

Carbon dioxide starvation, the development of C₄ ecosystems, and mammalian evolution

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The decline of atmospheric CO₂ over the last 65 million years (Ma) resulted in the 'CO₂-starvation' of terrestrial ecosystems and led to the widespread distribution of C₄ plants, which are less sensitive to CO₂ levels than are C₃ plants. Global expansion of C₄ biomass is recorded in the diets of mammals from Asia, Africa, North America, and South America during the interval from about 8 to 5 Ma. This was accompanied by the most significant Cenozoic faunal turnover on each of these continents, indicating that ecological changes at this time were an important factor in mammalian extinction. Further expansion of tropical C₄ biomass in Africa also occurred during the last glacial interval confirming the link between atmospheric CO₂ levels and C₄ biomass response. Changes in fauna and flora at the end of the Miocene, and between the last glacial and interglacial, have previously been attributed to changes in aridity; however, an alternative explanation for a global expansion of C₄ biomass is CO₂ starvation of C₃ plants when atmospheric CO₂ levels dropped below a threshold significant to C₃ plants. Aridity may also have been a factor in the expansion of C₄ ecosystems but one that was secondary to, and perhaps because of, gradually decreasing CO₂ concentrations in the atmosphere. Mammalian evolution in the late Neogene, then, may be related to the CO₂ starvation of C₃ ecosystems.

Keywords: Neogene, carbon isotopes, CO₂, grassland, evolution

1. INTRODUCTION

Almost all terrestrial faunal changes in the late Miocene are attributed to changes in aridity. In this paper we instead argue that gradually decreasing levels of atmospheric CO₂ led to 'CO₂-starvation' of C₃ plants in tropical, subtropical, and even some temperate regions. This CO₂-starvation was directly responsible for the increase in C₄ biomass with important evolutionary consequences for terrestrial mammals, including the evolution of humans. In the past 20 years the importance of CO₂ requirements for different photosynthetic pathways has become evident. This recognition leads us to propose that CO₂ concentrations in the atmosphere, as well as other factors such as aridity, may be important in ecosystem change with subsequent consequences for the evolution of terrestrial mammals. We focus on the last 15 million years (Ma) of Earth history in this discussion.

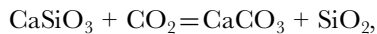
It has long been recognized that the last 6 to 8 Ma of Earth's terrestrial history are different from the entire previous history of Earth. Important changes in mammalian fauna have been recognized in both the Old World and the New World with the elements of modern faunas making their appearance in the Pliocene. In North America the Miocene Epoch was characterized by an increase in the number of equid genera in the Early to Middle Miocene (*ca.* 20 to 8 Ma) reaching a maximum of 12 genera, and by the development of hypsodonty (high crowned teeth) presumably to exploit grasses; this was followed by a crash in diversity in the latest Miocene,

with extinction of all but one genus by the Pleistocene (MacFadden 1992). Meanwhile, in Africa the great diversity and abundance of hominoid apes in the Miocene was reduced to a few apes, a few hominids, and an expansion of the monkeys. At the same time, a great diversity of bovids developed in Africa in the latest Miocene to early Pliocene (Vrba 1995). Faunal changes are conventionally attributed to increasing aridity in the late Miocene and early Pliocene. For example, in recent reviews of palaeoclimate and evolution (Janis 1993; Vrba *et al.* 1995), mammalian changes in Africa, Australia, Asia, North America, and South America are attributed primarily to aridity based on the recognition of mammals adapted to more open habitats. However, the geological evidence for aridity has not been very compelling (Bishop 1976). Geochemical investigation during the past decade has provided compelling evidence for the expansion of C₄ biomass, which consists of predominantly tropical to subtropical grasses and sedges, between 8 and 6 Ma (Cerling *et al.* 1993, 1997b).

