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No C_4 Plants Found at the Haibei Alpine Meadow Ecosystem Research Station in Qinghai, China: Evidence from Stable Carbon Isotope Studies

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Abstract: Using the measurement of stable carbon isotopes in leaves as a tool to investigate photosynthetic pathway of 102 plant species grown at an alpine meadow ecosystem, at the foot of the Qilian Mountain, Qinghai, China. The results indicate that the $\delta^{13}C$ values of plants have a narrow range from −28.24‰ to −24.84‰, which means that none of the species examined belongs to C_4 and crassulaceous acid metabolism (CAM) photosynthetic pathway and all of these species perform photosynthesis through the C_3 pathway. This is likely due to a long-term adaptation to environments at the alpine meadow ecosystem.
Key words: $\delta^{13}C$ value; photosynthetic pathway; alpine meadow; Qinghai-Xizang (Tibet) Plateau

Photosynthetic characteristics of plants have been interests to many scientists (Smith and Epstein, 1971; Hatterley, 1983; Lin and Guo, 1988; Lin *et al.*, 1989; Li, 1993a; 1993b; Yin and Li, 1997; Tang *et al.*, 1999a; 1999b; Qu *et al.*, 2001). To identify photosynthetic pathways, the following methods are always used: anatomy, physiological indicators, and activities of enzymes (Haines and Montague, 1979; Pinder and Kroh, 1987). Yin and Zhu (1990) based on variations in the ratios of ribulose diphosphate carboxylase (RUBPCase) to phosphoenolpyruvate carboxylase (PEPCase) activities in plant species and classified them into C_3 and C_4 plants (plant species with activity ratios of RUBPCase to PEPCase more than 1 is defined as C_3-type species, or as C_4-type species when the ratios are less than 1). Carbon isotope ratio has been found to be a very useful method in studying photosynthetic pathways in last thirty years. There are two naturally occurring stable carbon isotopes, ^{12}C and ^{13}C. Most of the carbon is ^{12}C (98.9%), with 1.1% being ^{13}C (Tang *et al.*, 1999b). The isotopes are unevenly distributed among and within different compounds, and this isotopic distribution can reveal information about the physical, chemical, and metabolic processes involved in carbon transformations. The overall abundance of ^{13}C relative to ^{12}C in plant tissues is commonly less than the carbon of atmospheric carbon dioxide, due to carbon isotope discrimination that occurs in the incorporation of CO_2 into plant biomass (Eickmeier, 1976). Plants utilizing the Hatch-Slack (C_4) pathway have $\delta^{13}C$ value ($^{13}C/^{12}C$) in the range from −6‰ to −19‰, with an average of −12.5‰, while those utilizing the Calvin (C_3) pathway have $\delta^{13}C$ value between −22‰ to −34‰ (Bender, 1971; Smith and Epstein, 1971; Thoughton, 1972). These variations have been related to the differences in heavy carbon isotope (^{13}C) discrimination by the primary carboxylases. Phospheonol pyruvate carboxylase, which has high affinity and low discrimination to ^{13}C, is associated with C_4 photosynthesis; and ribulose diphosphate carboxylase, which has lower affinity and higher discrimination to ^{13}C, is associated with C_3 photosynthesis. Waller and Lewis (1979) defined C_3 and C_4 photosynthetic pathways of North America pasture in 1979. In China, Lin and Guo (1988) first attempted to use stable carbon isotope to identify photosynthetic pathways of plant species grown in Guangdong area. Later, Yan *et al.* (1998) studied interspecific variations and temporal variation of $d^{13}C$ in leaves of broad-leaved forest in the temperate zone, and Tang *et al.* (1999a) distinguished photosynthetic types in Northeast China transect (NECT) area.

