Global vegetation change through the Miocene/Pliocene boundary

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Between 8 and 6 million years ago, there was a global increase in the biomass of plants using C_4 photosynthesis as indicated by changes in the carbon isotope ratios of fossil tooth enamel in Asia, Africa, North America and South America. This abrupt and widespread increase in C_4 biomass may be related to a decrease in atmospheric CO_2 concentrations below a threshold that favoured C_3-photosynthesizing plants. The change occurred earlier at lower latitudes, as the threshold for C_3 photosynthesis is higher at warmer temperatures.

The C_3 and C_4 photosynthetic pathways fractionate carbon isotopes to different degrees; C_3 and C_4 plants have $\delta^{13}C$ values ranging from about −22‰ to −30‰ and −10‰ to −14‰, respectively[1–5]. (Isotopic ratios are reported relative to the isotopic standard PDB, where $\delta^{13}C$ (in ‰) = $[(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard} - 1] \times 1{,}000$). So the carbon isotope composition of fossil tooth enamel reflects the C_3/C_4 composition of mammalian diet[6–9]. Soil organic matter preserves this isotopic distinction with little or no isotopic fractionation (<2‰), but both soil carbonate and carbonate in biogenic apatite from large mammals are significantly enriched in ^{13}C compared to source carbon[7,8,10]. Cerling *et al.*[9] have studied fossil soils and tooth enamel from Pakistan and North America and concluded that C_4 ecosystems underwent a global expansion between about 7 and 5 million years (Myr) ago in the late Miocene and early Pliocene epochs; they suggested that atmospheric CO_2 concentrations could have fallen below a threshold critical to C_3 photosynthesis. However, others[11–13], also studying fossil soils and tooth enamel, concluded that there was not a global expansion of C_4 biomass in the late Miocene, and that there was no link between changes in C_3/C_4 biomass and atmospheric chemistry. Hill[13] suggested that observed dietary changes in Africa ~7 Myr ago need not signify a vegetation change, but may be explained by faunal immigration or *in situ* speciation.

Here we report the results of stable carbon isotope analyses from more than 500 equids and other hypsodont (that is, having high-crowned teeth) large mammals from Asia, Africa, North America, South America and Europe. Our studies emphasized equids because modern equids are thought to be predominantly grazers, and equids are abundant in the fossil record. We also analysed other hypsodont large mammals because the record of equids is more limited in Europe, Asia, Africa and South America than it is in North America. Thus, from Europe, Asia and Africa we also report the results of analyses of fossil proboscideans (elephants and their allies), and from South America those of notoungulates (an extinct order of endemic South American mammals). There are several advantages of using mammalian teeth rather than soils for indications of C_4 biomass; first, identification is straightforward, and second, mammals enhance the isotope signal by selective feeding. In most cases C_4 diets are indicators of grazing although some C_4 dicots (for example, *Chenopodiaceae*) can be important components of the diets of certain mammals, especially in regions having saline soils. C_3 grasses today are important in some ecosystems, so that a C_3 diet does not necessarily indicate a browsing diet.

We first show that bioapatite (tooth enamel) in large mammals is ~14‰ enriched in ^{13}C compared to their diet. Using this discrimination factor we then show that large mammals with ages greater than 8 Myr from a global population all had diets compatible with a pure C_3, or C_3-dominated, diet. We then show that by 6 Myr ago equids and some other large mammals from low latitudes (<37°) had a C_4-dominated diet in Africa, South America, North America and southern Asia. No evidence is found suggesting a significant C_4 component in the diets of large mammals from western Europe at any time. Comparison of the quantum yields of C_3 and C_4 monocots, which are primarily grasses and sedges, indicates that C_4 monocots are favoured at atmospheric CO_2 concentrations less than 500 parts per million by volume (p.p.m.v.) when accompanied by high growing-season temperature. The persistance of significant C_4 biomass beginning about 6–8 Myr ago and continuing to the present is compatible with atmospheric CO_2 levels in the late Miocene declining below the 'crossover' point where C_4 grasses are favoured over C_3 grasses or other C_3 plants.

