Review

Chinese Science Bulletin

Geography

November 2012 Vol.57 No.31: 4024–4035
doi: 10.1007/s11434-012-5233-9

Spatial and temporal variations of C_3/C_4 relative abundance in global terrestrial ecosystem since the Last Glacial and its possible driving mechanisms

RAO ZhiGuo*, CHEN FaHu, ZHANG Xiao, XU YuanBin, XUE Qian & ZHANG PingYu

Key Laboratory of Western China's Environmental Systems (Ministry of Education), Lanzhou University, Lanzhou 730000, China

Received January 18, 2012; accepted March 31, 2012; published online June 17, 2012

The primary factor controlling C_3/C_4 relative abundance in terrestrial ecosystem since the Last Glacial has been widely debated. Now more and more researchers recognize that climate, rather than atmospheric CO_2 concentration, is the dominant factor. However, for a specific area, conflicting viewpoints regarding the more influential one between temperature and precipitation still exist. As temperature and precipitation in a specific area usually not only vary within limited ranges, but also covary with each other, it is difficult to get a clear understanding of the mechanism driving C_3/C_4 relative abundance. Therefore, systematic analysis on greater spatial scales may promote our understanding of the driving force. In this paper, records of C_3/C_4 relative abundance since the Last Glacial on a global scale have been reviewed, and we conclude that: except the Mediterranean climate zone, C_3 plants predominated the high latitudes during both the Last Glacial and the Holocene; from the Last Glacial to the Holocene, C_4 relative abundances increased in the middle latitudes, but decreased in the low latitudes. Combining with studies of modern process, we propose a simplified model to explain the variations of C_3/C_4 relative abundance in global ecosystem since the Last Glacial. On the background of atmospheric CO_2 concentration since the Last Glacial, temperature is the primary factor controlling C_3/C_4 relative abundance; when temperature is high enough, precipitation then exerts more influence. In detail, in low latitudes, temperature was high enough for the growth of C_4 plants during both the Last Glacial and the Holocene; but increased precipitation in the Holocene inhibited the growth of C_4 plants. In middle latitudes, rising temperature in the Holocene promoted the C_4 expansion. In high latitudes, temperature was too low to favor the growth of C_4 plants and the biomass was predominated by C_3 plants since the Last Glacial. Our review would benefit interpretation of newly gained records of C_3/C_4 relative abundance from different areas and different periods, and has its significance in the understanding of the driving mechanisms of C_3/C_4 variations on longer timescales (e.g., since the late Miocene) with reliable records of temperature and atmospheric CO_2 concentration.

C_3/C_4 plants, global ecosystem, Last Glacial, driving factor, temperature

Citation: Rao Z G, Chen F H, Zhang X, et al. Spatial and temporal variations of C_3/C_4 relative abundance in global terrestrial ecosystem since the Last Glacial and its possible driving mechanisms. Chin Sci Bull, 2012, 57: 4024–4035, doi: 10.1007/s11434-012-5233-9

Terrestrial higher plants assimilate atmospheric CO_2 mainly via two photosynthetic pathways, i.e. C_3 and C_4 pathways. Pure C_3 and C_4 plants show $\delta^{13}C$ values ranging from ca. −22‰ to −30‰ and from ca. −9‰ to −19‰ [1–4], respectively. Previously, numerous studies have already established stable carbon isotope fractionation model of terrestrial higher plants [4], as well as its relationship with environmental conditions [5]. Generally speaking, C_4 plants are considered to have competitive advantages over C_3 plants under warm, dry and lower atmospheric CO_2 concentration conditions [1–4]. Therefore, from the theoretical perspective, paleoclimatic and paleoenvironmental reconstruction based on records of past C_3/C_4 variations is feasible. But, in practice, varied environmental factors usually co-vary with each other, resulting in the stepwise understanding of the driving mechanisms of C_3/C_4 relative abundance.

In the late 1980s, C_4 expansion in the Indian subcontinent during the late Miocene (Siwalik in Figure 1) was initially

*Corresponding author (email: raozhg@lzu.edu.cn)

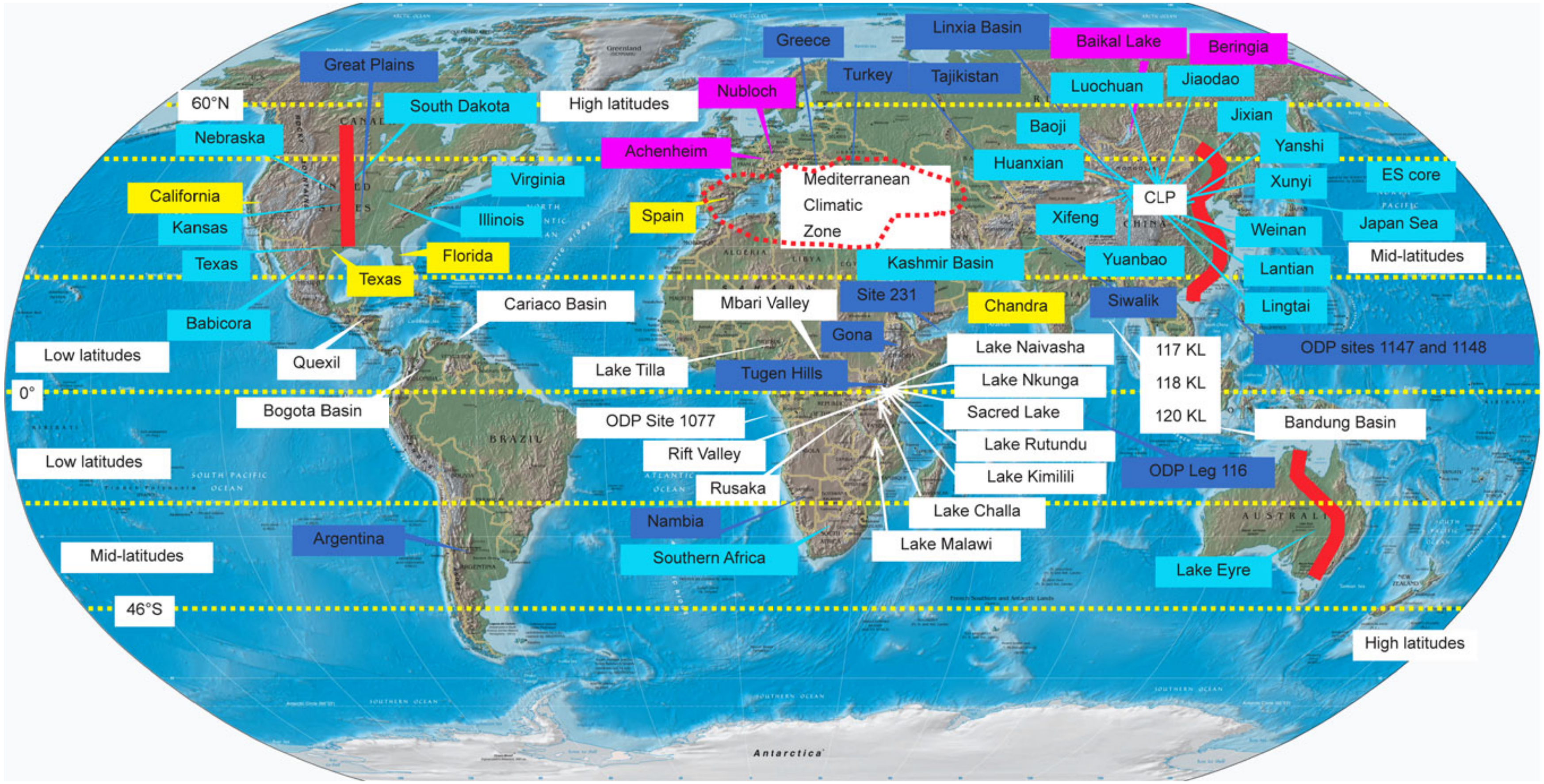

Figure 1 Distribution of the cited study sites in this paper. Red bars indicate areas for organic carbon isotopic studies of modern surface soils; yellow dashed lines represent inportant latitudinal boundaries; red dashed lines represent the Mediterranean climate zone; yellow background represent locations for investigations of modern C_4 species; white background indicate C_3/C_4 records since the Last Glacial from low latitudes; light blue background indicate C_3/C_4 records since the Last Glacial from mid-latitudes; purple backgournd indicate C_3/C_4 records since the Last Glacial from high latitudes; dark blue background represent locations of C_3/C_4 records since the late Miocene.

thought to be the response of local terrestrial ecosystem to the inception or a marked strengthening of the Asian monsoon system driven by uplift of the Tibetan Plateau [6]. Subsequently, synthesis of results from all over the world pointed out that C_4 expansion during the late Miocene may have occurred on a global scale, and remarkable decline of atmospheric CO_2 concentration was proposed as the main driving force [7,8]. However, due to limited knowledge of long-term atmospheric CO_2 history and the difficulty of reconstructing it over such a long geological period, studies of C_3/C_4 variations on a shorter timescales (especially since the Last Glacial) boomed quickly.

