Occurrence and altitudinal pattern of C_4 plants on Qinghai Plateau, Qinghai province, China

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Abstract

The natural occurrence and altitudinal pattern of species with C_4 photosynthesis were investigated on Qinghai Plateau, Qinghai province by using stable carbon isotopes in plant leaves and using additional data from references. A total of 58 species belonging to 10 families and 34 genera were identified using C_4 photosynthetic pathway, which is only 1.66 % of total 3 500 plant species in Qinghai province. The leading two families, *i.e.* Gramineae (23 species) and Chenopodiaceae (22 species) contain 77.6 % of all C_4 plants in the studied area. The number of C_4 species increased from 1 600 to 2 400 m a.s.l. and then decreases quickly till 4 400 m a.s.l. with one half of C_4 species distributing from 2 200 to 2 800 m a.s.l. (48 %). Eight plant species were found above 4 000 m a.s.l., but the distribution of these species is limited to the south of Qinghai province (low latitude area) where annual mean temperature is above 0 ºC, suggesting that low temperature may generally limit the distribution of C_4 plants.

Additional key words: altitude distribution; C_4 species; $\delta^{13}C$; Qinghai Plateau.

Introduction

The photosynthetic pathway composition, a fundamental ecological distinction in many ecosystems, has received much attention by scientists. The determination of photosynthetic pathway types will largely contribute to the research on exploring eco-physiological mechanism or evolution process of plant species under special environmental conditions (Akhani *et al*. 1997, Sage 2004, Sage *et al*. 2007). Continuously more attention has been paid since the work by Downton and Tregunna (1968) to C_4 plant species which were accepted widely as photosynthetic pathway from C_3 predecessors. A large number of studies have investigated the occurrence, distribution and evolution of C_4 plant species in tropical, subtropical or temporal ecosystems in the world wide (Downton 1975, Collins and Jones 1985, Redmann *et al*. 1995, Kalapos *et al*. 1997, Collatz *et al*. 1998, Pyankov *et al*. 2000, Wang 2002b, Zhang *et al*. 2003, Sage 2004, Sage *et al*. 2007). By contrast, investigation of C_4 plants in cold ecosystems, especially for high altitude alpine plants, is rather limited (Wang 2003a, Wang *et al*. 2004).

Qinghai Plateau, in Qinghai province with an area of 720 000 square kilometers, lies on the eastern part of the Qinghai-Tibet Plateau, occupying almost 30 % of the total area of Qinghai-Tibet Plateau distributed in China. The determination of photosynthetic pathways and distributions of plant species on the Plateau is of special interest by scientist (Wang 2003a). However, little work on the determination of plant photosynthetic pathway, especially C_4 photosynthesis, has been reported on Tibetan Plateau (Wang 2003a, Wang *et al*. 2004). Stable carbon isotope technique has become a useful method to investigate C_3 and C_4 photosynthetic pathways since the works by Bender (1971) and Smith and Epstein (1971) which showed that C_4 plants have $\delta^{13}C$ values in the range from –6 ‰ to –19 ‰, whereas –22 ‰ to –34 ‰ for C_3 plant species. The purpose of the present study was to investigate the occurrence of C_4 photosynthetic pathway on Qinghai Plateau by using stable carbon isotope compositions in plant leaves and comparing with related publications. Our study will contribute to better understanding the ecological response and adaptation of different photosynthetic pathway plants to high altitude environment.

Received 27 November 2008, *accepted* 1 June 2009.
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Acknowledgement: Financial support was provided by National Foundation of Natural Sciences of China (No. 30270217, 30671669).

Materials and methods

Study area and sample collection: The study was conducted on Qinghai Plateau, Qinghai province. The climate of Qinghai is affected by the southeast monsoon and high-pressure system of Siberia. The continental monsoon type climate has severe and long winter and short cool summer. It has a mean annual temperature with the range of –6 to 9 ºC, with maximum and minimum air temperatures of 40.3 and –48.1 ºC, respectively. The mean annual precipitation ranges from 16.2 to 746.9 mm, with the great part focused on summer. The average elevation of Qinghai Plateau is more than 3 000 m a.s.l., with 54 % of the area between 4 000 and 5 000 m a.s.l. Qinghai Plateau is primarily a mountain Plateau dominated by alpine meadow, accompanied with few forests, shrubs, steppes, alpine deserts, and polar deserts.