C_3- and C_4-dominated diets

The unambiguous detection of the presence of the C_4 signal is an important issue. C_3 plants have a considerable range in $\delta^{13}C$; water-stressed ecosystems are enriched in ^{13}C (as high as −22‰) compared to the average C_3 value of about −27‰, whereas closed canopies are depleted in ^{13}C, having values as low as −35‰ (refs 5, 14, 15). C_4 plants have a much more restricted $\delta^{13}C$ range, where plants using the NADP-me and NAD-me sub-pathways have average $\delta^{13}C$ values of about −11.4‰ and −12.7‰, respectively[16]. The isotopic fractionation between diet and bioapatites (such as tooth enamel) is not well established for large mammals. After reaction with H_3PO_4 and cryogenic purification, samples were reacted at 50 °C with silver wool to remove trace amounts of SO_2 gas which was occasionally identified in both modern and fossil samples; trace amounts of SO_2 in CO_2 can result in positive ^{13}C shifts greater than 4‰ (unpublished data). Table 1 shows the results of analyses from the hypergrazer alcelaphine bovids (hartebeest and wildebeest) from Kenya that have a diet of NADP-subpathway grasses (about −11.4‰; ref. 16), and from restricted feeders from the Hogel Zoo in Salt Lake City, Utah with a diet of meadow hay and alfalfa (−26.5‰). These results indicate an isotope fractionation factor for both C_3 and C_4 diets in large mammals: $\alpha_{\text{enamel-diet}}$ is 1.0143 to 1.0148, or $\delta^{13}C_{\text{enamel}} - \delta^{13}C_{\text{diet}} \approx 14.3‰$, where $\alpha_{\text{enamel-diet}} = (1{,}000 + \delta_{\text{enamel}})/(1{,}000 + \delta_{\text{diet}})$. This enrichment in ^{13}C of ~14.3‰ for tooth enamel in large mammals compared to their diet is greater than observed in laboratory experiments on very small mammals (mice)[17]. Therefore a $\delta^{13}C$ value for enamel of −8‰ would correspond to a dietary intake of −22‰ to −22.5‰, which is within the range of observed pure C_3 ecosystems and plants[1,2,5,14]. Water stress or high light conditions (or both) causes an enrichment of ^{13}C in C_3 plants[5,14] so that −8‰ for the $\delta^{13}C$ of enamel can be taken as conservative 'cut-off' value to exclude the possibility of a 'false positive' indicating a significant C_4 biomass in diet. For fossil samples, yet another correction should be considered: Friedli and others[18] and Marino and McElroy[19] have shown that the $\delta^{13}C$ of the atmosphere and plants, respectively, have become 1.5‰ more negative in the past 150 years because of fossil-fuel burning. Therefore, the 'cut-off' for a pure C_3 diet may be even more positive, perhaps even −7‰. Others[11] have used a 'cut-off' of −10.5‰ for tooth-enamel $\delta^{13}C$ values to indicate significant C_4 biomass, which we believe is too ^{13}C-depleted for the reasons discussed above.

We analysed 226 different mammals (bovids, camelids, equids, proboscideans, rhinocerids, suids, tapirids) older than 8 Myr and find no evidence for a significant C_4 component in diets of mammals from Europe, Africa, Asia, or the Americas. The average $\delta^{13}C$ value for this suite was $-10.6 \pm 1.3‰$ and only a single sample gave $\delta^{13}C > -8‰$ ($\delta^{13}C = -7.5‰$). These data are compatible with all the animals having diets from −22‰ to about −28‰, with an average diet of −25‰ which is in the range of the carbon isotopic composition for modern C_3 plants. Figure 1 shows the $\delta^{13}C$ values for 825 modern plants; also shown are $\delta^{13}C$ for tooth enamel for 309 modern mammals, and 226 fossil mammals with ages older than 8 Myr. The modern mammals show a distinction between C_3-dominated and C_4-dominated diets, and the >8-Myr mammals indicate diets compatible with an essentially pure C_3 diet.

The $\delta^{13}C$ of the primary dietary signal is preserved in the fossil record in tooth enamel and does not seem to be affected by diagenesis. This is illustrated in Fig. 2 where we show the $\delta^{13}C$ values for east African deinotheres (elephant-like ungulates of the order Proboscidea), other proboscideans, and equids through the past 20 million years. Deinotheres always have $\delta^{13}C$ values consistent with a pure C_3 diet, whereas the equids and proboscideans have $\delta^{13}C$ values consistent with a C_3 diet before 8 Myr, but consistent with a C_4-dominated diet after about 7 Myr. The deinotheres were collected from the same sedimentary deposits as the other fossils. In addition, palaeosols and other sedimentary carbonates from the Koobi Fora (Kenya) sequence[20] have $\delta^{13}C$ values intermediate between the $\delta^{13}C$ values for C_3 and C_4 endmembers.