In the early studies of C_3/C_4 variations since the Last Glacial, atmospheric CO_2 concentration was adopted as the dominant driving force too. Lacustrine $\delta^{13}C$ results from Sacred Lake (Figure 1) in Kenya, East Africa indicate that dominance of C_4 plants in this area during the Last Glacial was replaced by C_3 plants during the Holocene. Change of atmospheric CO_2 concentration was considered to be the main driving force responsible for this ecological shift [9]. Simulation results also suggested that change of CO_2 concentration alone could explain this observed vegetation shift in tropical Africa [10]. However, compound-specific $\delta^{13}C$ data of long-chain *n*-alkanes in lacustrine sediments from two lakes (Babicora and Quexi, Figure 1) in Mesoamerica record opposite C_3/C_4 trends since the Last Glacial, indicating that regional climate, especially the hydrological condition, exerts a stronger influence on the C_3/C_4 relative abundance [11]. Subsequently, climate as the dominant driving factor for terrestrial ecological C_3/C_4 variations has been widely recognized.

However, for a specific area, main climatic factors (such as temperature and precipitation) could covary during either historical or geological periods, which might further couple with terrestrial ecological C_3/C_4 variations. Therefore, conflicting viewpoints of the driving mechanisms may arise from the same C_3/C_4 records from a single location or a small area. For example, contrast to early report, newly gained data from East Africa emphasized the significant influence of hydrological conditions (precipitation) [12,13]. Similar change trends of the paleo-C_3/C_4 relative abundance also occurred along an altitudinal gradient in Basin Bogota, tropical Colombia (Figure 1). Some researchers believe that it was driven by variations of atmospheric CO_2 and temperature [14], while others consider that the influence of atmospheric CO_2 and precipitation is more important than that of temperature [15]. In the Chinese Loess Plateau (Figure 1), many researchers have recognized the increased C_4 relative abundance from the Last Glacial to the Holocene, and the variation of the intensity of the East Asian Summer Monsoon has been suggested as the primary driving force on glacial/interglacial timescales [16,17]; more recently, some scholars begin to emphasize the influence of temperature [18,19]. All these inconsistencies suggest that systematic analysis of the paleo-C_3/C_4 records from a vast space (global) since the Last Glacial is necessary for further understanding of the driving mechanisms, as well as providing better knowledge for more accurate paleoclimatic and paleoenvironmental reconstruction.

In this paper, C_3/C_4 records since the Last Glacial on a global scale have been reviewed. We summarize the basic spatial and temporal characteristics of C_3/C_4 relative abundance during the Last Glacial and the Holocene (frame of glacial/interglacial timescale). Then, combined with modern C_3/C_4 relative abundance revealed by $\delta^{13}C$ data from surface soils on continental scale, the relationships between C_3/C_4 relative abundance and environmental conditions, as well as its possible driving mechanisms, have been discussed. Our work aims at better reconstruction of paleoclimate and paleoenviroment based on paleo-C_3/C_4 records.

1 Global paleo-C_3/C_4 records since the Last Glacial

Records of C_3/C_4 relative abundance in terrestrial ecosystem since the Last Glacial reveal similar trends in adjacent regions, and dissimilar trends among different latitudes (Figures 1 and 2). We will introduce the paleo-C_3/C_4 records since the Last Glacial mainly based on the basically different change trends in different latitudes. However, the actual boundaries between these latitudinal regions are not easily to be well-determined. It is well-known that the vegetation types are not always distributed in parallel with the latitudes, due to the different areas, shapes and relative positions of the oceans and continents. So, the actual paleo-C_3/C_4 changes are not always necessarily following the latitudinal rule. What we present, in one word, is basically and globally characteristics of paleo-C_3/C_4 variations since the Last Glacial.

In the low-latitudes, in tropical Africa, organic $\delta^{13}C$ records from several mid-altitude lakes (2000–3000 m a.s.l.) and low-altitude lakes in mountains (Figure 1), (including Lake Sacred [9,20,21], Lake Nkunga [22,23] and Lake Rutundu [24] in Mt. Kenya, Lake Kimilili in Mt. Elgon [9] and Lake Challa in Mt. Killimanjaro [13], Lake Tilla in northeastern Nigeria [25] and Lake Malawi [12]), as well as a peat bog (Rusaka in Figure 1) in Burundi [26], show highly similar trends, which suggests C_4 vegetation dominated during the Last Glacial and C_3 dominated during the Holocene. $\delta^{13}C$ results of soil organic matter from profiles in the Kenya Rift Valley (Figure 1) also suggest that the boundary of forest and savanna advanced more than 300 m in altitude during the transition from the Last Glacial to the Holocene, indicating that C_4 plants expanded during the Last Glacial in that region [27]. This was confirmed by pollen records from Lake Naivasha (Figure 1) in Central Rift Valley of Kenya [28]. In the same latitudinal band, $\delta^{13}C$ evidence from low Bogota Basin, tropical Colombia (Figure 1) indicates similar ecological shift, i.e. predominance of C_4 plants during the Last Glacial was replaced by C_3 plants during the Holocene [14,15]. Sedimentological (lithologic) and palynological analyses of two cores from Indonesia (Bandung Basin in Figure 1) indicate that fresh water swamp forests during the Holocene replaced open swamp vegetation dominated by grasses and sedges during the Last Glacial [29]. Since all trees are C_3 plants and all C_4 plants are grasses, sedges and shrubs, results from these two cores may also indicate the decrease of C_4 relative abundance from the Last Glacial to the Holocene in this area (Bandung Basin in Figure 1). $\delta^{13}C$ data of both total organic matter and long-chain *n*-alkanes derived from terrestrial higher plants in marine sediment cores (117 KL, 118 KL and 120 KL, Figure 1) in the Bay of Bengal show similar change trends, that is more positive values occurring in the Last Glacial, indicating that terrestrial ecosystem in the source area (Himalayan Basin) was dominated by C_4 plants during the Last Glacial and by C_3 plants during the Holocene [30]. Compared to the Preboreal and Holocene, $\delta^{13}C$ values of *n*-alkanoic acids derived from terrestrial higher plants in marine sediments of Cariaco basin (Figure 1) are enriched by 4%–5‰ in the Last Glacial period, indicating greater ratios of waxes derived from C_4 plants during the relative cold and dry Last Glacial [31,32]. The overall change trend is similar to the results of compound-specific $\delta^{13}C$ data of long-chain *n*-alkanes along sediment core from Lake Quexil located in low-latitude Mesoamerica [11]. All the evidence, clearly demonstrates that C_4-predominated vegetation during the Last Glacial was replaced by C_3-predominated vegetation during the Holocene in low-latitudes. In other words, the relative abundance of C_4 plants decreased from the Last Glacial to the Holocene in those regions. Here, record from Lake Challa [13] (Figure 2(a)) is selected as a representative of C_3/C_4 variation since the Last Glacial in low-latitudes.

In the mid-latitudes, $\delta^{13}C$ records from more than ten loess/paleosol sequences (i.e. Luochuan, Jiaodao, Jixian, Yanshi, Xunyi, Weinan, Lantian, Lingtai, Yuanbao, Xifeng, Huanxian, Baoji, Figure 1) on the Chinese Loess Plateau (CLP) [18,19,33–35] show an increase of C_4 relative abundance from the Last Glacial to the Holocene. In the eastern and central CLP, the magnitude of C_4 increase in several profiles is ca. 40% [18,19,33,34]. Even in the Holocene with higher C_4 abundance, C_4 plants only dominated on the eastern edge of CLP (Yanshi [19] in Figure 1). Organic $\delta^{13}C$ data from the western edge of CLP indicate that this area was dominated by pure C_3 vegetation during the Last Glacial (Yuanbao [35] in Figure 1). Because $\delta^{13}C$ values of modern plants are variable under different environmental conditions [36–39], and to a certain extent, it will become more positive during the decomposition of plant remains [39,40]. It is worth to note that relative abundance of C_4 plants, especially during the glacial periods, may has been overestimated [39], if the highest frequent carbon isotopic values in modern C_3 and C_4 plants (normally, −27‰ and −13‰ [33]) were taken as the end-point values for estimation. Similar records of C_3/C_4 variation since the Last Glacial have been obtained from sediments of the Japan Sea [41]. In the Kashmir Basin (Figure 1), India, almost all the paleosols in the loess, indicating climate amelioration, support significant C_4 vegetation [42,43], which is similar to the results from the Chinese loess/paleosol sequences. Soil organic $\delta^{13}C$ records from the central Great Plains (including several sites in South Dakota and Nebraska, Figure 1) [44], and adjacent central and south-central Texas (Figure 1) [45,46], southeastern West Virginia (Figure 1) [47] and southwestern Kansas (Figure 1) in USA [48] also record an increase of C_4 vegetation from the late Pleistocene to the Holocene. $\delta^{13}C$ data of *n*-alkanes derived from terrestrial higher plants in the sediments of the North Pacific ES core (Figure 1) show significant variations from glacial (less positive) to interglacial (more positive), indicating changes of C_4/C_3 relative abundance in the source regions (central Asia) [49]. Obviously, from the Last Glacial to the Holocene, relative abundance of C_4 plants in the source regions increased; such a change trend is apparently similar to the compound-specific $\delta^{13}C$ record of sedimentary long-chain *n*-alkanes from Lake Babicora in mid-latitude Central America [11]. In the Southern Hemisphere, a review of pollen, phytolith and isotope evidence from southern Africa (Figure 1) concludes the paleovegetation variation trend in this area is opposite to that occurred in the tropic Africa with increased C_4 grass ratio during the Last Glacial Maximum [50]. Based on such a trend, we can speculate that C_4 relative abundance may have increased from the Last Glacial to the Holocene in southern Africa. Similarly, $\delta^{13}C$ results in fossil emu eggshell from Lake Eyre (Figure 1), South Australia indicate that C_4 abundance was the highest between 45000 and 65000 years ago, the lowest in the Last Glacial Maximum, and then rising in the Holocene [51]. Miller et al. [52] demonstrate that human colonization may have a significant influence on the paleovegetation change in the South Australia 45000 year ago. Nevertheless, C_4 abundance in that region increased from the Last Glacial to the Holocene was consistent with the general characteristics of the mid-latitude paleovegetation change. $\delta^{13}C$ record from Xunyi Profile [19] in the CLP is selected as a representative of C_3/C_4 variation since the Last Glacial in mid-latitude region (Figure 2(b)).

