidium dasystachys	M,G,P	–27.7		–27.5	C_3
	Bromus inermis	M,G,P		–26.9		C_3
	Elymus nutans	M,G,P	–27.1		–26.8	C_3
	Festuca ovina	M,G,P	–27.1			C_3

Table 2 (continued)

Family	Species	Basic characteristics	$\delta^{13}C$ values Menyuan	Henan	Maduo	Photosynthetic pathways
Gramineae	*Festuca rubra*	M,G,P	–26.0			C_3
	Helictotrichon tibeticum	M,G,P	–27.0			C_3
	Koeleria cristata	M,G,P		–25.5		C_3
	K. litvinowii	M,G,P	–28.1	–27.9		C_3
	Poa annua	M,G,A		–27.7	–27.6	C_3
	P. sinattenuata	M,G,A	–27.1			C_3
	Ptilagrostis concinna	M,G,P	–25.6			C_3
	P. dichotoma	M,G,P	–27.2			C_3
	Stipa penicillata	M,G,P	–25.4			C_3
	S. purpurea	M,G,P	–26.1		–25.7	C_3
Iridaceae	*Iris ionantha*	D,F,P			–26.8	C_3
	I. potaninii	D,F,P		–26.4		C_3
Labiatae	*Ajuga lupulina*	D,F,P	–26.9	–26.6		C_3
	Dracocephalum heterophyllum	M,F,P		–26.0		C_3
	Elsholtzia calycocarpa	D,F,A	–25.7			C_3
	E. densa	M,F,A		–29.0		C_3
	Lamiophlomis rotata	M,F,P		–27.3		C_3
	Mentha haplocalyx	D,F,P	–28.8			C_3
Leguminosae	*Astragalus adsurgens*	D,F,P			–25.8	C_3
	A. licentianus	D,F,P	–27.7	–26.4		C_3
	A. mattam	D,F,P			–26.9	C_3
	A. peduncularis	D,F,P	–26.6	–26.8		C_3
	A. polycladus	D,F,P	–26.8	–25.4		C_3
	Gueldenstaedtia diversifolia	D,F,P			–24.9	C_3
	G. multiflora	D,F,P	–25.1			C_3
	Medicago lupulina	D,F,A	–28.7			C_3
	Oxytropis caerulea	D,F,P	–27.1	–27.3		C_3
	O. falcata	D,F,P		–28.6	–27.5	C_3
	O. ochrocephala	D,F,P	–25.7			C_3
	Thermopsis lanceolata	D,F,P			–26.7	C_3
Liliaceae	*Allium chrysanthum*	M,F,P	–27.3			C_3
Papaveraceae	*Hepecoum leptocarpum*	D,F,P		–25.3		C_3
Plantaginaceae	*Plantago depresa*	D,F,P	–27.8	–27.0		C_3
Polygonaceae	*Polygonum alatum*	D,F,A	–27.9	–28.1		C_3
	P. macrophyllum	D,F,P	–28.0			C_3
	P. sibiricum	D,F,P	–28.1	–27.7	–26.5	C_3
	P. tenuifolium	D,F,P	–26.0		–25.8	C_3
	P. viviparum	D,F,P	–26.5	–26.4	–26.0	C_3
Potamogetonaceae	*Triglochin matitima*	M,F,P		–26.8		C_3
	T. palustre	M,F,P		–25.1		C_3
Primulaceae	*Androsace septentrionalis*	D,F,P	–27.1			C_3
	Glaux maritime	D,F,P	–27.6	–27.7	–26.4	C_3
Ranunculaceae	*Aconitum gymanandrum*	D,F,A	–27.7	–26.7	–26.6	C_3
	A. pendulum	D,F,P			–27.3	C_3
	Anemone obtusiloba	D,F,P	–25.3			C_3
	Delphinium candelabrum	D,F,P	–27.6		–27.3	C_3
	D. pylzowii	D,F,P	–26.9			C_3
	Halerpestes tricuspis	D,F,P	–27.6			C_3
	Oxygraphis glaoiabs	D,F,P		–27.2		C_3
	Ranunculus brotherusii	D,F,P			–25.0	C_3

Table 2 (continued)