Alpine meadow ecosystem, prevailing over Qinghai-Xizang (Tibet) Plateau, "the third pole of the world", is the ideal place for the research of structure, function of alpine meadow ecosystem and global changes. However, there is no report on $\delta^{13}C$ values and photosynthetic pathways of plants with the application of $\delta^{13}C$ value measurements at the Haibei Alpine Meadow Ecosystem Research Station (HAMERS) of The Chinese Academy of Sciences (CAS). It is necessary to examine the mode of CO_2 fixation pathways in a number of plant species grown at alpine meadow ecosystem because it is one of the most sensitive areas to

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global changes and has become the key area of International Geosphere-Biosphere Programme (IGBP).

1 Materials and Methods

1.1 Study area

This study was conducted at the HAMERS of CAS. The HAMERS was established in 1976 in order to understand the structure and function of alpine meadow ecosystem, form and development of biodiversity, the adaptive and evolutionary strategies of species, and the impact of global changes on grassland ecosystem. The HAMERS has been expanding as a field open station of CAS in 1988, one of the key stations of the Chinese Ecosystem Research Network (CERN) in 1992, the unique research station of International Tundra Experiment (ITEX) in 1998, a member of International Center for Integrated Mountain Development (ICIMOD), and Northern Sciences network (NSN) in 1999. It is situated in the northeast of Qinghai-Xizang Plateau at an altitude of 3 200 m, 37° 29 '–37° 45 ' N, 101° 12 '–101° 33' E, with an average annual temperature –1.7 ℃. There is no apparent four seasons with only warm season from May to October and cold season from November to April.

1.2 Stable carbon isotope analysis

Leaves were collected from individuals of common plant species for isotope analysis. All leaf samples were collected during the exuberant season (July to August) in 2002. Leaves were air dried indoors to constant mass in an oven at 70 ℃ for 48 h, ground finely, and dispatch to Finnigan MAT DELTA^{PLUS}XL isotope ratio spectrometer under element-analysis meter and spectrometer (EAMS) conditions. Interface is ConFIII. Operation condition: oxidizing furnace temperature is 900 ℃, reducing furnace is 680 ℃, pillar temperature is 40 ℃. The resulting CO_2 was purified in a vacuum line and injected in spectrometer (Finnegan Mat, Bermen, Germany) fitted with double inlet and collector systems. Standards were Peedee Belemnite (PDB) formation from South Carolina, USA (Craig, 1957). The results are expressed in $\delta\,^{13}C$ directly relative to the PDB standard in the conventional δ per mil notation as follows:

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

where $^{13}C/^{12}C$ is the isotopic ratio of sample (s) and PDB standard (sta). The overall (sample preparation plus analysis) analytical precision is ± 0.2‰.

2 Results and Discussion

One hundred and two plant species, representing 70 genus and 25 families have been examined and their $\delta\,^{13}C$ values are summarized in Table 1. Among the families examined, one each belongs to Chenopodiaceae, Dipsecaceae, Equisetaceae, Iridaceae, Liliaceae, Plantaginaceae, Salicaceae, Thymelaceae and Violaceae; 2 each to Borraginaceae, Umbelliferae, and Primulaceae; 3 each to Crucifeae, Labiatae and Papaveraceae; 4 to Polygonaceae; 6 each to Rosaceae, Scrophulariaceae and Leguminosae; 8 to Ranunculaceae; 10 to Cyperaceae; 11 to Gramineae; 12 to Gentianaceae and 13 to Compositae. Their habitats and basic characteristics of vascular plants were also given.

All the $\delta\,^{13}C$ values of species measured had a narrow range from –28.24‰ to –24.84‰ (Table 1). This indicates no C_4 species was found at HAMERS and all species examined belong to C_3 photosynthetic pathway. These results are somewhat contradictory to Wang and Yang (1981). They classified photosynthetic pathways of 51 species at the HAMERS via anatomical means (i.e. presence or absence of "Kranz" structure) and defined species such as *Elymus nutants, Helictotrichon tibeticum,* and *Aneurolepidium dasystachys* as C_4 type plants. Carbon stable isotope technology is sensitive and accurate to reveal photosynthetic pathway, the difference between their results and this study is probably related to different sampling processes, habitats or detective method. $\delta\,^{13}C$ values of species within the same genus have no significant difference, but having great variations under different living environments, such as alpine meadow, swamp meadow or alpine shrub. In general, species grown under swamp or northern slope have more negative $\delta\,^{13}C$ values than those under meadow or southern slope within the same genus (Table 1). Under the same living conditions, species within the same genus also have differences in $\delta\,^{13}C$ values due to the species specification. Furthermore, it is likely that $\delta\,^{13}C$ values of monocotyledonous species (–26.19‰) tend to be less negative than those of dicotyledonous (–26.50‰) under the same conditions (such as meadow). Thus grasses and sedges also tend to be less negative $\delta\,^{13}C$ values than those of forbs and shrubs because all grasses and sedges are monocotyledonous.