C_3/C_4 records from the high-latitudes are sparse relative to low- and mid-latitudes. However, sediments from Lake Baikal (Figure 1), Russia provides excellent materials for the reconstruction of paleo-C_3/C_4 changes. Although the total organic $\delta^{13}C$ values of the lake sediment are more positive during the Last Glacial than in the Holocene, *n*-alkanes of leaf waxes derived from terrestrial plants show remarkably uniform $\delta^{13}C$ values that consistent with those from modern C_3-plants throughout the entire core spanning the last 20 ka, indicating the predominance of C_3 vegetation in this high-latitude region occurred not only during the Last Glacial but also during the Holocene [53]. Although the loess region in the northwestern Europe is close to the mid-latitudes, its

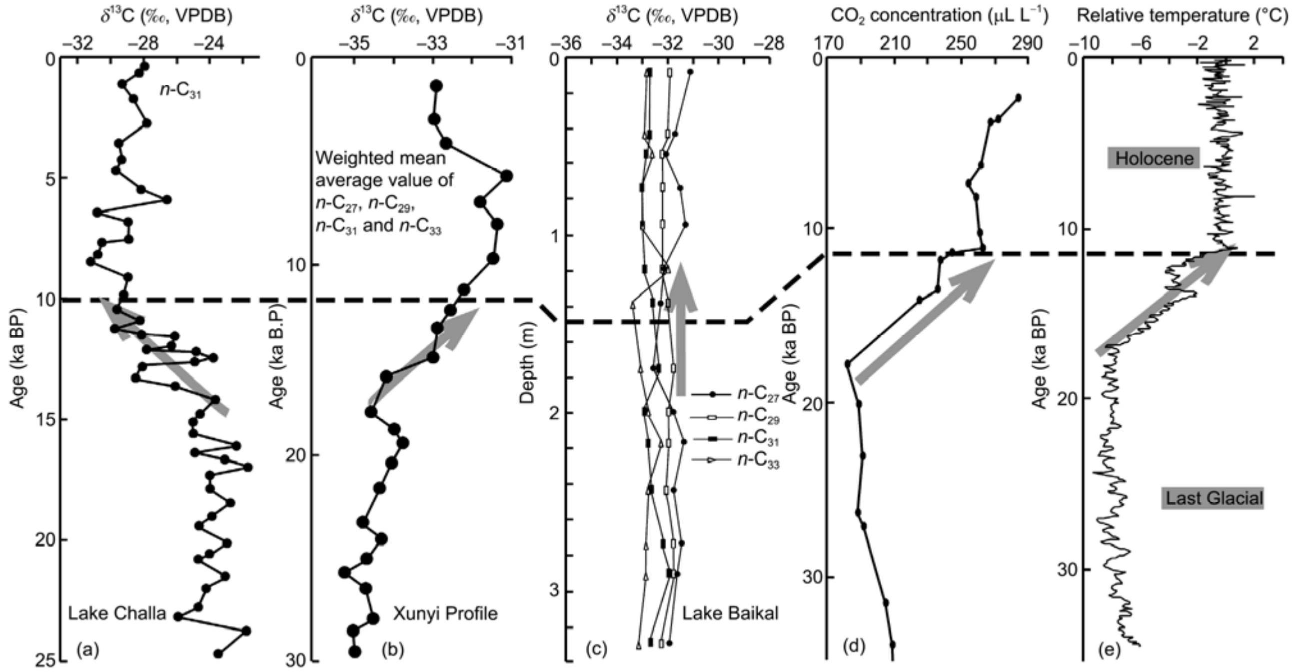

Figure 2 Comparison of the representative C_3/C_4 records since the Last Glacial from the low-latitudes (a) [13], mid-latitudes (b) [19], high-latitudes (c) [53] and records of atmospheric CO_2 concentration (d) [54] and global mean temperature since the Last Glacial (e) [55].

location in the west edge of the continent results in the lower regional temperature than that of the same latitude in the east edge of the continent. Therefore, C_3/C_4 variation in this region should be similar to that of the high-latitudes. $\delta^{13}C$ values of soil organic carbon from two high-resolution loess profiles in France and Germany (Achenheim and Nubloch in Figure 1) are quite negative (⩽–24‰), with more negative values in the Holocene and less negative in the Last Glacial [56–58]. The authors conclude that soil $\delta^{13}C$ from this area does not indicate the variation of C_3/C_4 abundance but $\delta^{13}C$ of pure C_3 plants under different climatic conditions. Their conclusion was confirmed by $\delta^{13}C$ results from modern C_3 plants [36–39]. $\delta^{13}C$ values of Beringian late Pleistocene mummified remains of several kinds of mega-herbivores demonstrate that local biomass (Figure 1) was predominated by C_3 plants during the Last Glacial [59]. All of these indicate that C_4 plants never become significant components of the local biomass in the high-latitudes during both the Last Glacial and Holocene. $\delta^{13}C$ record from Lake Baikal [53] is selected as a representative of C_3/C_4 variation since the Last Glacial in high-latitudes (Figure 2(c)).

Interestingly, the C_3/C_4 variations along the altitudinal gradient in the low latitudes are similar to that along the latitudinal gradient. $\delta^{13}C$ values of soil organic matter from four profiles along the altitudinal gradient in the Bogota Basin (Figure 1), Colombia [15] demonstrate that the carbon isotope stabilized at ca. –24‰ in the highest profile (3150 m a.s.l.), indicating pure C_3 vegetation in the high altitude since the Last Glacial (similar to records from the high-latitudes). At the same time, the $\delta^{13}C$ data from the two mid-altitude profiles (elevation are 2980 and 2850 m a.s.l.) indicate that the C_4 abundance increased from the Last Glacial to the Holocene (similar to records from mid-latitudes), and the $\delta^{13}C$ data of the lowest profile (2650 m a.s.l.) indicate that C_4-predominated vegetation during the Last Glacial was replaced by C_3 vegetation during the Holocene (similar to records from low-latitudes).

Obviously, the general pattern of global C_4/C_3 change since the Last Glacial is that C_4-dominant vegetation during the Last Glacial was replaced by C_3 vegetation during the Holocene in the low-latitudes; C_4 abundance increased from the Last Glacial to the Holocene in the mid-latitudes; and pure C_3 vegetation occupied the high-latitudes during both the Last Glacial and the Holocene.

2 Modern C_4 plants

2.1 Distribution of C_4 plant species

Due to the influence of local factors, such as landform and physiognomy, natural vegetation shows high diversity. Sage et al. [5] summarize global distribution of C_4 photosynthesis mainly based on the percentage representation of C_4 photosynthesis in regional grass floras (different to percentage contribution to primary production), and show that only few C_4 species distribute in limitedly small areas with relative warm environment above 60°N (Figure 1). In the region below 46°S (Figure 1), almost no C_4 plants have been found. Because the C_4 plants are extremely rare in these two regions, relative abundance of C_4 plants in local ecosystem should be extremely low and thus could be neglected. Their work also clearly shows that C_4 grasses prosper in the warm temperate zone with relative wet summers, such as Jacksonville in Florida and Chandra in India and Abilene in Texas (Figure 1). However, C_3 plants dominate the regions with Mediterranean climate characterized by a moist cool winter and dry warm summer, such as Pasadena in California and Seville in Spain (Figure 1). As a result, the authors conclude that temperature has an important control on the growth of C_4 plants [5].