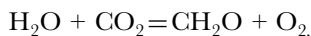
We review the history of atmospheric CO₂ over the last 100 Ma, discuss the implications for atmospheric CO₂ concentrations on the competition between C₃ and C₄ photosynthetic pathways, and then provide evidence that C₄ biomass expanded in tropical to temperate regions starting about 8 Ma. We show that important faunal changes occurred globally about the same time as the expansion of C₄ biomass, and that faunal and floral changes in the Pleistocene (including refugia in the tropics) may be related to effects of CO₂ starvation of C₃ plants.

2. HISTORY OF ATMOSPHERIC CO₂ IN THE LAST 100 MA

The concentration of carbon dioxide in the atmosphere is related to the injection of CO₂ into the atmosphere–hydrosphere due to volcanism, the extraction of CO₂ from the atmosphere by weathering and photosynthesis, and the burial of carbon in the oceans (Berner 1991, 1994). Important geochemical and biogeochemical reactions describing these reactions include:



and



where the first reaction describes weathering and the sink of carbon to the oceans in the form of carbonate sediments, and the second reaction describes the burial of organic carbon. For a planet with liquid water these reactions cause a net decrease in CO₂ in the planetary atmosphere over the life of the planet, as CO₂ in the atmosphere is converted to solids in the form of limestone or organic deposits. Tectonic movements, such as the uplift of the Himalayas due to the collision of the Indian subcontinent and the Asian continent, result in the consumption of prodigious amounts of CO₂ because of weathering (Raymo & Ruddiman 1992).

Although a detailed history of carbon dioxide in the atmosphere is still being developed, it is possible to place some important constraints on CO₂ concentrations at certain times in the Earth's history, with the result that general trends become apparent. The Mesozoic Era, from about 225 to 65 Ma is an interval of equable climate even in high latitudes. Global circulation models of the Cretaceous Period (145 to 65 Ma) show global warming compared to the present because of changes in ocean and continent configurations (Barron *et al.* 1989, 1993), but calculated temperatures for high latitude continental interiors are too low for the geological evidence. However, inclusion of significant amounts of greenhouse gases (e.g. $4 \times \text{CO}_2$; Barron *et al.* 1989, 1993) make the model runs compatible with temperatures based on geological evidence (palaeofloral and palaeofaunal analyses; Wolfe 1985). Berner (1991, 1994) modelled the carbon cycle and concluded that Cretaceous CO₂ levels were significantly higher than today's value of *ca.* 280 ppmv (the pre-Industrial Revolution value). Cerling (1991) proposed a palaeo-CO₂ (pCO₂) barometer based on diffusional transport of CO₂ in soils and its preservation as oxidized carbon in soils and palaeosols. The work of Cerling (Cerling 1991, 1997*b*; Ehleringer & Cerling 1995), and others (summarized in Berner (1997)), suggests that CO₂ levels for most of the Mesozoic were well above 1000 ppmv, and that the Cenozoic Era (65 Ma to the present) is characterized by lower levels than the Mesozoic, being less than 1000 ppmv. The results of this pCO₂ barometer, and others (stomatal densities, Kürschner *et al.* 1996; marine biomarkers, Freeman & Hayes 1992), indicate lower CO₂ levels for the last 65 Ma are in general agreement with Berner's model of CO₂ concentrations over the last 200 Ma.

The geological record of atmospheric CO₂ during glacial intervals is very well established for the last

200 000 years, and stable isotope studies of marine carbonates indicate a cyclicity that can be reasonably extrapolated to about 700 000 years ago. CO₂ concentrations in ice cores show that CO₂ levels in interglacial intervals were about 270 ppmv but about 180 ppmv during glacial maxima (Jouzel *et al.* 1987; Neftel *et al.* 1988; Leuenberger *et al.* 1992). These values are very robust as they are based on air preserved in bubbles in the ice cores. The glacial–interglacial cyclicity of the last 200 000 years in the ice cores correlates with isotope cyclicities in marine sediment cores. The periodicity of these cores extends back to about 700 000 years ago, when a different cyclicity becomes apparent (DeMenocal 1995). The last 700 000 years of Earth's climate has a dominant cycle of 110 000 years (a characteristic Milankovitch frequency), whereas from 0.7 to 2.4 Ma the 110 000 cycle is not apparent and is dominated by the secondary 21 000 and 41 000 cycles (also Milankovitch cycles).