C_4 ecosystem development in Neogene times

The striking change from C_3 to C_4 ecosystems was first noted in palaeosol carbonates in the Siwalik sediments of Pakistan[21] which showed a change in $\delta^{13}C$ starting about 7 Myr ago with values averaging about −10‰ and reaching about 0‰ by about 5 Myr ago. This can be compared to the record of equid and proboscidean tooth enamel from the same time interval (Fig. 2). These data show a significant C_4 component in both the equid and proboscidean diet between 8 and 7 Myr, but that the C_4 endmember diet was not reached until about 5 Myr (perhaps as early as 6 Myr). The transition begins at about 7.8 Myr using the palaeomagnetic timescale of Cande and Kent[22], or 7.3 Myr using the older palaeomagnetic timescale of Berggren[23]. Equids first appear in the Pakistan sequence about 10.5 Myr, the time of the 'Hipparion datum' and become widespread throughout much of Europe, Africa and Asia. Notably, the earliest equids in the Siwalik sequence have a C_3-dominated diet.

East Africa has an abundant fossil record of proboscideans and equids. We report data from Maboko, Fort Ternan, the Turkana basin and the Suguta depression, and include in our discussion previously published data from the Baringo basin[11]. Both elephantids and equids changed from a C_3-dominated diet to a C_4-dominated diet between about 8 and 7 Myr, while deinotheres retained a C_3-dominated diet (Fig. 2). Equids appear in east Africa by about 10 Myr, and in two sites older than 9 Myr equids have a C_3 diet. The equids have transitional diets at about 8 Myr as recorded in the Samburu Hills, and have largely adapted to a C_4-dominated diet by the time of the oldest sediments in the Lothagam sequence, estimated to be about 7.5 Myr. Elephantids show a similar pattern although they seem to lag the equids in making the transition to a C_4-dominated diet.

The South American record was sampled from deposits in Argentina and in southern Bolivia. Equids entered South America very late, so notoungulates were also included in our analysis. The ages of the samples in Fig. 2 are based primarily on the South American Land Mammal Ages (SALMA), although several samples are also included from well-dated Neogene (Pliocene + Miocene) deposits in northern Argentina[24]. Securely dated notoungulates have a C_3 diet before 8 Myr, but show evidence for a significant C_4