2.2 C_3/C_4 relative abundance in modern vegetation

Relative to C_4 percentage in regional grass floras, contribution of C_4 plants to primary production in local vegetation is more concerned, because $\delta^{13}C$ from most sediment can only reveal the C_4/C_3 contributions in primary production. Until now, few investigations reveal the basic characteristics of C_4/C_3 composition in modern vegetation on continental scale. Previous study of the phytolith $\delta^{13}C$ in the surface soil of eastern China (Figure 1) indicates that along the latitudinal gradient, C_4 abundance increases at first and then decreased, with the highest C_4 abundance in both grasslands and grasslands under forest between 34° and 40°N [60]. Our newly gained $\delta^{13}C$ data of both long-chain *n*-alkanes and total organic matter of surface soils [61,62] in eastern China with higher spatial resolution further confirm that of phytoliths in surface soils [60]. Together, all these three datasets demonstrate that relatively higher C_4 abundance in modern vegetation of the eastern China occurs in mid-latitudes spanning from ca. 30° to 40°N (represented by $\delta^{13}C$ data of total organic matter of surface soils from this region, Figure 3(a)). In North America, data of soil organic $\delta^{13}C$ along a latitudinal gradient in USA and Canada (Figure 1) show a clearly vegetation shift from almost pure C_4 vegetation around ca. 30°–40°N to pure C_3 vegetation around ca. 50°–55°N [63] (Figure 3(b)). Similar investigation conducted in Australia (Figure 1) [64] indicates that the relatively higher C_4 abundance occurs in grasslands and savannas spanning from ca. 14° to 25°S, and gradually decrease both southward and northward (Figure 3(c)). Our analysis of these evidences [62] indicates that, although the specific latitudes are different in these three continents, a basic pattern is that the highest C_4 abundance in modern vegetation occurs in the mid-latitudes. A simple evidence that is most of the low-latitudes are occupied

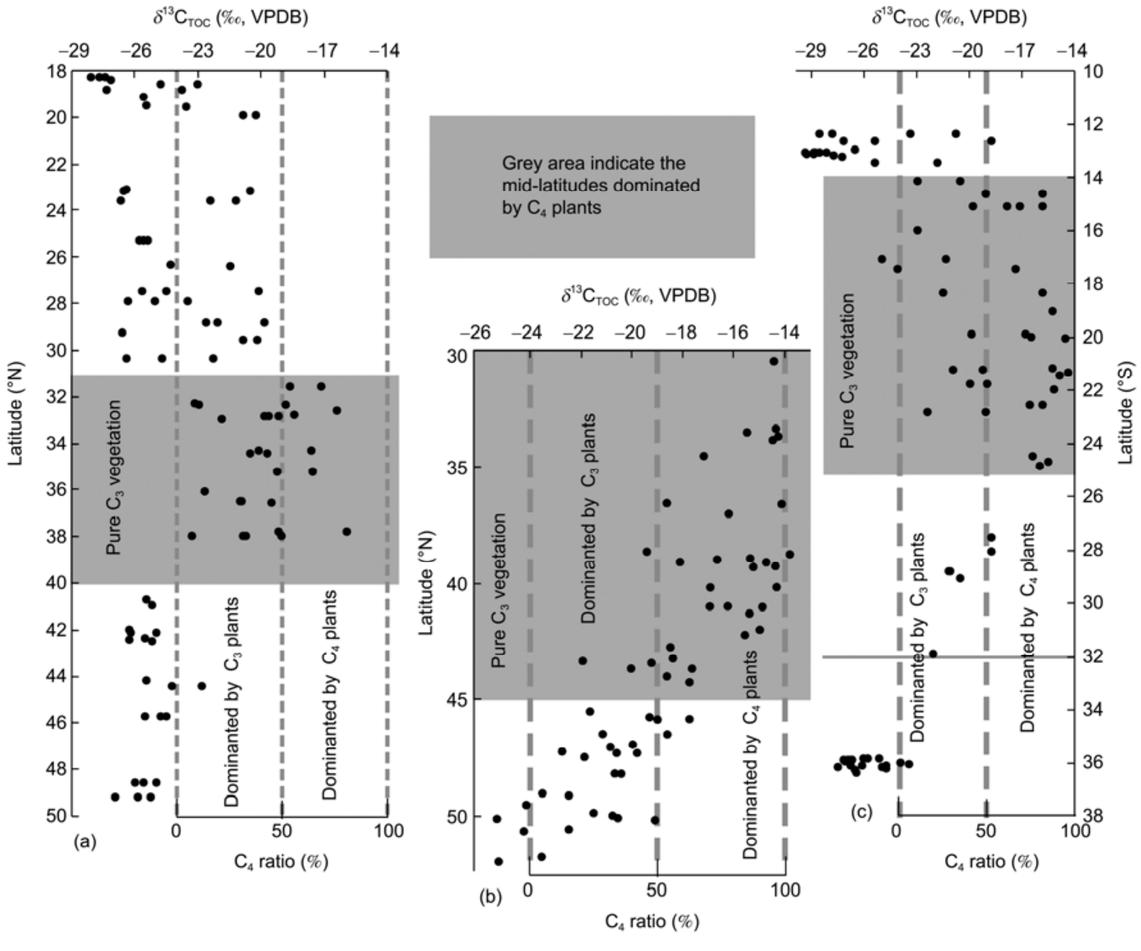

Figure 3 C_3/C_4 relative abundance in modern vegetation indicated by $\delta^{13}C$ of total organic matter of surface soils on continental scales along latitudinal gradients in eastern China (a), the Great Plains in North America (b) and Australia (c) (modified from [62]).

by tropical rainforest or sub-tropical seasonal rainforest while Savanna vegetation (typical C_4 vegetation) occupies its two swings and no C_4 plants dominate the high-latitudes [5], therefore, C_3/C_4 relative abundance in modern vegetation revealed by surface soil $\delta^{13}C$ values should be reliable.

3 Discussion on driving mechanisms and its significance

3.1 Driving mechanisms

It is well-known that C_4 plants generally get competitive advantages under the warm, dry and low atmospheric CO_2 concentration conditions [1–4]. Compared to the Holocene, environment conditions during the Last Glacial period were characterized by lower temperature [55], lower atmospheric CO_2 concentration [54] (Figure 2(d) and (e)), and relatively arid. Anyway, the decrease of temperature from the low- to the high-latitudes, which is the same during both the Last Glacial and the Holocene, may explain the dissimilar C_3/C_4 change trends in different latitudes. In the low-latitudes, temperature is high enough to allow the growth of C_4 plants during both the Last Glacial and Holocene, relatively arid condition in this region during the Last Glacial promoted C_4 expansion while the increased precipitation during the Holocene is adverse for the growth of C_4 plants. In the high-latitudes, during both the Last Glacial and Holocene, the temperature is too low to support the growth of C_4 plants. And in the mid-latitudes, although the increase of precipitation and atmospheric CO_2 concentration from the Last Glacial to the Holocene is adverse for the growth of C_4 plants, the increased temperature efficiently increased the relative C_4 abundance in this region.

As mentioned above, climate exerts more significant influence on the global C_3/C_4 variations since the Last Glacial, especially the effect of temperature on the growth and distribution of C_4 plants. When environmental temperature is below the "threshold value", especially during the growing seasons, C_4 plants will be absent in local ecosystem, such as the reconstructed paleovegetation in the high-latitudes since the Last Glacial [53,56,59] and that during the Last Glacial on the western edge of the CLP [35]. When environmental temperature is higher than the "threshold value", extremely arid, especially during the growing seasons, could also be adverse to the growth of C_4 plants, such as the modern vegetation in the Mediterranean climate zone (Pasadena in California and Seville in Spain [5] in Figure 1). Carbon isotopic evidence of carbonates and fossil teeth from Greece and Turkey in Mediterranean climate zone indicates that the local terrestrial ecosystem was dominated by C_3 vegetation over the past 11 Ma, as it is today in this region [65]. The Mediterranean climate condition was also proposed as the main controlling factor on the C_3-predominated vegetation over the past 1.77 Ma in Tajikistan (Figure 1) indicated by $\delta^{13}C$ values of soil organic matter of loess [66]. Obviously, high temperature associated with high precipitation favors C_3 trees and inhibits the growth of C_4 grasses, as evidenced from the present and Holocene vegetation in the low-latitudes [9,14]. Only the combination of high enough temperature and moderate aridity (or moderate humidity) remarkably favor the growth of C_4 plants, as exemplified by the Holocene vegetation in the mid-latitudes [18,19] and the Last Glacial vegetation in the low-latitudes [9,14].