The last major change in atmospheric CO₂ has been due entirely to humans whose appetite for energy, with the resultant fossil fuel burning, has resulted in an increase in atmospheric CO₂ levels from 280 ppmv in 1850 to over 360 ppmv today.

The history of CO₂ abundance in the atmosphere over the last 100 Ma, during which oscillations of CO₂ levels were imposed by orbital forcing, has been one of decline. This decline was probably driven in large part, by the uplift and weathering of the Himalayas which consumes a huge amount of carbon dioxide (Raymo & Ruddiman 1992). It is likely that the Himalayan uplift, like the proverbial straw which broke the camel's back, drove the present Earth system into a very low-CO₂ world. It is in this low-CO₂ world that humans evolved. A low-CO₂ world has important implications for photosynthesis because, as also will be shown, it led to CO₂ starvation of C₃ plants and their replacement by plants using the C₄ photosynthetic pathway which is more efficient in CO₂ starved conditions.

In summary, CO₂ levels were in the order of 1000 ppmv or higher at the end of the Cretaceous, some 65 Ma. The Cenozoic was an era of CO₂ decline, with the present-day glacial–interglacial oscillation being reached by 0.7 Ma. It is likely that CO₂ levels fluctuated from interglacial highs ranging between 250 and 300 ppmv to glacial lows ranging between 175 and 225 ppmv for the last 700 000 years with a cyclicity of about 110 000 years. In the last 150 years CO₂ levels have risen to over 350 ppmv, conditions not experienced on Earth in the previous million years or longer. Figure 1 shows a schematic diagram showing the general decrease in atmospheric CO₂ over the last 65 Ma.

3. EFFECT OF ATMOSPHERIC CO₂ ON PHOTOSYNTHESIS

There are three photosynthetic pathways used by plants, known as the C₃, the C₄ and the CAM pathways. The C₃ pathway is the least advanced pathway and was used by the earliest plants, from the early history of the Earth when CO₂ was the most abundant gas in the atmosphere to the present day. The C₄ and CAM pathway evolved more recently, apparently in response to lower atmospheric CO₂ levels (Ehleringer *et al.* 1991). C₃ plants make

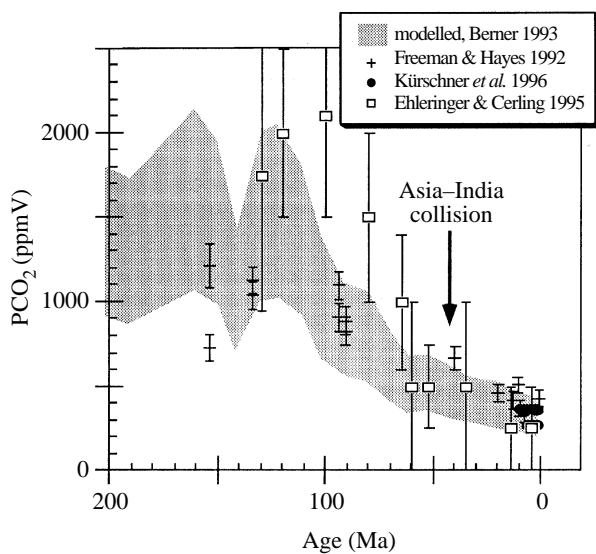


Figure 1. Modelled and calculated CO_2 levels from 200 Ma to the present. The model is from Berner (1991, 1994, 1997), and calculated values are based on marine biomarkers (Freeman & Hayes 1992), stomatal densities (Kürschner *et al.* 1996), and pedogenic carbonates (Ehleringer & Cerling 1995). Other modelling experiments (Barron *et al.* 1989, 1993) favour CO_2 levels > 1200 ppmv for the Cretaceous.

up most of the global biomass; C_4 plants make up about 18% of the global terrestrial productivity (based on data from Mellilo *et al.* (1993); summarized in Cerling (1997a)); and CAM plants have a lower global productivity than both C_3 and C_4 plants. Here, we will discuss the differences between C_3 and C_4 plants, although some of the principles apply to CAM plants as well.