Family	Species	Basic characteristics	$\delta^{13}C$ values Menyuan	Henan	Maduo	Photosynthetic pathways
Ranunculaceae	*Ranunculus pulchellus*	D,F,P	–25.9			C_3
	R. tanguticus	D,F,P	–27.0	–26.2		C_3
	Thalictrum alpinum	D,F,P	–26.8			C_3
	Trollius chinenses	D,F,P		–26.4		C_3
	T. pumilus	D,F,P	–28.0			C_3
Rosaceae	*Coluria longifolia*	D,F,P			–27.2	C_3
	Dasiphora fruticosa	D,Sh,P	–26.1	–26.0		C_3
	Potentilla acaulis	D,F,P		–26.5		C_3
	P. anserina	D,F,P	–28.1		–27.2	C_3
	P. bifurca	D,F,P		–28.1	–26.9	C_3
	P. multiceps	D,F,P			–26.0	C_3
	P. nivea	D,F,P	–27.5			C_3
	Sibiracea angustata	D,Sh,P	–26.6			C_3
	Spiraea alpina	D,Sh,P			–25.3	C_3
Rubiaceae	*Galium boreale*	D,F,P	–25.8			C_3
	G.. verum	D,F,P	–27.2			C_3
Salicaceae	*Salix oritrepha*	D,P	–28			C_3
Scrophulariaceae	*Euphrasia tatarica*	D,F,A,	–29.2			C_3
	Lagotis brachystachya	D,F,P			–27.1	C_3
	Lancea tibetica	D,F,P	–26.8	–26.0	–26.3	C_3
	Pedicularis alaschanica	D,F,P	–28.0	–27.2		C_3
	P. kansuensis	D,F,A	–27.8	–29.1	–27.0	C_3
	P. longiflora	D,F,A		–28.6	–26.8	C_3
	P. muscicola	D,F,P		–27.1		C_3
	P. przewalskii	D,F,P			–27.5	C_3
	P. roylei	D,F,P		–26.3		C_3
	Veronica biloba	D,F,A	–27.8	–27.3		C_3
	V. ciliata	D,F,P				C_3
Solanaceae	*Przewalskia tangutica*	D,F,P			–26.0	C_3
Thymelaceae	*Stellera chamaejasme*	D,F,P	–26.9		–26.8	C_3
Umbelliferae	*Bupleurum condensatum*	D,F,P	–27.7			C_3
	Notopterygium frobesii	D,F,P	–26.3			C_3
	N. incisum	D,F,P	–28.1	–26.7		C_3
	Sphallerocarpus gracilis	D,F,P			–25.8	C_3

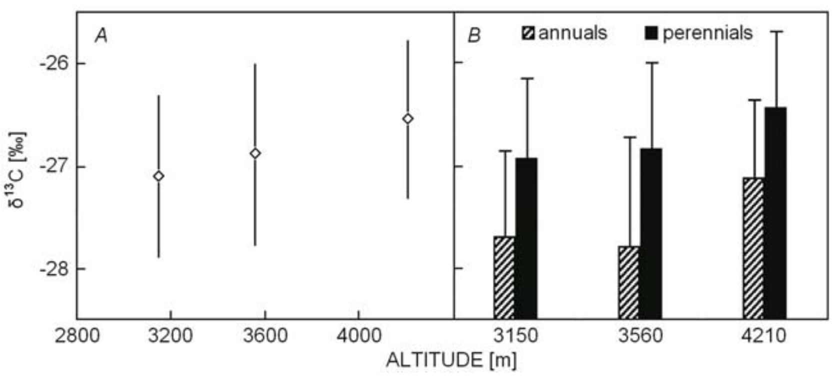

Fig. 1. Average $\delta^{13}C$ values of (*A*) plants collected from different altitude, (*B*) annuals and perennials at different altitudes.

Results

The $\delta^{13}C$ values of 161 plants collected at three considered sites (Table 1) had a narrow range from –29.2 to –24.6 ‰ (Table 2). The stable carbon isotope ratios for plants in the three sites ranged from –29.2 to –25.1 ‰, –29.1 to –24.6 ‰, –28.8 to –24.9 ‰, respectively, and the average $\delta^{13}C$ values at each site tended to be more positive with the increase of altitude (Fig. 1*A*).

There were no significant differences between the average $\delta^{13}C$ values of monocotyledonous species (–27.0 ‰) and those of dicotyledonous ones (–26.9 ‰). Thus forbs and shrubs had no different $\delta^{13}C$ values from monocotyledonous grasses and sedges. Under the same environmental conditions, species with different life span (annuals and perennials) at three sites had significant difference in $\delta^{13}C$ values ($p<0.05$). Mean $\delta^{3}C$ values of annual species tended to be more negative than those of perennial species at each site (Fig. 1*B*).

Discussion

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 in the eastern Tibetan Plateau. Considering the climate, the low temperature may be the limiting factor for C_4 plant species.

The increase of $\delta^{13}C$ values of leaves along the considered altitudinal gradient, is in accordance with the results of Körner *et al.* (1988, 1991), Morecroft *et al.* (1990), or Marshall and Zhang (1994). In addition, the $\delta^{13}C$ values indicate that perennial plants (long-lived plants) have more positive $\delta^{13}C$ values than annual plants (short-lived plants), according to Ehleringer and Cooper (1988). The significance of isotopic variation lies in its broad correlation with photosynthetic water-use efficiency (WUE) (Farquhar *et al.* 1982, Hultine and Marshall 2000). Farquhar and Richards (1984) and William *et al.* (1992) showed a positive relationship between WUE and plant longevity based on $\delta^{13}C$ measurements. Therefore, the results of this study suggest that species with longer lifespan have greater WUE, *i.e.* perennials are more advantageous than annuals in water-limited environments of the Tibetan Plateau.

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