Due to the obviously different trends in C_3/C_4 changes in different latitudes, variation of atmospheric CO_2 concentration since the Last Glacial (ca. 170–360 $\mu L\ L^{-1}$; Figure 2(d)) shows no significant control on the growth and distribution of C_4 plants. However, it is undoubtedly that, as the "carbon resource", atmospheric CO_2 concentration can influence the competition between C_4 and C_3 plants. The key is the change magnitude of concentration of atmospheric CO_2. The concentration of atmospheric CO_2 from the Last Glacial to present may not reach a "threshold value" that would affect the growth of C_4 plants significantly, therefore, atmospheric CO_2 concentration since the Last Glacial (ca. 170–360 $\mu L\ L^{-1}$) should be in the range of the so-called "low atmospheric CO_2 concentration" that suitable for the growth of C_4 plants. A field experimental study over eight years carried out in the United States demonstrates that atmospheric CO_2 concentration shows no significant influence on the relative C_4 biomass production even if it reaches twice of the natural concentrations [67].

Other factors have been proposed as the controlling factors for the past C_4/C_3 change, e.g. seasonality. Such interpretation is not in conflict with our understanding, given the different spatial and temporal scales. For example, the studies on $\delta^{13}C$ of carbonate and organic matter from a loess-paleosol profile in Illinois (Figure 1) propose that carbonate $\delta^{13}C$ can be treated as a warm-season proxy that have recorded the glacial variations at submillennial scales during the Last Glacial [68,69]. In addition, $\delta^{13}C$ values of organic matter in cave sediments from the same region show the regional C_3/C_4 changes on glacial/interglacial timescales, with more C_4 plants during the middle Holocene and more C_3 plants during the Last Glacial Maximum [70]. Obviously, on glacial/interglacial timescales, regional vegetation changes in Illinois are consistent with the characteristics of the mid-latitudes, i.e. C_4 abundance increased from the Last Glacial to the Holocene.

3.2 Significance of the driving mechanisms

In our knowledge, the replacement of C_4-predominated vegetation during the Last Glacial by C_3 plants during the Holocene in the low-latitudes mainly reflects the increase in humidity during the transition. The large-scale African vegetation changes recorded by low-latitude marine sediments (ODP Site 1077 in Figure 1) with a longer timescale demonstrate that they were controlled by the changes in aridity driven by the strength of the African monsoon [71].

During the Holocene, organic $\delta^{13}C$ of sediments in the southeast of Central African Republic (Mbari Valley in Figure 1) indicates that higher C_4 ratio in local biomass was a response to arid condition indicated by low lake level of Lake Chad [72]. Variation of C_3/C_4 relative abundance in tropical Africa mainly controlled by the humidity has been accepted by more and more researchers. Recently-gained 23 ka record of C_3/C_4 relative abundance from sediments in Lake Malawi has been used to reconstruct the evolution history of aridity in this area [12]. Lake Challa (Figure 1) on the southeast slope of Mt. Killimanjaro [13] is a low-altitude lake (ca. 880 m a.s.l.) on the boundary area between Kenya and Tanzania. Newly obtained $\delta^{13}C$ data from Lake Challa further confirm the decrease of C_4 plants from the Last Glacial to the Holocene, as reported from several other lake sediments. Detailed analysis also clearly demonstrates the initial time of the decrease of C_4 relative abundance was synchronous with precipitation increase indicated by the enhanced intensity of African monsoon, 1500 years later than the increase of the concentration of atmospheric CO_2 and 3500 years latter than the temperature increase [13]. All these evidence indicates that the arid condition has an important influence on the vegetation in Africa, especially in low-latitude tropical Africa. More significantly, this study implies that new records with higher resolution of C_3/C_4 variations in this region (low-latitudes) could be used to reconstruct the history of regional aridity or monsoonal precipitation.

In the high-latitudes, the temperature is too low to support the growth of C_4 plants during both the Last Glacial and Holocene, so, the terrestrial ecosystem in this region has been predominated by C_3 plants since the Last Glacial [53,56–59]. Numerous study results of modern C_3 plants indicate that their $\delta^{13}C$ values are negatively correlated with the precipitation, i.e. $\delta^{13}C$ of modern C_3 plants will be more negative with increasing precipitation [36–39]. Therefore, $\delta^{13}C$ data derived from terrestrial higher plants in this region (high-latitudes) should record the $\delta^{13}C$ response of predominant C_3 plants to the variation of climate factors (mainly precipitation). Based on detailed studies of modern process and sedimentary records, paleoprecipitation reconstruction may be feasible in this region. In Europe, paleoprecipitaiton reconstruction based on the organic $\delta^{13}C$ of the loess/paleosol sequences since the Last Glacial has been conducted [57,58]. On the western edge area of the CLP, organic $\delta^{13}C$ data indicate that the local biomass was predominated by C_3 plants during the Last Glacial period, consequently, the $\delta^{13}C$ data have been attempted to be used in paleoprecipitation reconstruction [35].

In the mid-latitudes, increased C_4 relative abundance from the Last Glacial to the Holocene has been proposed as the ecological response to the increased temperature [18,19], our review of the global paleo-C_3/C_4 records supports such a viewpoint. However, temperature since the Last Glacial in the mid-latitudes may just varied around the "threshold value", while the precipitation (or humidity) may be different in various locations, the driving mechanisms of paleo-C_3/C_4 variations in this region may be complicated and need to be analyzed specifically and carefully. We speculate that in the arid or semi-arid inland areas of the mid-latitudes, the humidity may keep in the "relative arid" range suitable for the growth of C_4 plants during both the Last Glacial and the Holocene. Therefore, variation of temperature could either significantly promote or suppress C_4 relative abundance in such areas, which means variation of the C_4 ratio in these areas could serve as an indicator of paleotemperature variation. In semi-humid or humid areas of the mid-latitudes, due to the coupled effect of temperature and precipitation, the main controlling factor or its climatic significance of the variations of C_4 relative abundance may be different during different geological periods (such as the Last Glacial and the Holocene).

On longer timescales, the main controlling factor for C_4 expansion since the late Miocene has been widely debated during the past two decades. A dramatic ecological shift from C_3 to C_4 dominated biomass during the late Miocene indicated by pedogenic carbonate $\delta^{13}C$ from Siwalik Group in northern Pakistan [6,7,73] (Figure 1) was initially thought to be a possible mark of the inception or a marked strengthening of the Asian monsoon system driven by uplift of the Tibetan Plateau [6]. Subsequently, Cerling et al. [7,8] believe that there was a global C_4 expansion through the Miocene/Pliocene boundary and proposed such an expansion may be related to lower atmospheric CO_2 concentration. The proposition of Cerling et al. [7,8] has been challenged on the scale of the C_4 expansion [74,75], on the process of the transition from the Miocene to the Pliocene [76], and on the relationship between environmental factors and vegetation evolution [77–80]. We summarize the C_3/C_4 records [6–8,73–75,81–92] since the late Miocene, the results are shown in Table 1. Obviously, there are not contemporaneous C_4 expansions recorded by paleoecological proxies since the late Miocene. Such as, $\delta^{13}C$ data of pedogenic carbonate [6,73], total organic matter [73,82], fossil animals [7,8,81], long-chain *n*-alkanes [83] of higher plant origins from Siwalik sediments in Indian subcontinent and marine sediments in the Bay of Bengal (Figure 1) indicate the remarkable C_4 expansion during the late Miocene in this area, and the main expansion happened among 7–5 Ma. However, in the north of the Tibet Plateau, carbon isotopic data of fossil animals from the Linxia Basin (Figure 1) indicate that only during the Quaternary, C_4 plants become a significant fraction of the local vegetation [85]. Similarly, $\delta^{13}C$ data of fossil eggshell from Namibia demonstrate that C_4 plants become a significant fraction of local biomass only in the Quaternary since about 2 Ma ago [86]. Evidence from northeastern Argentina indicates that main C_4 expansion in this area happened around 4 Ma [74]. However, evidence from the Great Plains in the North America indicates that main C_4 expansion in this area happened between 6–4 Ma, and the C_4 abundance reached modern level about 2.5 Ma ago [75,90]. There seems no contemporaneous C_4 expansion during the late Miocene, which denies a global driving factor (such as the significant decrease of atmospheric CO_2 concentration) for C_4 expansion in the late Miocene.