Why there is no distribution of C_4 type species at the HAMERS? It is necessary to solve this question by understanding the environmental conditions of these species. As mentioned above, the HAMERS is situated in the region of the Qinghai-Xizang Plateau, in a large valley oriented NW-SE surrounded on all sides by the Qilian Mountains with 37° 29' –37° 45' N and 101° 12' –101° 23' E. The average altitude of mountain area is 4 000 m above sea level and 3 200 m for valley area. The climate of the HAMERS is dominated by the southeast monsoon and

Table 1 $\delta^{13}C$ values and habitat of plant species grown at Haibei Alpine Meadow Ecosystem Research Station (HAMERS)

Family	Species	Habitat	Basic characteristics	$\delta^{13}C$ values	Photosynthetic pathways
Borraginaceae	*Microula sikkimensis*	Yard	D, F	-27.44	C_3
	Trigonotis peduncularis	Yard	D, F	-26.13	C_3
Chenopodiaceae	*Atriplex fera*	Yard	D, F	-26.17	C_3
Compositae	*Ajania tenuifolia*	Alpine meadow	D, F	-26.76	C_3
	Anaphalis flaccidus	Alpine meadow	D, F	-27.04	C_3
	A. lacteal	Alpine meadow	D, F	-28.24	C_3
	Artemisia sieversiara	Yard	D, F	-26.50	C_3
	Leontopodium nanum	Alpine meadow	D, F	-25.12	C_3
	L. virgaurea	Alpine shrub	D, F	-26.46	C_3
	Ligularia purdomii	Alpine shrub	D, F	-26.87	C_3
	Lihularia sagitta	Alpine meadow	D, F	-27.73	C_3
	Saussurea katochaete	Swamp meadow	D, F	-25.89	C_3
	S. kokonorensis	Swamp meadow	D, F	-25.85	C_3
	S. stella	Swamp meadow	D, F	-26.30	C_3
	S. superba	Alpine meadow	D, F	-25.13	C_3
	Taraxacum mongolicum	Alpine meadow	D, F	-25.32	C_3
Crucifeae	*Capsella bursa-pastoris*	Alpine meadow	D, F	-27.52	C_3
	Descurainia sophia	Yard	D, F	-27.05	C_3
	Draba oreades	Yard	D, F	-26.19	C_3
Cyperaceae	*Blysmus sinocompressus*	Swamp meadow	M, S	-27.04	C_3
	Carex atro-fusca	Alpine meadow	M, S	-26.83	C_3
	C. crebra	Alpine meadow	M, S	-26.54	C_3
	C. moorcroftii	Swamp meadow	M, S	-27.32	C_3
	Kobresia bellardii	Northern slope	M, S	-27.45	C_3
	K. capillifolia	Northern slope	M, S	-27.20	C_3
	K. humulis	Alpine meadow	M, S	-26.83	C_3
	K. pygmaea	Southern slope	M, S	-26.13	C_3
	K. tibetica	Swamp meadow	M, S	-27.63	C_3
	Scirpus distigmaticus	Alpine meadow	M, S	-26.51	C_3
Dipsecaceae	*Morina chinensis*	Alpine meadow	D, F	-25.25	C_3
Equisetaceae	*Equisetum arvense*	Riverside	D, F	-25.32	C_3
Gentianaceae	*Gentiana aristata*	Alpine meadow	D, F	-26.03	C_3
	G. aristta	Alpine meadow	D, F	-26.69	C_3
	G. farreri	Alpine meadow	D, F	-26.90	C_3
	G. leucomeloena	Swamp meadow	D, F	-26.95	C_3
	G. squarrosa	Alpine meadow	D, F	-26.58	C_3
	G. straminea	Alpine meadow	D, F	-26.92	C_3
	Gentianopsis paludosa	Alpine meadow	D, F	-27.24	C_3
	Lomatogonium rotatum	Southern slope	D, F	-27.01	C_3
	Swertia bifolia	Northern slope	D, F	-28.11	C_3
	S. przewalskii	Northern slope	D, F	-27.95	C_3
	S. tetraptera	Alpine meadow	D, F	-26.59	C_3
	S. tetraptera	Alpine shrub	D, F	-26.78	C_3
	Aneurolepidium dasystachys	Alpine meadow	M, G	-27.45	C_3
	Bromus inermis	Alpine meadow	M, G	-27.36	C_3
	Elymus nutans	Alpine meadow	M, G	-26.32	C_3
	Festuca ovina	Alpine meadow	M, G	-26.80	C_3
	F. rubra	Alpine meadow	M, G	-26.43	C_3
	Helictotrichon tibeticum	Alpine meadow	M, G	-25.01	C_3
	Koeleria cristata	Alpine meadow	M, G	-24.87	C_3
	Poa sinattenuata	Alpine meadow	M, G	-25.48	C_3
	Ptilagrostis concinna	Alpine meadow	M, G	-25.03	C_3
	P. dichotoma	Alpine meadow	M, G	-25.62	C_3
	Stipa penicillata	Alpine meadow	M, G	-25.80	C_3