The plant species were obtained by flora of Qinghai and lists of local plants in some related references (Wang and Yang 1981, Lin and Guo 1988, Li *et al.* 2006). By compiling C_3 or C_4 related publications from 1978 to 2006 (Raghavendra and Das 1978, Wang and Yang 1981, Li 1993a,b, Redmann *et al.* 1995, Yin and Wang 1997, Yin and Li 1997, Lin and Guo 1988, Tang 1999, Pyankov *et al.* 2000, Wang 2002a,b, 2003a,b, 2004a,b, Li *et al.* 2006), the photosynthetic pathways were preliminarily determined. The distribution range of plant species was obtained from flora of Qinghai. During the growing season (July–August) in 2003 and 2005 we twice collected the selected C_4 plants as much as possible. Also, a large number of dominant and common plant species were collected (Li *et al.* 2006). Each leaf sample consisted of 15-20 leaves from ten individual plants per one species. Leaves were oven dried to constant mass at 75 ºC, ground finely, and then sub-sampled for isotopic analysis. If field sampling was not available, samples for isotopic analyses were collected from specimens. In addition, some plant isotope values were obtained from published references (for details *see* Results).

Stable carbon isotope analysis: Carbon isotope ratios ($\delta^{13}C$) were determined by an isotope ratio mass spectrometer (*MAT DELTA^PLUS^XL, Thermo Finnigan*, San Jose, CA, US) 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 ratios of content of the carbon isotopes in a sample (s) and the standard (sta), respectively. The standard is carbonate taken from the fossil *Belemnitella americana* from the Cretaceous Pee Dee formation in South Carolina (PDB). The overall analytical precision is ± 0.2 ‰, which means differences between duplicates are always less than 0.2 ‰. Values are presented as the mean value of the two subsamples.

Results

C_4 plant species composition: The stable carbon isotope values of the list of 56 plant species have a narrow range from –16.9 ‰ to –11.2 ‰ (Table 1), indicating the C_4 photosynthetic pathway type of the considered species. Of the indentified species, 34 species were found in Dicotyledonae, whereas 24 in Monocotyledoneae. Among the families examined, 23 species were in Gramineae, 22 in Chenopodiaceae, 4 in Amaranthaceae, 3 in Compositae, and 1 each in Convolvulaceae, Crassulaceae, Euphorbiaceae, Polygonaceae, Potamogetonaceae and Zygophyllaeceae, respectively. 77.6 % of the total C_4 plant species were found in Gramineae (39.7 %) and Chenopodiaceae (37.9 %), whereas the other 22.4% existed in 8 families. In addition, the proportion of annuals (70.7 %) in the total 58 species was largely higher than that of perennials (29.3 %) (Table 1).

Altitudinal pattern of C_4 species: The C_4 type plant species on Qinghai Plateau were distributed in the range from 1 600 to 4 400 m a.s.l., with almost half of the number of C_4 species occurring from 2 200 to 2 800 m (Table 1). The number of C_4 species varied significantly with altitude (r^2 = 0.8031, Fig. 1), with increasing number from 1 600 to 2 400 m and then decreasing quickly from 2 400 to 4 400 m a.s.l. A total of 8 C_4 species were distributed at the altitudes higher than 4 000 m a.s.l. (Table 1).

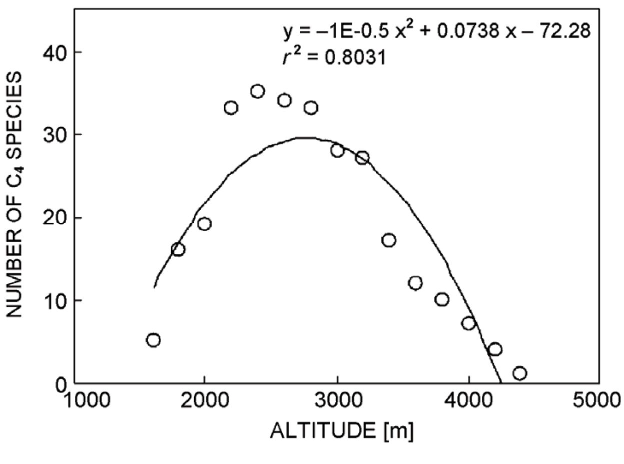

Fig. 1. Variation in number of C_4 species along the altitudinal gradient on Qinghai Plateau.

Table 1. Stable carbon isotope ($\delta^{13}C$) values, altitudinal distribution, and basic characteristics of C_4 plant species identified on Qinghai Plateau, Qinghai province, China. A – annual, P – perennial, D – dicotyledon, M – monocotyledon, F – forb, G – grass, Sh – shrub. Asterisk shows that the stable carbon isotope ratios of plants are from Tang and Liu (2001).