There are two important aspects of photosynthetic efficiency that are of importance in this discussion. These are the inherent quantum yield of the pathways (and subpathways) under optimal conditions, and environmental conditions that reduce efficiency of the pathways (in particular, photorespiration). The quantum yield of CO_2 uptake in plants, which is the ratio of CO_2 molecules gained to the number of photons absorbed, is expected to be higher in C_3 plants than in C_4 plants because C_4 plants have extra energy requirements related to the regeneration of phosphoenol pyruvate from pyruvate in the first part of the C_4 cycle. However, the operation of the 'CO₂-pump' in C_4 photosynthesis has a net benefit—photorespiration is avoided. Under low CO_2 conditions the quantum yield of C_3 plants is reduced due to photorespiration where O_2 is absorbed and CO_2 is given off. In particular, high temperatures and low CO_2/O_2 ratios lead to increased photorespiration in C_3 plants.

Cerling *et al.* (1997) and Ehleringer *et al.* (1997) have modelled the 'crossover' for C_4 photosynthesis relative to C_3 photosynthesis for grasses and for dicots. This model is based on the model of Farquhar & von Caemmerer (1982) for leaf level photosynthesis, uses the parameters of Jordan & Ogren (1984), and experimentally measured quantum yields from a variety of studies (summarized in Ehleringer *et al.* (1997)). For modern levels of CO_2 (*ca.* 350 ppmv) and high temperature (*ca.* 30 °C), C_3 monocots and dicots have quantum yields of about $52 \mu\text{mol mol}^{-1}$, compared to *ca.*

$65 \mu\text{mol mol}^{-1}$ for NADP-me C_4 monocots. Other C_4 groups have lower quantum yields: NAD-me monocots have a quantum yield of about $60 \mu\text{mol mol}^{-1}$, and NADP-me and NAD-me dicots have quantum yields of about 60 and $53 \mu\text{mol mol}^{-1}$, respectively (Ehleringer *et al.* 1997).

While the quantum yield of C_4 photosynthesis is independent of temperature, that of C_3 photosynthesis is inversely related to temperature because of photorespiration. The crossover model of Cerling *et al.* (1997) and Ehleringer *et al.* (1997) indicates that C_4 monocots should be favoured over C_3 monocots and dicots above growing season temperatures of about 20–25 °C, which is corroborated by many studies (summarized in Ehleringer *et al.* (1997)).

Figure 2 shows the crossover model of Cerling *et al.* (1997) and Ehleringer *et al.* (1997). This model has important implications about ecosystems when considered in the light of the history of atmospheric CO_2 on Earth. The 'natural' level of CO_2 in Holocene interglacial conditions is about 270 ppmv (the pre-Industrial Revolution concentration), which is clearly in the range that represents CO_2 -starvation for C_3 plants in the warmer parts of the planet. In particular, such conditions favour the C_4 monocots; C_4 dicots are generally not favoured over C_3 dicots except during the interglacial CO_2 lows. A possible reason for the paucity of C_4 dicots may be that they were favoured only in the interglacial lows, which did not persist long enough for them to flourish (Ehleringer *et al.* 1997).

The Earth has been in this 'CO₂-starved' mode, where C_4 monocots make up a significant fraction of the Earth's total biomass, for some 7 Ma, a condition rarely (if ever) attained in the earlier history of the Earth's atmosphere. This paucity of CO_2 had enormous consequences on global ecosystems and evolution, as we will show below.

4. EVIDENCE OF C_4 EXPANSION

Two important intervals of C_4 expansion are evident in the geological record. (1) At the end of the Miocene there was a global expansion of C_4 biomass, probably when atmospheric CO_2 levels declined below about 500 ppmv; and (2) in some tropical and subtropical ecosystems during Pleistocene glacial maxima. In this section we will summarize the evidence for C_4 expansion in these two intervals of Earth's history.

