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Vegetational ecotype of the Gyirong Basin in Tibet, China and its response in stable carbon isotopes of mammal tooth enamel

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Abstract **Carbon isotope analysis of modern herbaceous plants in the Gyirong Basin (Tibet, China) indicates that although C_3 plants are dominant, C_4 plants rarely comprise of the vegetation in the area at 4000 m above sea level. The C_4 plants discovered in the Gyirong Basin are *Salsola nepalensis* of Chenopodiaceae and *Pennisetum flaccidum* of Gramineae, affirming that C_4 plants affected by high solar gain can be distributed at high altitude, which supports the opinion that some C_4 plants can exist in areas of high elevation. Carbon isotope analysis of herbivore tooth enamel from the Gyirong Basin indicates that carbon isotopes of structural carbonate in biogenic apatite at high altitude still keep a stable enrichment relationship with those of plants in their diet. Carbon isotopes in tooth enamel are therefore an accurate proxy for vegetation ecotypes and should reflect climatic and environmental features.**

Keywords: vegetation, mammal, carbon isotope, Tibetan Plateau, climate and environment.

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Within the recent two decades, stable carbon isotopic compositions of mammalian tooth enamel have become widely used as an effective method to reconstruct climatic and environmental features during past geological periods. The principle of this method is that stable carbon isotopes of tissues, such as bones and teeth of herbivore mammals, have a close relationship with those of grasses in their diet, and $\delta^{13}C$ is enriched in tissues of these mammals by a range of about 12‰—15‰[1,2]. Stable carbon isotopic compositions of C_3 and C_4 plants are distinct, with $\delta^{13}C$ values of C_3 plants ranging from −22‰ to −35‰ and C_4 plants ranging from −8‰ to −16‰[3,4]. Fossil tooth enamel has been shown more resistant to diagenesis than other biogenic apatite materials, so distributions of C_3 and C_4 plants when mammals lived can be inferred according to the stable carbon isotopic composition of tooth enamel[5,6]. Unfortunately, most stable carbon isotope analyses of modern mammals have been performed on bones. Measurements on modern tooth enamel are comparatively scarce, especially from the Chinese mainland[7].

It is generally accepted that grasses at high altitude are C_3 plants. Recently, however, it was reported that some C_4 vegetation is distributed at high altitude[8−12]. The elevation of the Gyirong Basin in Tibet, China is about 4000 m, but previous reports about stable carbon isotopes of grasses are rare at high altitude in the Tibetan Plateau[11−15]. Also, very few studies have been done on the relationship between carbon isotopes of tooth enamel of modern herbivores and vegetation at high altitude. The goal of our study is to characterize the vegetational ecotype and the response of stable carbon isotopes in herbivore tooth enamel to modern vegetation at high altitude in the Tibetan Plateau, which will provide basis for explaining carbon isotopes of fossil tooth enamel and building hard theoretic foundation to reconstruct paleovegetation and paleoenvironment.

1 Materials and methods

1.1 Plant material

Fifty-three herbaceous species were collected from Oma Village in Gyirong County, Tibet, China (geographical location: 28°46′00″N, 85°18′16″E; elevation: 3968 m; see Fig. 1), including all grasses found in this area. With the exception of two species of artificially planted crops (highland barley and rape), other 51 species are wild plants. Plant samples were collected from 11:00 a.m. to 12:00 noon on sunny days in July 2001, and all were completely unfolded, fresh leaf blades, which commonly have the most representative photosynthetic ability. Each sample was commonly a mix of 3—5 different individuals of the same species.

1.2 Animal material

Tooth samples of three herbivores, horses (*Equus caballus*), goats (*Capra hircus*) and yaks (*Bos mutus*), were collected from Oma. All samples were from local individuals that fed on naturally occurring forage. Seven to ten samples, each from different individuals, were analyzed for each mammal species. Biogenic apatite, which makes up 95% of tooth enamel in mammals, contains about 1% structural carbonate, mainly as carbonate ion in place of hydroxyl or phosphate ions. Judged by tooth eruption and abrasion, all individuals sampled are adult. Samples belong to cheek teeth, including premolars and molars. The sampled dates for animals are the same as those for plants.