Family	Species	Basic characteristics	$\delta^{13}C$ [‰]	Altitude [m]
Amaranthaceae	*Amaranthus paniculatus*	D,F,A	–13.6	2 100–2 800
	Amaranthus hypochondriacus	D,F,A	–14.9	1 600–2 300
	Amaranthus retroflexus	D,F,A	–13.1	2 200–2 800
	Amaranthus tricolor	D,F,A	–13.6	1 600–2 500
Chenopodiaceae	*Agriophyllum squarrosum*	D,F,A	–11.2	2 900–3 200
	Atriplex centralasiatica	D,F,A	–13.9	3 000–4 300
	Atriplex patens	D,F,A	–16.1	2 900
	Atriplex sibirica	D,F,A	–15.4	1 900–3 100
	Atriplex tatarica	D,F,A	–13.9	3 000–3 100
	Axyris amarantoides	D,F,A	–11.4*	2 400–4 100
	Bassia dasyphylla	D,F,A	–15.6	2 700–3 200
	Chenopodium acuminatum	D,F,A	–14.1	2 500–2 700
	Chenopodium album	D,F,A	–11.5*	1 700–4 200
	Chenopodium hybridum	D,F,A	–12.4*	2 300–3 500
	Halogeton glomeratus	D,F,A	–12.8	3 000–3 500
	Haloxylon ammodendron	D,Sh,P	–12.4*	2 600–3 000
	Kochia melanoptera	D,F,A	–15.9	1 900–2 600
	Kochia prostrate	D,Sh,P	–16.3	2 550
	Kochia scoporia	D,F,A	–14.9	2 300–3 300
	Kochia sieversiana	D,F,A	–13.1	2 600–2 900
	Salsola abrotanoides	D,Sh,P	–14.6	2 800–3 500
	Salsola collina	D,F,A	–14.1	1 700–4 000
	Salsola monoptera	D,F,A	–13.3	3 300–3 400
	Salsola paulsenii	D,F,A	–14.3	3 400
	Salsola pellucida	D,F,A	–13.8	2 300–3 200
	Salsola ruthenica	D,F,A	–12.9	2 900–3 300
Compositae	*Artemisia dracunculus*	D,F,P	–13.9*	3 100–3 900
	Artemista anethifolia	D,F,P	–13.6	2 230–3 230
	Tephroseris kirilowii	D,F,P	–13.9	2 500–3 500
Convolvulaceae	*Cuscuta europaea*	D,F,A	–16.6	2 500–4 300
Crassulaceae	*Orostachys fimbriatus*	D,F,P	–15.6*	1 900–3 500
Euphorbiaceae	*Euphorbia humifusa*	D,F,A	–13.9	1 900–3 250
Gramineae	*Aristida adscensionis*	M,G, A	–16.3	1 800
	Bothriochloa ischcemum	M,G,P	–14.3	1 800–2 600
	Buchloe dactyloides	M,G,P	–14.5	2 200
	Chloris virgata	M,G,A	–15.6	1 850–2 600
	Cleistogenes chinensis	M,G,P	–14.0*	2 100
	Cleistogenes squarrosa	M,G,P	–15.1	3 300
	Cleistogenes songorica	M,G,P	–16.0	2 400–2 800
	Digitaria violascens	M,G,A	–12.6	2 260
	Echinochloa crusgalli	M,G,A	–12.9	2 200–2 520
	Enneapogon brachystachyus	M,G,A	–14.3	1 890–3 200
	Eragrostis cilianensis	M,G,A	–13.5	1 880–2 800
	Eragrostis minor	M,G,A	–13.2	2 200–2 600
	Eragrostis nigra	M,G,A	–13.6	1 700–3 600
	Hierochloe glabra	M,G,P	–14.1	2 200–3 800
	Orinus kokonorica	M,G,P	–13.9	2 230–4 400
	Panicum miliaceum	M,G,A	–16.9	2 200–2 900
	Pennisetum longissimum	M,G,P	–13.6	2 230–3 800
	Pennisetum centrasiaticum	M,G,P	–15.1	1 850–4 000
	Setaria viridis	M,G,A	–15.7	1 800–3 600
	Setaria glauca	M,G,A	–16.8	2 100–2 500
	Tragus racemosus	M,G,A	–16.3	2 200–2 900

Table 1 (continued)

Family	Species	Basic characteristics	$\delta^{13}C$ [‰]	Altitude [m]
Gramineae	*Tragus berteronianus*	M,GA	–12.8	2 230–2 800
	Zea mays	M,G,A	–14.1	2 000
Polygonaceae	*Calligonum mongolicum*	D,Sh,P	–12.6*	2 800–3 000
Potamogetonaceae	*Potamogeton crispus*	M,F,P	–14.9	2 300
Zygophyllaeceae	*Tribulus terrestris*	D,F,A	–14.3	1 880–3 250