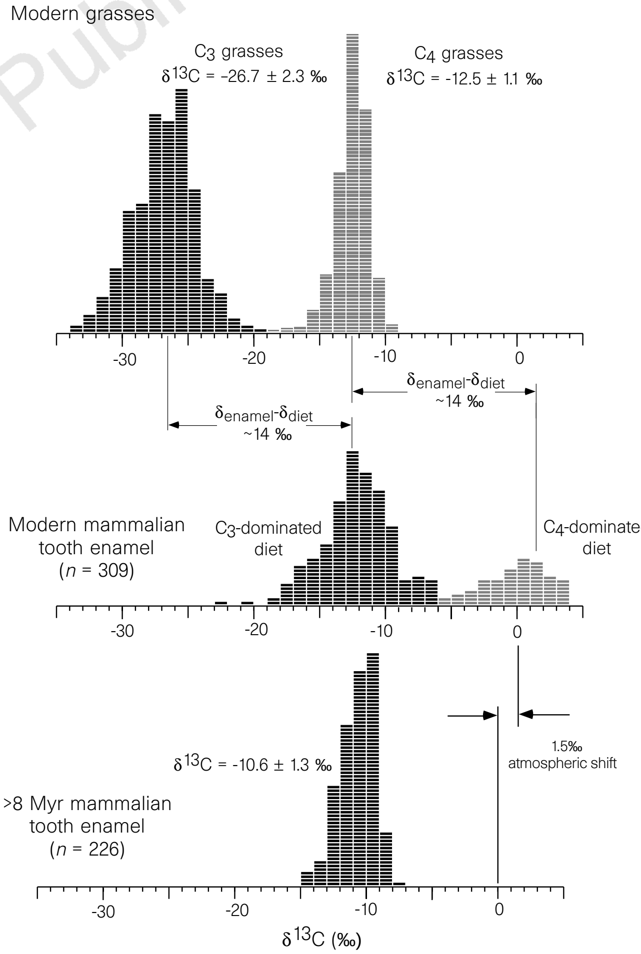

Figure 1 Histograms of $\delta^{13}C$ for modern grasses (compiled from refs 5–8, and unpublished University of Utah data), modern tooth enamel, and fossil tooth enamel >8 Myr. The $\delta^{13}C$ for modern and fossil mammalian enamel is from Europe, Asia, Africa, North America and South America, and represents all samples analysed in our laboratory of these age intervals. Fossil samples include bovids, equids, giraffids, notoungulates, proboscideans and rhinocerids. The $\delta^{13}C$ axis of fossil tooth enamel is shifted by an additional 1.5‰ to adjust for the anthropogenic shift in $\delta^{13}C$ in the atmosphere (and therefore diet and enamel) resulting from fossil-fuel burning[18,19].

component (−4.8‰) by 7.6 Myr (ref. 24).

We divided the North American data in a ‘low-latitude’ (<37° N) and a ‘high-latitude’ group (>37° N), 37° N represents a convenient dividing line placed at the northern boundaries of Oklahoma, New Mexico and Arizona, and is the approximate boundary between the southern Great Plains and the northern Great Plains. We report data from more than 300 fossil equids from North America. The low-latitude group includes samples from Mexico, Florida, Texas, Oklahoma, New Mexico, Arizona and southern California. It shows a significant isotopic change in the late Hemphillian. All sites with ages older than 7 Myr have δ^{13}C values between −8‰ and −15‰, but are as high as −2.7‰ at 6.8 Myr at Coffee Ranch in northern Texas. Late Hemphillian sites in Mexico have δ^{13}C values up to +1.7‰ by 5.7 Myr. Equids in the low-latitude region of North America show considerable scatter in the δ^{13}C values, probably indicating a reliance on both C_3 and C_4 grasses possibly during different times of the year.

High-latitude sites from North America included Alaska, northern California, Idaho, Nebraska, Nevada, North Dakota, Oregon, South Dakota, Washington and Wyoming. Equids from these sites consumed a smaller fraction of C_4 biomass than did the low-latitude equids. This is to be expected because of the lower abundance of C_4 grasses in northern North America compared to southern North America[25]. Of the high-latitude sites, only those in Nebraska show significant C_4 biomass in the diet where one δ^{13}C enamel value reaches −3‰.

European sites in Fig. 2 are from Spain and France, between 38° and 48° N. Neither equids nor proboscideans show any evidence of a significant C_4 biomass in their diets at any time during the past 20 Myr. This is consistent with the dominance of C_3 plants in the region today, and agrees with data obtained from additional samples of equids and other ungulates from the eastern Mediterranean (for example, Samos, Pikermi, Pasalar)[26,27] and from Morocco and Algeria in North Africa (unpublished data). These data suggest that C_4 plants have not been a significant component of the biomass in western European or Mediterranean ecosystems at any time.

There is now evidence from four different widely separated regions (Pakistan, East Africa, low-latitude North America, and South America) for a significant expansion of C_4 biomass between about 8 and 6 Myr. All samples older than about 8 Myr have δ^{13}C values between −8‰ and −15‰, yet by 6.8 Myr regions have at least some δ^{13}C values that indicate a C_4-dominated diet (>−4‰), and reach $\delta^{13}\mathrm{C} \approx 0$‰ by about 5 Myr or earlier. Meanwhile, fossil hypsodont herbivores from high-latitude North America show a subdued increase of C_4 biomass in their diets, whereas those from Europe exhibit no increase. The pattern of dietary change with latitude (Fig. 3) in equids and proboscideans is compatible with conditions that would favour C_4 biomass in hotter regions, but conditions that also promote C_4 biomass expansion simultaneously in widespread parts of the globe. Figure 3 shows that we sampled both the northern and southern limbs of the C_3/C_4 transition, which is between about 25° and 40° latitude in both hemispheres. The high variability in the C_4 component of diet in such intermediate latitudes may be the result of several factors, such as the variability in growing season for different regions (for example, Mediterranean climates at about 35° have fewer C_4 plants than monsoonal climates at the same latitude), variability in C_4 biomass during different parts of the growing season (for example, spring versus summer conditions) or long-term climate fluctuations (for example, glacial versus interglacial). Equatorial sites show low isotopic variability for equid diets (Fig. 3).