(Continued)

Iridaceae	*Iris potaninii*	Alpine meadow	D, F	-26.47	C_3
Labiatae	*Ajuga lupulina*	Alpine meadow	D, F	-26.92	C_3
	Elsholtzia calycocarpa	Alpine meadow	D, F	-25.79	C_3
	Mentha haplocalyx	Alpine meadow	D, F	-26.69	C_3
Leguminosae	*Astragalus adsurgens*	Alpine meadow	D, F	-24.84	C_3
	Gueldenstaedtia diversifolia	Alpine meadow	D, F	-24.84	C_3
	Oxytropis caerulea	Alpine meadow	D, F	-26.83	C_3
	Oxytropis ochrocephala	Alpine meadow	D, F	-25.77	C_3
	Thermopsis lenceolata	Southern slope	D, F	-25.56	C_3
	Trigonella ruthenica	Alpine meadow	D, F	-27.75	C_3
Liliaceae	*Allium chysanthum*	Northern slope	M, F	-27.86	C_3
Papaveraceae	*Hepecoum leptocarpum*	Alpine meadow	D, F	-28.22	C_3
	Notopterygium incisum	Alpine meadow	D, F	-27.41	C_3
	Pleurospermum foetens	Riverside	D, F	-27.16	C_3
Plantaginaceae	*Plantago depresa*	Alpine meadow	D, F	-26.13	C_3
Polygonaceae	*Polygonum sibiricum*	Alpine meadow	D, F	-27.74	C_3
	Polygonum sphaerostachyum	Northern slope	D, F	-27.56	C_3
	Polygonum tenuifolium	Alpine meadow	D, F	-26.06	C_3
	Polygonum viviparum	Alpine meadow	D, F	-26.52	C_3
Primulaceae	*Androsace septentrionalis*	Swamp meadow	D, F	-26.41	C_3
	Glaux maritime	Alpine meadow	D, F	-27.12	C_3
Ranunculaceae	*Aconiytum gymanandrum*	Alpine meadow	D, F	-26.76	C_3
	Anemone obtusiloba	Alpine meadow	D, F	-25.32	C_3
	Delphinium pylzowii	Alpine meadow	D, F	-26.68	C_3
	Halerpestes tricuspis	Alpine meadow	D, F	-27.09	C_3
	Ranunculus brotherusii	Alpine meadow	D, F	-26.13	C_3
	R. pulchellus	Alpine meadow	D, F	-25.68	C_3
	Thalictrum alpinum	Alpine meadow	D, F	-26.40	C_3
	Trollius pumilus	Alpine meadow	D, F	-26.02	C_3
Rosaceae	*Dasiphora fruticosa*	Alpine shrub	D, Sh	-26.34	C_3
	Potantilla anserine	Alpine meadow	D, F	-26.02	C_3
	P. bifurca	Alpine meadow	D, F	-26.49	C_3
	P. nivea	Alpine meadow	D, F	-25.84	C_3
	Sibiracea angustata	Northern slope	D, Sh	-26.51	C_3
	Spiraea alpina	Northern slope	D, Sh	-26.40	C_3
Rubiaceae	*Galium bungei*	Southern slope	D, F	-25.74	C_3
	G. verum	Southern slope	D, F	-25.93	C_3
Salicaceae	*Salix oritrepha*	Northern slope	D, Sh	-25.82	C_3
Scrophulariaceae	*Euphrasia tatarica*	Alpine meadow	D, F	-28.20	C_3
	Lancea tibetica	Alpine meadow	D, F	-24.87	C_3
	Pedicularis alaschanica	Alpine meadow	D, F	-27.24	C_3
	P. kansuensis	Alpine meadow	D, F	-26.66	C_3
	P. longiflora	Riverside	D, F	-28.15	C_3
	Veronica ciliata	Alpine meadow	D, F	-27.29	C_3
Thymelaceae	*Stellera chamaejasme*	Southern slope	D, F	-24.97	C_3
Umbelliferae	*Bupleurum condensatum*	Southern slope	D, F	-27.62	C_3
	Notopterygium frobesiide	Southern slope	D, F	-25.36	C_3
Violaceae	*Viola yedoensis*	Alpine meadow	D, F	-25.45	C_3