1.3 Analytical methods

Plant samples were washed ultrasonically with clear water, and oven-dried at 85℃. Depending on their size, 5—20 leaf blades were chosen at random from each dry

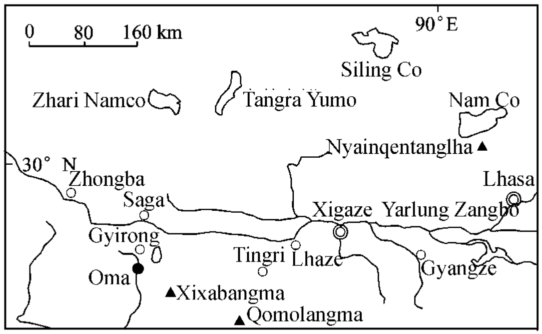

Fig. 1. Map of the Gyirong Basin in Tibet, China showing the locality referred to in this work.

sample ground into powder to produce approximately equal amount. CO_2 was produced from the combustion of a sample with CuO and Pt thread in evacuated quartz tubes at 500℃ for 24 h.

Pure enamel was physically separated from dentine, cement and bone, and soaked in 0.6% acetic acid for 16 h. It was then thoroughly rinsed with distilled water, dried, and ground into 75-μm powder with agate mortar. The powder was reacted with 10% H_2O_2 for 16 h, rinsed repeatedly, centrifuged, and reacted with 0.6% acetic acid for 16 h. It was again rinsed with distilled water several times, centrifuged and dried. CO_2 was produced by using the phosphoric acid method, and purified.

The $\delta^{13}C$ values of the resultant CO_2 were determined on MAT-252 mass spectrometer. Pretreatments and analyses of these samples were performed in the Isotope Laboratory of the Institute of Geology and Geophysics of the Chinese Academy of Sciences.

The carbon isotopic composition is reported in the standard notation as

$$\delta^{13}C\ (‰) = (R_{sample}/R_{standard} - 1) \times 1000,$$

where R = $^{13}C/^{12}C$, and the Cretaceous marine fossil Pee Dee belemnite (PDB) is adopted as the standard sample. Results of repeated measurements show that the analytical precision is better than 0.2‰.

2 Result and discussion

The analytical result indicates that among 53 herbaceous species in the Gyirong Basin, 51 species are C_3 plants with $\delta^{13}C$ values from −21.8‰ to −29.1‰ (average −25.3‰), including three genera and four species of Polygonaceae, one species of Chenopodiaceae, one species of Caryophyllaceae, two genera and two species of Ranunculaceae, one species of Papaveraceae, three genera and three species of Cruciferae, one genus and two species of Rosaceae, four genera and five species of Fabaceae, one species of Geraniaceae, one species of Malvaceae, two genera and two species of Thymelaeaceae, two genera and two species of Umbelliferae, one species of Gentianaceae, three genera and three species of Borraginaceae, two genera and two species of Labiatae, one species of Solanaceae, one species of Scrophulariaceae, one species of Plantaginaceae, six genera and twelve species of Compositae, four genera and four species of Gramineae, and one species of Liliaceae. Two species, *Salsola nepalensis* of Chenopodiaceae and *Pennisetum flaccidum* of Gramineae, are C_4 plants with $\delta^{13}C$ values of −11.5‰ and −11.2‰ respectively (average −11.3‰) (Table 1). C_3 plants make up 96.2% of all grasses, while C_4 plants make up only 3.8% (Fig. 2). All grasses from Oma Village in the Gyirong Basin have an average $\delta^{13}C$ value of −24.8‰.

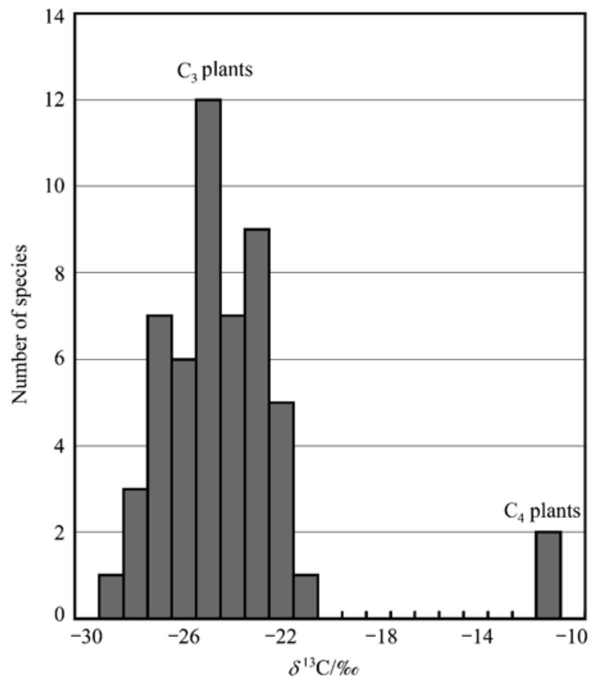

Fig. 2. Distributions of C_3 and C_4 plants in the Gyirong Basin in Tibet, China.