Because C_3/C_4 records since the late Miocene mainly come from the low- and mid-latitudes (Figure 1), and modern temperature in these regions is in the range suitable for the growth of C_4 plants as we discussed previously. Long-term record indicates that the global mean temperature has gradually decreased since the late Miocene [93] (Figure 4(a)). Therefore, temperature should not be the factor driving C_4 expansion in these areas since the late Miocene. Reconstructed atmospheric CO_2 concentration based on marine sediments are not exactly similar, and the time resolutions are significantly different. However, almost all the reconstructed

Table 1 Primary characteristics of the C_4 expansion in different continents since the late Miocene

Region	Time of initial C_4 signal	Main period of C_4 expansion	C_4 ratio after expansion	Reference
Indian subcontinent	9.4 Ma	6 Ma	ca. 100%	[6–8,73,81–83]
East Asia	20 Ma	2 Ma	< 40%	[84]
Linxia Basin		2 Ma	< 40%	[85]
Northeastern Argentina	7.6 Ma	4 Ma	ca. 40%–60%	[74]
Namibia		After the Miocene		[86]
Northeastern Africa		After 3.4 Ma	ca. 50%–65%	[88,89]
Kenya	15.3 Ma			[81,87]
Great Plains		6.4–4.0 Ma	ca. 50%–80%	[75,90]

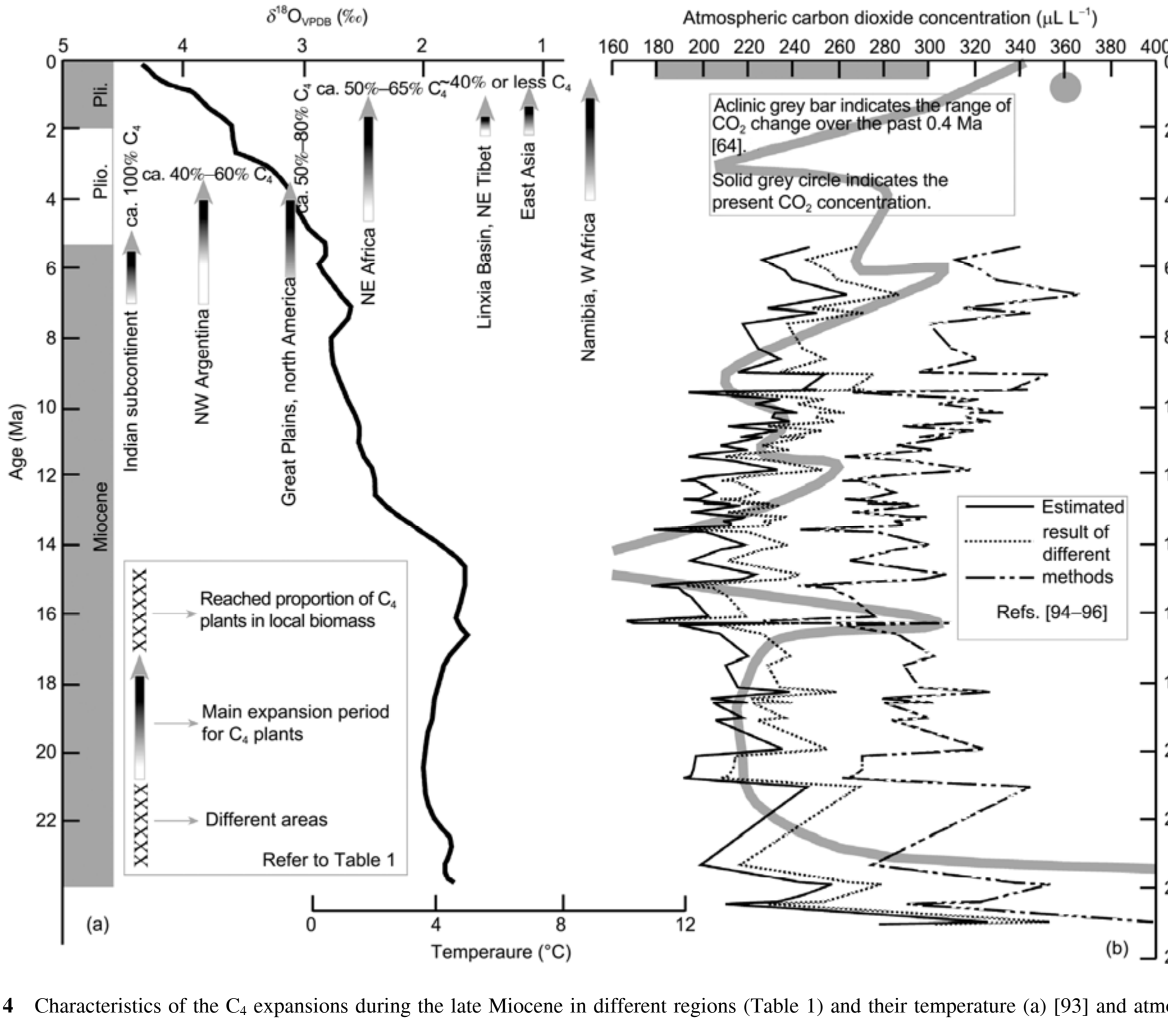

Figure 4 Characteristics of the C_4 expansions during the late Miocene in different regions (Table 1) and their temperature (a) [93] and atmospheric CO_2 background (b) [94–96].

records indicated that the concentration of atmospheric CO_2 is relatively stable during the past 14–15 Ma, without significant decrease [94–96] (Figure 4(b)). Assuming that the reconstructed temperature and atmospheric CO_2 are reliable, based on the global C_3/C_4 records since the Last Glacial and C_3/C_4 relative abundance in modern vegetation, we can reasonably consider that the asynchronous C_4 expansions in different regions since the late Miocene are mainly the terrestrial ecological response to the change of regional hydrological conditions (humidity or aridity). That may explain why on the same global background of temperature and atmospheric CO_2 concentration, C_4 expansions since the late Miocene show so significant differences in different regions. The most possible interpretation is that the beginning time and degree of aridification is different in different regions. Indeed, our speculation needs more works to confirm. Recently reported data demonstrate that the C_4 expansion in Arabia and Indian Subcontinent during the late Miocene was mainly driven by large-scale variation of hydrological conditions [97].

4 Conclusions

Investigation on the distribution of modern C_4 plant species indicates that above 60°N and below 46°S, C_4 plants are extremely rare or absent. Surface soil organic $\delta^{13}C$ data on continental scales indicate that the highest contribution of modern C_4 plants to primary production of local terrestrial ecosystem occurs in the mid-latitudes. Since the Last Glacial, C_3/C_4 records on a global scale show obviously latitudinal characteristics: predominated C_4 during the Last Glacial was replaced by C_3 plants during the Holocene in the low-latitudes; the relative abundance of C_4 plants increased from the Last Glacial to the Holocene in the mid-latitudes; and the terrestrial ecosystem in the high-latitudes was predominated by C_3 plants since the Last Glacial. Based on all these, we put forward a simplified model to explain the relationship between the C_4 relative abundance and the corresponding climatic conditions. The effect of temperature on the growth of C_4 plants is vital in that below the "threshold value" of temperature, the growth of C_4 plants will be inhibited. When the environmental temperature is favorable, both extremely humid and arid condition (especially extremely humid and arid growing seasons) could be adverse for the growth of C_4 plants. Only enough high temperature combine with moderate humidity (or aridity) favor the growth of C_4 plants. Such a model is in effect on the global/continental scale, glacial/interglacial timescale and on the background of atmospheric CO_2 concentration since the Last Glacial to present. Paleoclimatic interpretation of newly grained C_3/C_4 records with higher resolution and the understanding of the driving mechanisms of the variations of C_3/C_4 relative abundance since the late Miocene in different regions will benefit from this work.

Thanks are due all the authors cited in this paper for their pioneering work. This work was supported by the National Basic Research Program of China (*2010CB950202*), *the Key Project of the Chinese Ministry of Education* (*109151*), *the National Natural Science Foundation of China* (*40901055 and 41171091*), *the Fundamental Research Funds for the Central Universities of Lanzhou University* (*lzujbky-2012-k49*) *and the Program for New Century Excellent Talents in University* (*NCET-10-0468*).