D, F, G, M, S and Sh stand for Dicotyledonous, Forb, Grass, Monocotyledonous, Sedge, and Shrub, respectively.

the high-pressure system of Siberia. It has a continental monsoon type climate with severe and long winters and short cool summers. The annual average air temperature is −1.7 ℃ with extremes of maximum at 27.6 ℃ and minimum at −37.1 ℃. During winter months, the average temperature can drop to −15 ℃ to −20 ℃ in highland area. In summer, the average temperature in the warmest month (July) is 14 ℃ to 22 ℃ in the valleys and 4 ℃ to 10 ℃ in the mountains. Average annual precipitation ranges from 426–860 mm, 80% of which falls in the short summer growing season from May to September. It is reported that C_4 type species are commonly found under dry and high temperature of tropical and subtropical areas, which indicates that these conditions favor the evolution of C_4 and CAM plant species (Black, 1977). For example, Winter *et al.* (1976) reported that Mediterranean species predominantly had $\delta^{13}C$ values indicating the C_3 pathway of photosynthesis. By contrast, nearly all species belong to the Sahara-Arabian and/or Sudanian group with a C_4-like carbon isotope composition. It is reasonable to suggest that the absence of C_4 type species at HAMERS is closely related to or is the long-term adaptation to these typical environmental factors, especially under the severe low temperatures at Qinghai-Xizang Plateau alpine ecosystems. Thus, along a geographical gradient of decreasing aridity and temperature, the proportion of C_4 type in plant communities may decrease or diminish.

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海北高寒草甸生态系统研究定位站没有发现 C_4 植物——来自于稳定性碳同位素的证据

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摘要： 通过对海北高寒草甸生态系统研究站25个科、70个属、102种植物叶片的稳定性碳同位素的测定，以确定植物群落的光合型。结果表明，所测定的102种植物的稳定性碳同位素比值（$\delta^{13}C$）介于-28.24‰和-24.84‰之间，说明这102种植物均属于C_3植物，无C_4植物或CAM植物。植物这种光合型的分布与该生态系统中的环境因子密切相关，是低温、强辐射等环境因素长期作用的结果，也反映了植物对这种特殊环境的适应。

关键词： $\delta^{13}C$；光合途径；高寒草甸；青藏高原

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