Faunal change in the latest Miocene

The period in the late Miocene and Pliocene when we have identified significant change in diet was also a period of worldwide faunal change. Significant faunal turnover is observed in Pakistan,

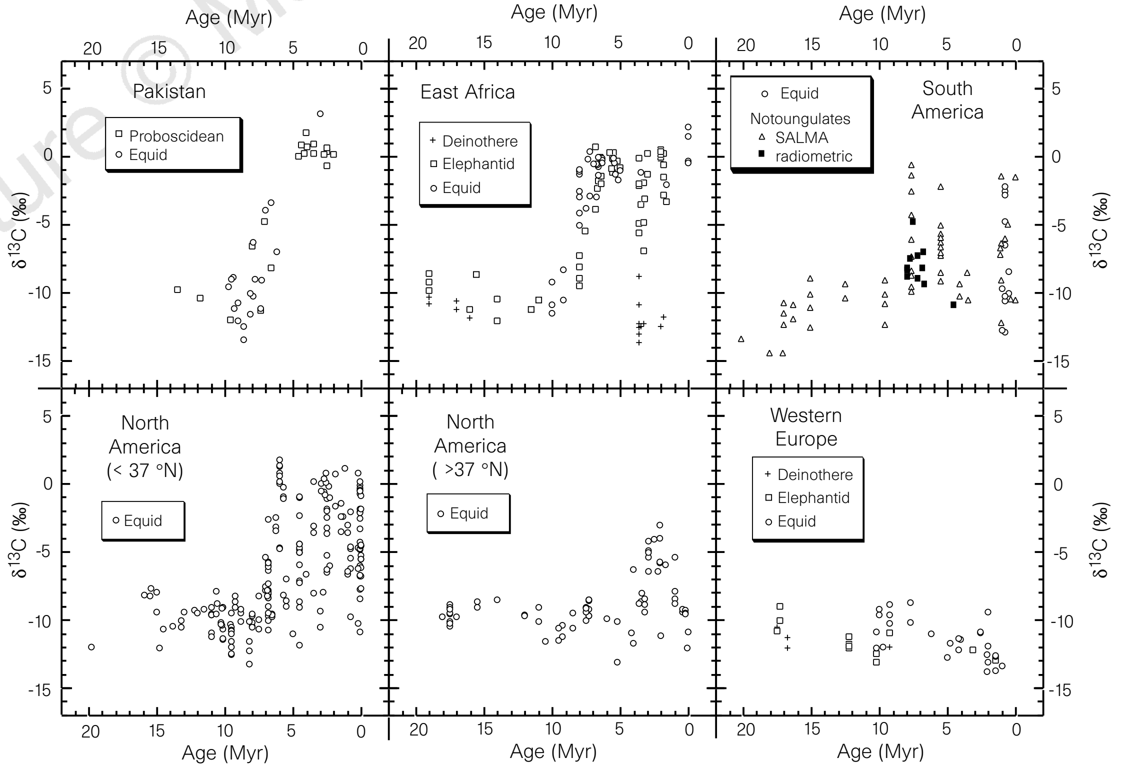

Figure 2 Changes in δ^{13}C of equid and some other hypsodont mammals in the Neogene. Although most of the data in this are new, we also include previously published data from Pakistan[8,9,41], North America[42], South America[24,43], and Africa[11,36]. South American samples in bold are samples from a well-dated site[24] and the others[43] are shown as the average age according to their respective South American Land Mammal Age (SALMA)[44].