The $\delta^{13}C$ values of tooth enamel of 10 horse samples range between −12.8‰ and −13.8‰, with an average of −13.2‰; those of 9 goat samples are −8.8‰ to −12.1‰, with an average of −10.5‰; those of 7 yak samples are −10.7‰ to −14.2‰, with an average of −12.6‰ (Table 2, Fig. 3). All tooth enamel samples have an average $\delta^{13}C$ value of −12.1‰. Apparently, the $\delta^{13}C$ values of herbivore tooth enamel in the Gyirong Basin are more enriched by 12.7‰ than those of plants in their diet. This enrichment is consistent with results from other regions and falls within the enrichment range between 12‰ and 15‰. Carbon isotope analyses of structural carbonate in tooth enamel of the modern herbivores in Kenya and other places, such as giraffes, buffalos, gazelles, zebras, hippopotamuses, warthogs, white-tailed deer, and domestic cows, suggest that the $\delta^{13}C$ value of a mammal with pure C_3 diet is about −13.5‰, and that with pure C_4 diet is about +1‰, having an enrichment range of about 13‰[16]. An analysis to tooth enamel of several species of modern

Table 1 Carbon isotopic compositions of grasses in the Gyirong Basin in Tibet, China

Family	Genus and species	$\delta^{13}C$ (‰)	Family	Genus and species	$\delta^{13}C$ (‰)
Ranunculaceae	*Clematis tangutica*	−22.1	Borraginaceae	*Arnebia euchroma*	−26.9
	Thalictrum rutifolium	−23.9		*Lappula redowskii*	−26.9
Papaveraceae	*Corydalis stricta*	−23.0		*Onosma hookeri*	−24.3
Cruciferae	*Brassia campestris*	−27.2	Labiatae	*Dracocephalum heterophyllum*	−25.4
	Lepidium apetalum	−25.8		*Lophanthus tibeticus*	−24.4
	Rorippa elata	−25.0	Solanaceae	*Mandragora caulescens*	−21.8
Polygonaceae	*Fagopyrum tataricum*	−25.7	Scrophulariaceae	*Scrophularia dentate*	−22.8
	Polygonum avieulare	−27.9	Plantaginaceae	*Plantago depressa*	−25.9
	Polygonum sibiricum	−28.6	Compositae	*Artemisia edgeworthii*	−25.3
	Rumex nepalensis	−24.2		*Artemisia gmelinii*	−22.6
Chenopodiaceae	*Chenopodium prostratum*	−29.1		*Artemisia hedinii*	−26.6
	Salsola nepalensis	−11.5		*Artemisia macrocephala*	−28.9
Caryophyllaceae	*Silene caespitella*	−25.1		*Artemisia roxburghiana*	−26.8
Rosaceae	*Potentilla anserine*	−26.8		*Artemisia taimingensis*	−27.4
	Potentilla bifurca	−25.7		*Cirsium griseum*	−23.1
Fabaceae	*Astragalus kialensis*	−25.0		*Gnaphalium affine*	−24.7
	Astragalus oplites	−23.8		*Heteropappus boweri*	−27.5
	Cicer microphyllum	−24.7		*Heteropappus crenatifolius*	−27.4
	Oxytropis glacialis	−24.6		*Taraxacum tibetanum*	−23.8
	Trigonella emodi	−25.3		*Zxeris versicolor*	−26.2
Geraniaceae	*Erodium stephanianum*	−25.2	Gramineae	*Avena fatua*	−27.9
Malvaceae	*Malva rotundifolia*	−28.1		*Hordeum vulgare*	−22.2
Thymelaeaceae	*Stellera chamaejasma*	−23.0		*Oryzopsis lateralis*	−23.6
	Wikstroemia stenophylla	−23.1		*Pennisetum flaccidum*	−11.2
Umbelliferae	*Carum carvi*	−27.5		*Stipa breviflora*	−23.2
	Pimpinella acuminata	−25.3	Liliaceae	*Allium sikkimense*	−24.1
Gentianaceae	*Gentiana crassicaulis*	−22.7	Average		−24.8

Table 2 Carbon isotopic compositions of herbivore tooth enamel from the Gyirong Basin in Tibet, China