1 Denies P. The isotopic composition of reduced organic carbon. In: Fritz P, Fontes J C. Handbook of Environmental Isotope Geochemistry, Vol. 1. The Terrestrial Environment. Amsterdam: Elsevier Scientific Publishing Company, 1980. 339–345
2 O'Leary M H. Carbon isotope fractionation in plants. Phytochemistry, 1981, 20: 553–567
3 O'Leary M H. Carbon isotope in photosynthesis. BioScience, 1988, 38: 328–336
4 Farquhar G D, Ehleringer J R, Hubick K T. Carbon isotope discrimination and photosynthesis. Ann Rev Plant Physiol Mol Biol, 1989, 40: 503–537
5 Sage R F, Wedin D A, Li M R. The biogeography of C_4 photosynthesis: Patterns and controlling factors. In: Sage R F, Monson R K, eds. C_4 Plan Biology. San Diego: Academic Press, 1999. 313–373
6 Quade J, Cerling T E, Bowman J R. Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. Nature, 1989, 342: 163–166
7 Cerling T E, Wang Y, Quade J. Expansion of C_4 ecosystems as in indicator of global ecological change in the late Miocene. Nature, 1993, 361: 344–345
8 Cerling T E, Harris J M, MacFadden B J, et al. Global vegetation change through the Miocene/ Pliocene boundary. Nature, 1997, 389: 153–158
9 Street-Perrott F A, Huang Y S, Perrott R A, et al. Impact of lower atmospheric carbon dioxide on tropical mountain ecosystems. Science, 1997, 278: 1422–1426
10 Jolly D, Haxeltine A. Effect of low glacial atmospheric CO_2 on tropical African montane vegetation. Science, 1997, 276: 786–788
11 Huang Y S, Street-Perrott F A, Metcalfe S E, et al. Climate change as the dominant control on glacial-interglacial variation in C_3 and C_4 plant abundance. Science, 2001, 293: 1647–1651
12 Castañeda I S, Werne J P, Johnson T C, et al. Late Quaternary vegetation history of southeast Africa: The molecular isotopic record from Lake Malawi. Palaeogeogr Palaeoclimatol Palaeoecol, 2009, 275: 100–112
13 Damsté J S S, Verschuren D, Ossebaar J, et al. A 25000-year record of climate-induced changes in lowland vegetation of eastern equatorial Africa revealed by the stable carbon-isotopic composition of fossil plant leaf waxes. Earth Planet Sci Lett, 2011, 302: 236–246
14 Boom A, Marchant R, Hooghiemstra H, et al. CO_2- and temperature-controlled altitudinal shifts of C_4- and C_3-dominated grasslands allow reconstruction of palaeoatmospheric pCO_2. Palaeogeogr Palaeoclimatol Palaeoecol, 2002, 177: 151–168
15 Mora G, Pratt L M. Carbon isotopic evidence from paleosols for mixed C_3/C_4 vegetation in the Bogota Basin, Colombia. Quat Sci Rev, 2002, 21: 985–995
16 Lin B H, Liu R M, An Z S. Preliminary research on stable isotopic compositions of Chinese Loess (in Chinese). In: Liu D S, ed. Loess Environment and Global Change. Beijing: Science Press, 1991. 124–131
17 Lin B H, Liu R M. The stable isotopic evidence of the monsoon variation on Chinese Loess Plateau since the last 800 ka years (in Chinese). Chin Sci Bull (Chin Ver), 1992, 37: 1691–1693
18 Gu Z Y, Liu Q, Xu B, et al. Climate as the dominant control on C_3 and C_4 plant abundance in the Loess Plateau: Organic carbon isotope evidence from the last glacial-interglacial loess-soil sequences. Chin Sci Bull, 2003, 48: 1271–1276
19 Zhang Z H, Zhao M X, Lu H Y, et al. Lower temperature as the main cause of C_4 plant declines during the glacial periods on the Chinese Loess Plateau. Earth Planet Sci Lett, 2003, 214: 467–481
20 Huang Y S, Freeman K H, Eglinton T I, et al. $\delta^{13}C$ analyses of indi-

vidual lignin phenols in Quaternary lake sediments: A novel proxy for deciphering past terrestrial vegetation changes. Geology, 1999, 27: 471–474

21 Huang Y S, Street-Perrott F A, Perrott R A, et al. Glacial-interglacial environmental changes inferred from molecular and compound-specific $\delta^{13}C$ analyses of sediments from Sacred Lake, Mt. Kenya. Geochim Cosmochim Acta, 1999, 63: 1383–1404

22 Ficken K J, Street-Perrott F A, Perrott R A, et al. Glacial/interglacial variations in carbon cycling revealed by molecular and isotope stratigraphy of Lake Nkunga, Mt. Kenya, East Africa. Org Geochem, 1998, 29: 1701–1719

23 Olago D O, Street-Perrott F A, Perrott R A, et al. Late Quaternary glacial-interglacial cycle of climatic and environmental change on Mount Kenya, Kenya. J Afr Earth Sci, 1999, 29: 593–618

24 Ficken K J, Woller M J, Swain D L, et al. Reconstruction of a subalpine grass-dominated ecosystem, Lake Rutundu, Mt. Kenya: A novel multi-proxy approach. Palaeogeogr Palaeoclimatol Palaeoecol, 2002, 177: 137–149

25 Salzmann U, Hoelzmann P, Morczinek I. Late quaternary climate and vegetation of the Sudanian Zone of Northeast Nigeria. Quat Res, 2002, 58: 73–83

26 Aucour A-M, Bonnefille R, Hillaire-Marcel C. Sources and accumulation rates of organic carbon in an equatorial peat bog (Burundi, East Africa) during the Holocene: Carbon isotope constraints. Palaeogeogr Palaeoclimatol Palaeoecol, 1999, 150: 179–189

27 Ambrose S H, Sikes N E. Soil carbon isotope evidence for Holocene habitat change in the Kenya Rift Valley. Science, 1991, 253: 1402–1405

28 Maitima J M. Vegetation response to climatic change in Central Rift Valley, Kenya. Quat Res, 1991, 35: 234–245

29 Kaars S V D, Dam R. Vegetation and climate change in West-Java, Indonesia during the last 135000 years. Quat Int, 1997, 37: 67–71

30 Galy V, François L, France-Lanord C, et al. C_4 plants decline in the Himalayan basin since the Last Glacial Maximum. Quat Sci Rev, 2008, 27: 1396–1409

31 Hughen K A, Eglinton T I, Xu L, et al. Abrupt tropical vegetation response to rapid climate changes. Science, 2004, 304: 1955–1959

32 Makou M C, Hughen K A, Xu L, et al. Isotopic records of tropical vegetation and climate change from terrestrial vascular plant biomarkers preserved in Cariaco Basin sediments. Org Geochem, 2007, 38: 1680–1691

33 Vidic N J, Montañez I P. Climatically driven glacial-interglacial variations in C_3 and C_4 plant proportions on the Chinese Loess Plateau. Geology, 2004, 32: 337–340

34 Liu W G, Huang Y S, An Z S, et al. Summer monsoon intensity controls C_4/C_3 plants abundance during the last 35 ka in the Chinese Loess Plateau: Carbon isotope evidence from bulk organic matter and individual leaf waxes. Palaeogeogr Palaeoclimatol Palaeoecol, 2005, 220: 243–254

35 Chen F H, Rao Z G, Zhang J W, et al. Variations of organic carbon isotopic composition and its environmental significance during the Last Glacial on western Chinese Loess Plateau. Chin Sci Bull, 2006, 51: 1593–1602

36 Stewart G R, Turnbull M H, Schmidt S, et al. ^{13}C natural abundance in plant communities along a rainfall gradient: A biological integrator of water availability. Aust J Plant Physiol, 1995, 22: 51–55

37 Wang G A, Han J M, Liu T S. The carbon isotope composition of C_3 herbaceous plants in loess area of northern China. Sci China Ser D-Earth Sci, 2003, 46: 1069–1076

38 Diefendorfa A F, Muellerb K E, Wing S L, et al. Global patterns in leaf ^{13}C discrimination and implications for studies of past and future climate. Proc Natl Acad Sci USA, 2010, 107: 5738–5743

39 Wang G A, Feng X, Han J M, et al. Paleovegetation reconstruction using $\delta^{13}C$ of Soil Organic Matter. Biogeosciences, 2008, 5: 1325–1337

40 Melillo J M, Aber J D, Linkins A E, et al. Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter. Plant Soil, 1989, 115: 189–198

41 Yamada K, Ishiwatari R. Carbon isotopic composition of long-chain *n*-alkanes in the Japan Sea sediments: Implication for paleoenvironmental changes over the past 85 kyr. Org Geochem, 1999, 30: 367–377

42 Krishnamurthy R V, DeNiro M J. Isotope evidence for Pleistocene climatic changes in Kashmir, India. Nature, 1982, 298: 640–641

43 Krishnamurthy R V, Bhattacharya S K. Paleovegetational history in the Kashmir basin, India, derived from $^{13}C/^{12}C$ ratio in paleosols. Earth Planet Sci Lett, 1989, 95: 291–296

44 Johnson W C, Willey K L. Isotopic and rock magnetic expression of environmental change at the Pleistocene-Holocene transition in the central Great Plains. Quat Int, 2000, 67: 89–106

45 Nordt L C, Boutton T W, Hallmark C T, et al. Late Quaternary vegetation and climate changes in central texas based on the isotopic composition of organic carbon. Quat Res, 1994, 41: 109–120

46 Nordt L C, Boutton T W, Jacob J S, et al. C_4 Plant productivity and Climate-CO_2 variation in South-Central Texas during the Late Quaternary. Quat Res, 2002, 58: 182–188

47 Driese S G, Li Z H, Horn S P. Late Pleistocene and Holocene climate and geomorphic histories as interpreted from a 23000 ^{14}C yr B.P. paleosol and floodplain soils, southeastern West Virginia, USA. Quat Res, 2005, 63: 136–149

48 Olson C G, Porter D A. Isotopic and Geomorphic evidence for Holocene Climate, Southwestern Kansas. Quat Int, 2002, 87: 29–44

49 Ratnayake N P, Suzuki N, Okada M, et al. The variations of stable carbon isotope ratio of land plant-derived *n*-alkanes in deep-sea sediments from the Bearing Sea and the North Pacific Ocean during the last 250000 years. Chem Geol, 2006, 228: 197–208

50 Scott L. Grassland development under glacial and interglacial conditions in southern Africa: Review of pollen, phytolith and isotope evidence. Palaeogeogr Palaeoclimatol Palaeoecol, 2002, 177: 47–57