Table 1 δ^{13}C values for modern mammals and their diet

δ^{13}C (‰)	Name	Name
Wild grazers, Athi plains, Kenya (year of death, 1969): estimated $\delta^{13}C_{diet}$, $-$ 11.4‰*		
3.1	Coke's hartebeest	*Alcelaphus buselaphus cokii*
1.9	Coke's hartebeest	*Alcelaphus buselaphus cokii*
3.0	Coke's hartebeest	*Alcelaphus buselaphus cokii*
3.2	Coke's hartebeest	*Alcelaphus buselaphus cokii*
3.8	Coke's hartebeest	*Alcelaphus buselaphus cokii*
2.9	Wildebeest	*Connochaetes taurinus albojubatus*
3.9	Wildebeest	*Connochaetes taurinus albojubatus*
3.2	Wildebeest	*Connochaetes taurinus albojubatus*
3.9	Wildebeest	*Connochaetes taurinus albojubatus*
3.7	Wildebeest	*Connochaetes taurinus albojubatus*
3.2 ± 0.6	($\delta^{13}C_{enamel} - \delta^{13}C_{diet} = 14.6$)‡	
Hogel Zoo animals: estimated $\delta^{13}C_{diet}$ $-$ 26.5‰ ($n = 5$)†		
–12.8	African elephant	*Loxodonta africana*
–12.7	African elephant	*Loxodonta africana*
–13.7	Bactrian camel	*Camelus bactrianus*
–12.9	Bactrian camel	*Camelus bactrianus*
–13.0	Giraffe	*Giraffa camelopardalis*
–12.0	Pigmy hippopotamus	*Choeropsis liberiensis*
–12.8	Pigmy hippopotamus	*Choeropsis liberiensis*
–12.0	Zebra	*Equus burchelli grantii*
–12.0	Zebra	*Equus burchelli grantii*
–12.4	Zebra	*Equus burchelli grantii*
$-$ 12.6 ± 0.5	($\delta^{13}C_{enamel} - \delta^{13}C_{diet} = 13.9$‰)‡	

Hartebeest and wildebeest of East Africa are hypergrazers and have δ^{13}C values 1–2‰ more positive than zebra of the same year of death and from the same location (unpublished data). The large mammals from the Hogel Zoo in Salt Lake City, Utah, all have a diet that is primarily meadow hay.

* The average δ^{13}C of C_4 grasses using the NADP sub-pathway is –11.4‰ (ref. 16). C_4 grasses in the Athi plains predominantly use this subpathway.

† Five samples of meadow hay and alfalfa pellets collected in 1991 give $\delta^{13}C = -26.5 \pm 0.7$‰. Year of death for these animals was between 1980 and 1990.

‡ The ~14.3% difference between diet and enamel is compatible with the data in Bocherens *et al.*[50]

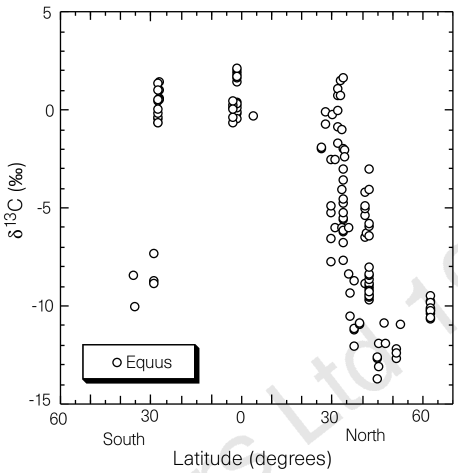

Figure 3 δ^{13}C of modern and fossil *Equus* versus latitude (all samples below 2,000 m elevation); we include data from Thackarey and Lee-Thorp[45] and data from Fig. 2. The equatorial dominance of C_4 grasses, the transition to C_3 grasses in intermediate latitudes (30–40°), and the dominance of C_3 grasses at high latitudes (~>45°), can be seen.

North America, South America, Europe and Africa. There has been debate as to whether such changes were in response to local climate change, immigration or other factors[13,28], but it is now clear from stable carbon isotope studies that an important global ecological change was underway at this time.

In Pakistan, many woodland-adapted mammals were replaced by more open-habitat representatives between 8 and 7 Myr (refs 29, 30). Tragulids are replaced by hypsodont artiodactyls, and true giraffes appear in the post-7.5 Myr assemblages, along with hippopotamid species[30]. After 7.4 Myr, local assemblages are dominated by hypsodont ungulates. Among the primates, *Sivapithecus* (a large-bodied hominoid) and lorisids became extinct in Asia between 8 and 7 Myr ago, their place eventually being taken by cercopithecids (Old World monkeys) that appeared in the latest Neogene[31]. Late Miocene changes among the small mammals include extinction of dormice, and the appearance of more open-adapted advanced rhyzomyids and hares[31].