Family	Genus and species	$\delta^{13}C$ (‰)										Average $\delta^{13}C$ (‰)
Equidae	Horse (*Equus caballus*)	−13.0	−13.1	−13.1	−13.3	−12.8	−12.8	−13.1	−13.4	−13.7	−13.8	−13.2
Bovidae	Yak (*Bos mutus*)	−14.0	−14.2	−13.7	−11.3	−10.7	−12.5	−11.9				−10.5
	Goat (*Capra hircus*)	−9.0	−8.8	−11.1	−11.4	−11.0	−12.1	−11.7	−9.0	−10.0		−12.6

herbivores shows that their $\delta^{13}C$ values are from −15.6‰ to −12.7‰, with an average of −13.6‰, and their diet has pure C_3 plants with an average $\delta^{13}C$ value of −27.5‰, so the enrichment range is 13.9‰[17]. As a result, herbivore tooth enamel in the Gyirong Basin completely follows a common enrichment rule of carbon isotopes. In other words, the carbon isotopic composition of herbivore tooth enamel is indeed regarded as a proxy for the photosynthetic pathways of vegetation. Distribution of C_3 and C_4 plants is closely related to climate and environment, so that carbon isotopes of tooth enamel have a direct response to climatic and environmental changes. Among herbivores on the savanna dominated by C_4 plants in Kenya, Cape buffalos and waterbucks of Bovidae have tooth enamel $\delta^{13}C$ values of −2.1‰ and −2.3‰, respectively, and zebras of Equidae have a $\delta^{13}C$ value of −0.8‰[16]. Comparing the Gyirong Basin with the Kenya savanna, it is implied that carbon isotopic compositions of mammals are related to plants in their diet but unrelated to their systematic positions.

C_3 plants grow in a cold or cool climate, including not only plants in the frigid zone but also those in cold niches of the temperate and tropic zones. 85% of known terrestrial plants, which includes trees, most shrubs and grasses at high latitude or high altitude, are C_3 plants. Modern C_3 grasses in North America, for example, are distributed at high latitude and altitude where temperature is relatively low during their growing season[18]. Evidence from alpine regions indicates that C_3 and C_4 plants have a marked vertical zonation. In Mt. Kenya, for instance, vegetation is entirely C_3 above 3000 m elevation, a mix of C_3 and C_4 plants between 3000 and 2000 m elevation, and entirely C_4 below 2000 m elevation[19]. An analysis of vegetation at different elevations in the arid Argentine temperate zone

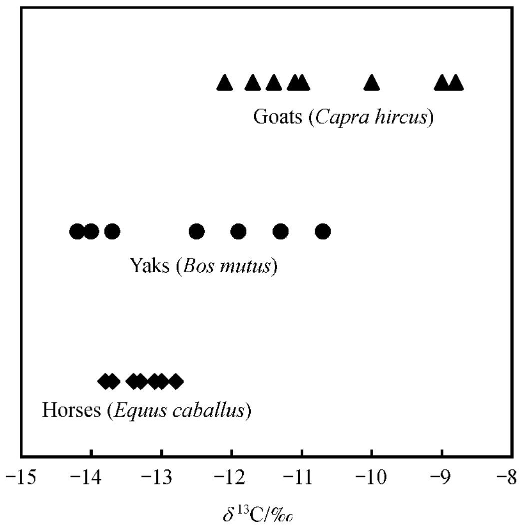

Fig. 3. Carbon isotopic range of herbivore tooth enamel from the Gyirong Basin in Tibet, China.

indicates that the abundance of C_4 plants decreases markedly with increasing elevation, and the proportion of C_4 plants is reduced to 20% by 2400 m elevation[20]. In the Bolivian and Venezuelan Andes, the vegetation is completely C_3 above 3500 m elevation[14,21]. Based on analyses for plant samples, additionally, no C_4 plants were found in Anapurna, Nepal between 4100 and 5610 m elevation on the southern slope of the Himalayas or the mountains above 3500 m elevation in Papua New Guinea[14]. All plant samples collected in the eastern part of the Tibetan Plateau are categorized as C_3 on the basis of isotope analyses[13,15]. Some recent studies, however, have reported that a few C_4 plants are found at high altitude in Tibet, even at a height of 4520 m[11,12]. A C_4 species (*Muhlenbergia richardsonis*) of Gramineae was recorded at 3960 m elevation in the western part of North America[10]. In East Africa, two species of C_4 plants were present up to 4000 m elevation[8] and the alpine vegetation in northwestern Argentina was found to be 1% C_4 at 4100—4500 m elevation[9].