Discussion

A total of more than 1 700 C_4 species belonging to about 22 families and 293 genera have been identified world wide (Li 1993a,b). On Qinghai Plateau, the eastern part of Qinghai-Tibet Plateau, only 58 C_4 species representing 10 families and 34 genera have been found, which is even less than occurred in Tibet plateau (79 C_4 species, Wang 2003a). In addition, the number of C_4 species on Qinghai Plateau is much lower compared with other regions in China (Yin and Li 1997, Yin and Wang 1997, Tang and Liu 2001, Wang 2002a,b, 2003b, 2004a, Liu *et al*. 2004) although the biodiversity is very abundant in this area (about 3 500 plant species). The two leading families, *i.e.* Gramineae and Chenopodiaceae, contain about 77.6 % of the total 58 C_4 species, suggesting that C_4 species mainly occur in very few families. Wang (2003a) compiled the C_4 species on Tibet Plateau and found that the leading two families including C_4 species are Gramineae and Cyperaceae, which is partly different from the present study. No Cyperaceae C_4 species was found on Qinghai Plateau whereas Cyperaceae is the second leading family in the study of Wang (2003a), suggesting that there may be large difference in species evolution between Qinghai and Tibet Plateaus. It is interesting to note that the number of annuals (41) was significantly higher than that of perennials (17), which is in contrast to the proportion of annuals and perennials in C_3 plants on Qinghai Plateau (Li *et al*. 2006). They found that in the total of 161 species collected from three altitudinal regions the number of annuals was significantly lower than that of perennials (26 vs. 135 for annuals and perennials). These may indicate that C_4 plants with shorter lifespan are more advantageous than C_4 species with longer lifespan under extremely environmental condition on Qinghai Plateau, whereas C_3 species may show the opposite dependency. Further study should pay more attention to the eco-physiological mechanism of adaptation to environmental conditions for C_3 or C_4 species with different lifespans.

Li *et al*. (2006) collected common and dominant species in three altitudinal regions from 3 150 to 4 210 m and found no C_4 occurrence at the landscape scale as a result of the extremely low air temperature. By contrast, a total of 8 C_4 species are found at the altitude above 4 000 m a.s.l. in this study. By investigating the distributions of these species, we found that the C_4 species distributing above 4 000 m only occur in the south of Qinghai Plateau, *i.e.* in the lower latitude area. The decrease of latitude partly compensates for the increase of altitude, which makes annual air temperature increase. For example, the mean annual air temperatures of Banma, Nangqian, Yushu and Zaduo counties are 2.4, 0.1, 2.9 and 0.5 ºC, respectively although altitude of each these county is above 4 000 m a.s.l. The annual average air temperature below 0 ºC may limit the distribution of C_4 species on Qinghai Plateau. The altitudinal pattern of C_4 species is very similar to the study of Wang (2003a) on C_4 species variation with altitude in Tibet Plateau, *i.e.* a decline trend after an initial increase. In this study area, only a small part of region is at the altitude below 2 000 m and is almost occupied by crops, which may lead to the decrease of C_4 species at lower altitude. The rapid decrease of air temperature results in the rapid decline in occurrence of C_4 species with the altitude varied from 2 400 to 4 400 m a.s.l.

In the present study, some plant species published in previous studies as C_4 plants including *Achnatherum splendens* (Wang 2002b, 2003a, Yin and Wang 1997), *Helictotrichon tibeticum* (Wang 2003a), *Artemisia sieversiana* and *Chenopodium glaucum* (Yin and Li 1997, Tang and Liu 2001), and *Elymus nutans* and *Potentilla anserina* (Yin and Wang 1997, Yin and Li 1997) should be identified using C_3 photosynthetic pathways according to their $\delta^{13}C$ values. The $\delta^{13}C$ values and relative characteristics are listed in Appendix.

Appendix

The C_3 plant species identified using stable carbon isotopes. These species occurring on Qinghai Plateau were identified in previous publications as C_4 ones. $\delta^{13}C$ values and basic characteristics of species are presented. A – annual, P – perennial, D – dicotyledon, M – monocotyledon, F – forb, G – grass.

Family	Species	Basic characteristics	$\delta^{13}C$ (‰)	Photosynthetic pathway
Compositae	*Artemisia sieversiana*	D,F,A	–27.3	C_3
Chenopodiaceae	*Chenopodium glaucum*	D,F,A	–28.1	C_3
Gramineae	*Achnatherum splendens*	M,G,P	–27.8	C_3
Gramineae	*Elymus nutans*	M,G,P	–26.8	C_3
Gramineae	*Helictotrichon tibeticum*	M,G,P	–26.1	C_3
Rosaceae	*Potentilla anserina*	D,F,P	–27.2	C_3

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