In North America, equids reached their maximum diversity in the middle Miocene but their diversity was greatly reduced in the Hemphillian (late Miocene and earliest Pliocene, or about 7 to 4.5 Myr ago)[32,33]. Camelids, antilocaprids, palaeomerycids and gomphotheres were likewise greatly reduced in diversity during this interval. In general, the more hypsodont lineages from these families were favoured in the Pliocene. This Hemphillian episode of extinction was the most severe to be documented in the North American Neogene, exceeding in extent the late-Pleistocene extinction event[32].

East African mammal faunas showed a marked shift in their community structure during the Neogene[34,35]. Early Miocene mammalian faunas in east Africa had a tropical-forest character with common taxa including hominoids, hyraxes, suids, rhinos and proboscideans. The Pliocene witnessed a sharp increase in seasonality with the faunas evolving a savanna-mosaic character. Grazing antelopes and hippos replaced chevrotains and anthracotheres as the dominant artiodactyls. Among the perissodactyls, three-toed equids replaced the browsing rhinos and hyraxes. High-crowned elephantids replaced bunodont long-jawed gomphotheres. Monkeys underwent a major radiation, replacing the diverse early and middle Miocene hominoid assemblage. During the terminal Miocene, open wooded-grassland habitats replaced the earlier less seasonal woodland/forest habitats; the Lothagam fauna seems to be transitional between the archaic earlier Miocene and the advanced Plio-Pleistocene faunas[36].

It is now clear that the expansion of C_4 grasses was a global phenomena beginning in the late Miocene and persisting to the present day. It was accompanied by important faunal changes in many parts of the world. It is not likely that the expansion of C_4 biomass in the late Miocene is due solely to higher temperature or to the development of arid conditions. There have always been some parts of the Earth with hot, dry climates yet it seems that the C_4 expansion was triggered by a single phenomenon as this expansion occurred simultaneously in widespread regions of the world that were separated by oceans (for example, the Old World, South America, North America). Significantly, C_4 plants in the cooler parts of the planet did not respond as effectively as in the hotter regions. Thus the C_4 expansion is not documented in the enamel of equids and proboscideans from the late Miocene and early Pliocene of western Europe, although by the lower Ruscinian of Europe hipparions (that were so abundant in the Miocene) have virtually disappeared, probably because of changing climate conditions[37].

Quantum yields, temperature and atmospheric CO_2

Plant metabolism responds directly to atmospheric CO_2 concentrations[38,39]. C_3 plants respond to changes in atmospheric

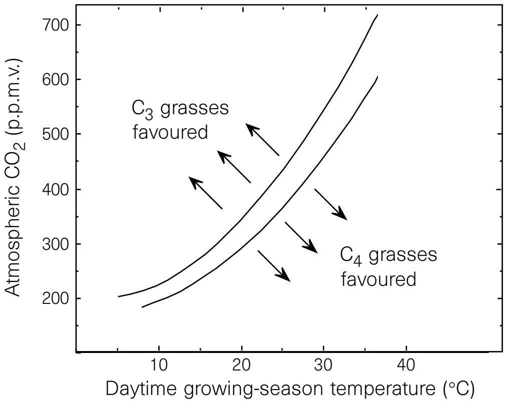

Figure 4 Results of a model for predicting C_3/C_4 dominance of grasses related to temperature and partial pressure of CO_2 according to which photosynthetic pathway has the greater quantum yield; here 'temperature' is the daytime growing-season temperature. This model is based on the equations of Farquhar and von Caemmerer[39] using constants determined by Jordan and Ogren[46]. Parameters of the model, including quantum yield-patterns of C_3 and C_4 grasses, have been verified by comparing the model results with published observations[47–49].

CO_2 with decreased maximum net photosynthetic rates that are related to lowered CO_2 levels because of both inherent CO_2 substrate limitations and higher photorespiration rates. C_4 plants are less sensitive to atmospheric CO_2 levels.