The dominance of C_3 plants in the Gyirong Basin is consistent not only with distribution features of C_3 plants, but also with analytical data of other regions at high altitude. The δ^{13}C values of C_3 plants increase with increasing elevation[14,15], and the vegetation in the Gyirong Basin has the same trend. The C_3 grasses at about 200 m elevation, for example, have an average δ^{13}C value of about −29‰[14], much more negative than the average value of −25.3‰ for C_3 plants in the Gyirong Basin. Analyses of individual plant species show the same trend. In the northeastern part of the Tibetan Plateau, for example, the δ^{13}C value of the genus *Stellera* is −24.3‰ at 3500 m elevation, and that of the genus *Potentilla* is −27.4‰ at 3140 m elevation[15]. In the Gyirong Basin at about 4000 m elevation, the δ^{13}C value of *Stellera chamaejasma* is −23.0‰, and those of the two species of *Potentilla* are −26.8‰ and −25.7‰, markedly more positive than data of the same genus at lower altitude.

Plants in arid or semiarid regions have more positive δ^{13}C than plants in humid or subhumid regions. In the subhumid region of the central Loess Plateau in northern China, for example, the C_3 plants have an average δ^{13}C value of −27.5‰, whereas in the semiarid and arid regions of the western Loess Plateau the average δ^{13}C is −26.2‰[22]. Correspondingly, the δ^{13}C values of C_3 grasses in the Gyirong Basin also respond to arid environment, and they have a mean of −25.3‰, which apparently reflects an extremely arid climatic condition. In fact, plants in arid regions may close their stomas or decrease stomatal conductance (g) in order to reduce evaporation of water. As a result, the ratio of intercellular to ambient CO_2 concentration (c_i) decreases and the δ^{13}C value of photosynthetic product becomes enriched[23].

In spite of only two species, on the other hand, the discovery of *Pennisetum flaccidum* and *Salsola nepalensis* in the Gyirong Basin demonstrates that C_4 plants are indeed distributed at high altitude, since the elevation of the sample locality Oma is close to 4000 m above sea level. This is consistent with other recent reports of C_4 plants found at high altitude in Tibet[11,12]. Among two species of C_4 plants found in the Gyirong Basin, *Pennisetum flaccidum* of Gramineae has a δ^{13}C value of −11.2‰, and *Salsola nepalensis* of Chenopodiaceae has a δ^{13}C value of −11.5‰, both of them belonging to the typical C_4 plants according to their carbon isotopic compositions. Based on the characteristic Kranz structure and CO_2 compensation concentration in C_4 plants, *Pennisetum flaccidum* has been demonstrated a C_4 plant[24]. Although *Salsola nepalensis* has not been directly reported as a C_4 plant until now, all other 54 species of the genus *Salsola* with known photosynthetic pathway belong to C_4 plants[25], and another C_4 species of this genus, *S. ruthenica*, is also found in Tibet[11,12]. As a result, it is reasonable to conclude that *S. nepalensis* is a C_4 plant. Consequently, it is unquestionable that rare C_4 plants exist in Oma, Gyirong at about 4000 m elevation.

Global vegetation studies indicate that temperature is the key climatic variable in determining whether C_4 photosynthetic pathway occurs[10,18,20,25−28]. On the other hand, there are different opinions about the influence of moisture condition on C_4 plants. Surveys of C_4 Gramineae plants on the Indian subcontinent and of C_4 Chenopodiaceae plants in China show that their geographical distributions are closely negatively correlated with moisture[28]. Some authors, however, report that the comparatively humid summer climate in the Tibetan Plateau is favorable to growth of C_4 plants[12]. Actually, the annual average temperature is −4—0℃ in the Tibetan Plateau between 27°—40° N where 76 species of C_4 plants have been reported in Tibet, Qinghai and western Sichuan of the cold temperate zone[28]. Among the known C_4 plants in China, species of

Gramineae, Chenopodiaceae, Cyperaceae, and Amaranthaceae are dominant, but the last two families are absent in the Gyirong Basin. This raises the interesting question of how C_4 plants came to be distributed, even in small abundances, in alpine areas. Some authors suggest that it might be the result of the expansion of C_4 plants, which originated from the tropic zone. Another intriguing possibility is that some C_4 plants had different origins[25,29,30]. High solar gain and summer wetness were regarded as conditions for the distribution of C_4 plants at high altitude in the Tibetan Plateau[12]. A study of a Gramineae species at high altitude in western North America shows that daily leaf temperature can reach a range favorable to C_4 photosynthesis in microsites with high solar gain on south-facing slopes[10]. The Gyirong Basin is located on the southern slope of the Himalayas. It is temperate and semiarid, and has a monsoon climate, receiving most of its 350 mm annual rainfall in summer. Additionally it receives over 3000 h sunlight annually. All these conditions are favorable for the presence of rare C_4 plants of Gramineae and Chenopodiaceae, and may be enough to counteract the effects of high altitude.

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