51 Johnson B J, Miller G H, Fogel M L, et al. 65000 years of vegetation change in central Australia and the Australian Summer Monsoon. Science, 1999, 284: 1150–1152

52 Miller G H, Fogel M L, Magee J W, et al. Ecosystem collapse in Pleistocene Australia and a human role in Megafaunal extinction. Science, 2005, 309: 287–290

53 Brincat D, Yamada K, Ishiwatayi R, et al. Molecular-isotopic stratigraphy of long-chain *n*-alkanes in Lake Baikal Holocene and glacial age sediments. Org Geochem, 2000, 31: 287–294

54 Petit J R, Jouzel J, Raynaud D, et al. Climate an atmospheric history of the past 420000 years from the Vostok ice core, Antarctica. Nature, 1999, 399: 429–435

55 Jouzel J, Lorius C, Petit J R, et al. Vostok ice core: A continuous isotopic temperature record over the last climatic cycle (160000 years). Nature, 1987, 329: 402–408

56 Hatté C, Antoine P, Fontugne M, et al. New chronology and organic matter $\delta^{13}C$ paleoclimatic significance of Nuβloch loess sequence (Rhine Valley, Germany). Quat Int, 1999, 62: 85–91

57 Hatté C, Fontugne M, Rousseau D-D, et al. $\delta^{13}C$ variations of loess organic matter as a record of the vegetation response to climatic changes during the Weichselian. Geology, 1998, 26: 583–586

58 Hatté C, Antoine P, Fontugne M, et al. $\delta^{13}C$ of loess organic matter as a potential proxy for paleoprecipitation. Quat Res, 2001, 55: 33–38

59 Bombin M, Muehlenbachs K. $^{13}C/^{12}C$ ratios of Pleistocene mummified remains from Beringia. Quat Res, 1985, 23: 123–129

60 Lü H Y, Wang Y J, Wang G A, et al. Analysis of carbon isotope in phytoliths from C_3 and C_4 plants and modern soils. Chin Sci Bull, 2000, 45: 1804–1808

61 Rao Z G, Jia G D, Zhu Z Y, et al. Comparison of the carbon isotope composition of total organic carbon and long-chain *n*-alkanes from surface soils in eastern China and their significance. Chin Sci Bull, 2008, 53: 3921–3927

62 Rao Z G, Zhu Z Y, Jia G D, et al. Relationship between climatic conditions and the relative abundance of modern C_3 and C_4 plants in three regions around the North Pacific. Chin Sci Bull, 2010, 55: 1931–1936

63 Tieszen L L, Reed B C, Bliss L B, et al. NDVI, C_3 and C_4 production and distributions in Great Plains grassland land cover classes. Ecol Appl, 1997, 7: 59–78

64 Bird M I, Pousai P. Variations of Delta ^{13}C in the surface soil organic carbon pool. Glob Biogeochem Cycle, 1997, 11: 313–322
65 Quade J, Solounias N, Cerling T E. Stable isotopic evidence from paleosol carbonate and fossil teeth in Greece for forest or woodlands over the past 11 Ma. Palaeogeogr Palaeoclimatol Palaeoecol, 1994, 108: 41–53
66 Yang S L, Ding Z L. Winter-spring precipitation as the principle control on predominance of C_3 plants in Central Asia over the past 1.77 Myr: Evidence from $\delta^{13}C$ of loess organic matter in Tajikistan. Palaeogeogr Palaeoclimatol Palaeoecol, 2006, 235: 330–339
67 Owensby C E, Ham J M, Knapp A K, et al. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. Glob Change Biol, 1999, 5: 497–506
68 Wang H, Follme L R, Liu J C-L. Isotope evidence of paleo-EI Niño-Southern Oscillation cycles in loess-paleosol record in the central United States. Geology, 2000, 28: 771–774
69 Wang H, Ambrose S T, Fouke B W. Evidence of long-term seasonal climate forcing in rhizolith isotopes during the last glaciation. Geophys Res Lett, 2004, 31: L13203
70 Panno S V, Curry B B, Wang H, et al. Climate change in southern Illinois, USA, based on the age and $\delta^{13}C$ of organic matter in cave sediments. Quat Res, 2004, 61: 301–313
71 Schefuß E, Schouten S, Jansen J H F, et al. African vegetation controlled by tropical sea surface temperatures in the mid-Pleistocene period. Nature, 2003, 422: 418–421
72 Runge J. Holocene landscape history and palaeohydrology evidenced by stable carbon isotope ($\delta^{13}C$) analysis of alluvial sediments in the Mbari valley (5°N/23°E), Central African Republic. Catena, 2002, 48: 67–87
73 Quade J, Cerling T E. Expansion of C_4 grasses in the Late Miocene of northern Pakistan: Evidence from stable isotopes in paleosols. Palaeogeogr Palaeoclimatol Palaeoecol, 1995, 115: 91–116
74 Latorre C, Quade J, McIntosh W C. The expansion of C_4 grasses and global change in the late Miocene: Stable isotope evidence from the Americas. Earth Planet Sci Lett, 1997, 146: 83–96
75 Fox D L, Koch P L. Tertiary history of C_4 biomass in the Great Plains, USA. Geology, 2003, 31: 809–812
76 Köhler M, Moyà-Solà S, Agusti J. Miocene/Pliocene shift: One step or several? Nature, 1998, 393: 126
77 Cerling T E, Quade J, Wang Y. Expansion and emergence of C_4 plants. Nature, 1994, 371: 112–113
78 Cowling S A. Plants and temperature-CO_2 uncoupling. Science, 1999, 285: 1500–1501
79 Boutton T W, Archer S R, Nordt L C. Climate, CO_2 and plant abundance. Nature, 1994, 372: 625–626
80 Robinson J M. Atmospheric CO_2 and plants. Nature, 1994, 368: 105–106
81 Morgan M E, Kingston J D, Marino B D. Carbon isotopic evidence for the emergence of C_4 plants in the Neogene from Pakistan and Kenya. Nature, 1994, 367: 162–165
82 Sanyal P, Bhattacharya S K, Kumar R, et al. Mio-Pliocene monsoonal record from Himalayan foreland basin (Indian Siwalik) and its relation to vegetational change. Palaeogeogr Palaeoclimatol Palaeoecol, 2004, 205: 23–41
83 Freeman K H, Colarusso L A. Molecular and isotopic records of C_4 grassland expansion in the late Miocene. Geochim Cosmochim Acta, 2001, 65: 1439–1454
84 Jia G D, Peng P A, Zhao Q H, et al. Changes in terrestrial ecosystem since 30 Ma in East Asia: Stable isotope evidence from black carbon in the South China Sea. Geology, 2003, 31: 1093–1096
85 Wang Y, Deng T. A 25 m.y. isotopic record of paleodiet and environmental change from fossil mammals and paleosols from the NE margin of the Tibetan Plateau. Earth Planet Sci Lett, 2005, 236: 322–338
86 Ségalen L, Renard M, Lee-Thorp J A, et al. Neogene climate change and emergence of C_4 grasses in the Namib, southwestern Africa, as reflected in ratite ^{13}C and ^{18}O. Earth Planet Sci Lett, 2006, 244: 725–734
87 Kingston J D, Marino B D, Hill A. Isotopic evidence for Neogene Hominid paleoenvironments in the Kenya Rifa Valley. Science, 1994, 264: 955–959
88 Feakins S J, deMenocal P B, Eglinton T I. Biomarker records of late Neogene changes in northeast African vegetation. Geology, 2005, 33: 977–980
89 Levin N E, Quade J, Simpson S W, et al. Isotopic evidence for Plio-Pleistocene environmental change at Gona, Ethiopia. Earth Planet Sci Lett, 2004, 219: 93–110
90 Fox D L, Koch P L. Carbon and oxygen isotopic variability in Neogene paleosol carbonates: Constraints on the evolution of the C_4-grasslands of the Great Plains, USA. Palaeogeogr Palaeoclimatol Palaeoecol, 2004, 207: 305–329
91 Tripple B J, Pagani M. The early origins of terrestrial C_4 photosynthesis. Annu Rev Earth Planet Sci, 2007, 35: 435–461
92 Edwards E J, Osborne C P, Strömberg C A E, et al. The origins of C_4 grasslands: Integrating evolutionary and ecosystem science. Science, 2010, 328: 587–591
93 Zachos J, Pagani M, Sloan L, et al. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science, 2001, 292: 686–693
94 Pagani M, Freeman K H, Arthur M A. Late Miocene atmospheric CO_2 concentration and the expansion of C_4 grasses. Science, 1999, 285: 876–879
95 Pagani M, Zachos J C, Freeman K H, et al. Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. Science, 2005, 309: 600–603
96 Pearson P N, Palmer M R. Atmospheric carbon dioxide concentrations over the past 60 million years. Nature, 2000, 406: 695–699
97 Huang Y S, Clemens S C, Liu W G, et al. Large-scale hydrological change drove the late Miocene C_4 plant expansion in the Himalayan foreland and Arabian Peninsula. Geology, 2007, 35: 531–534