The quantum yield (photosynthetic efficiency) of C_3 grasses relative to C_4 grasses varies with both atmospheric CO_2 levels and temperature (Fig. 4). The crossover point favouring C_3 over C_4 grasses is dependent on temperature and partial pressure of CO_2 (p_{CO_2}) such that C_4-dominated ecosystems are favoured under low p_{CO_2} conditions when accompanied by elevated temperature. The modern world is a 'C_4-world' where C_4 plants make up an important biomass in tropical, sub-tropical and some temperate ecosystems. When atmospheric CO_2 levels are high, above about 500 p.p.m.v., the C_3 photosynthetic pathway would be favoured in all conditions except those with extremely high temperatures. The 'C_3-world', where C_4 plants do not make up a significant fraction of the biomass even in tropical regions, is predicted to have been the more productive pathway from the origin of terrestrial vascular plants at about 400 Myr ago until the late Miocene between 8 to 6 Myr when the 'C_4-world' became established. A possible exception to this could have been during the late-Carboniferous to Permian glaciation if p_{CO_2} levels were low enough and some plants independently evolved the C_4 pathway, which was subsequently lost in the Mesozoic when CO_2 levels were again high.

The model of Fig. 4 explains some interesting features of the temporal change in diets of mammals shown in Fig. 2 and in the spatial change in diets shown in Fig. 3. The change from C_3 to C_4 diet in equids occurred somewhat earlier in tropical regions than in higher latitudes. In East Africa (3° S to 5° N), the transition is very rapid and is complete between 8 to 7.5 Myr; in Pakistan (32–33° N) the transition is slightly more gradual and occurs between about 7.8 and 6 Myr; in southern North America (20–37° N) it takes place between 6.8 and 5.5 Myr; in central North America (Nebraska; 40–43° N) the oldest sample analysed so far with a definite C_4 signal is about 4 Myr and no samples have $\delta^{13}C$ values above −2‰; in western Europe (between 40° and 50° N), there is no indication of a C_4 diet at any time. This is compatible with a history where the 'crossover' of quantum yields favouring C_4 plants over C_3 plants was reached first at low latitudes, and at later times at successively higher latitudes (because of lower temperature) as atmospheric CO_2 levels declined during the Neogene. It further implies we are unlikely to find evidence for widespread C_4 plants in periods of the Earth's history where p_{CO_2} was higher than about 500 p.p.m.v.

The modern spatial pattern of C_4 and C_3 grasses shows that C_4 grasses dominate in tropical and subtropical regions, that the transition to C_3 grasses takes place between about 30° and 45° latitude, and that C_3 grasses dominate at high latitudes (Fig. 3). Figure 4 shows that the crossover for the modern atmospheric level of CO_2 (280 p.p.m.v. for the pre-industrial value of CO_2) is between 16 °C and 20 °C (daytime growing-season temperature), with C_3 grasses being favoured in cooler regions (such as high latitudes and high altitudes).

This model is compatible with gradually decreasing CO_2 in the atmosphere during the Tertiary, and crossing a threshold important to C_3 photosynthesis near the end of the Miocene. Changes in atmospheric CO_2 levels are related to continental weathering; increased weathering rates during the past 40 Myr, especially in the tectonically active Himalayan–Tibetan region, have resulted in a lowering of CO_2 (ref. 40). The culminating effect is a world where C_3 plants are increasingly starved by decreasing atmospheric CO_2 levels in the late Neogene, a world where C_4 plants have an advantage over C_3 plants in many environments.

This model also has important implications concerning the present glacial–interglacial period of Earth's history, and the future of the Earth where atmospheric CO_2 concentrations are increasing because of fossil fuel burning. First, this model implies that at very low CO_2 conditions, such as during the glacial periods, C_3 grasses would have been at a great disadvantage worldwide so that at intermediate and low latitudes an expansion of C_4 grasses would be expected. The CO_2 concentration minima of about 160 to 180 p.p.m.v., reached during the Last Glacial Maximum, seems to be near the limit for successful competition of C_3 grasses with respect to C_4 grasses. Second, this model implies that C_4 grasses will be at an increasing disadvantage as CO_2 levels increase owing to humankind's energy appetite, in agreement with other models. This has further evolutionary implications because the past 7 Myr of evolution, including the evolution of hominids, has been in the 'C_4-world'. By increasing atmospheric CO_2 concentrations humans may be changing the Earth's atmosphere to conditions not favourable to a 'C_4-world', which were the conditions in which they originally evolved. ☐

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