(a) Latest Miocene to early Pliocene

Mammals are excellent indicators of the presence or absence of C_4 biomass in Cenozoic biotas because: (i) mammalian fossils are abundant in the geological record, (ii) mammalian tooth enamel preserves dietary preferences without modification by diagenesis, (iii) the isotopic composition of C_3 biomass is easily distinguished from C_4 biomass, and (iv) mammalian herbivores are selective feeders and their teeth should enhance any ecological signal provided by their diet.

The $\delta^{13}\text{C}$ of modern C_3 plants averages about -26.7‰ compared to that of C_4 plants which average about -12.5‰ (Bender 1971; Deines 1980; see also figure 3). Most of the analyses used to determine this distribution were collected in the 1970s to 1990s, after the atmosphere had changed by about 1.5‰ compared to the

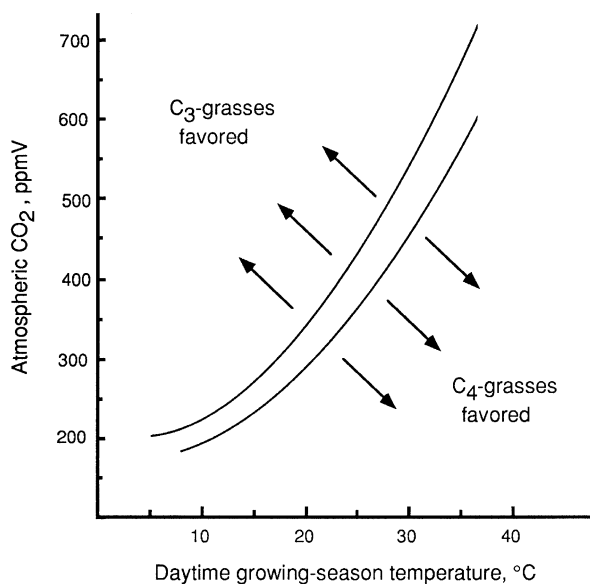


Figure 2. Crossover model of C_3/C_4 photosynthesis based on quantum yield of C_3 and C_4 plants. Modified from Cerling *et al.* (1997) and Ehleringer *et al.* (1997).

pre-Industrial Revolution value because of fossil fuel burning (Friedli *et al.* 1986), so that it is likely that pre-1850 plants are also enriched in ^{13}C by about 1.5‰ compared to modern plants (Marino & McElroy 1991). Therefore the $\delta^{13}C$ of ancient C_3 and C_4 plants probably had average values of about -25‰ and -11‰ , respectively. C_3 plants have a large variation in $\delta^{13}C$ values with ^{13}C depleted C_3 plants being found under closed canopy conditions (-30 to -35‰ ; van der Merwe & Medina 1989) and ^{13}C enriched plants (-24 to -22‰) being found in water stressed environments (Farquhar *et al.* 1989; Ehleringer *et al.* 1993). The isotopic composition of modern tooth enamel is about 14.3‰ enriched compared to their diet (Cerling *et al.* 1997b), so that mammals with average C_3 - and C_4 -diets have $\delta^{13}C$ values of about -12.4‰ and $+1.8\text{‰}$, respectively. However, mammals do not select 'average' $\delta^{13}C$ plants, but select from what is available. Thus modern mammals from closed canopy settings have $\delta^{13}C$ values from about -16 to -22‰ , whereas browsers from water stressed environments would have $\delta^{13}C$ values of about -10 to -8‰ . In East Africa the teeth of the hypergrazer *Connochaetes taurinus albojubatus* (white-bearded wildebeest) today have $\delta^{13}C$ values averaging $+3.5\text{‰}$ (Cerling *et al.* 1997b) because of its exclusive diet of C_4 plants using the NADP-subpathway ($\delta^{13}C$ ca. 11.4‰ ; Hattersley 1982). Due to the anthropogenic isotope effect, we would expect these values to be shifted by about 1.5‰ for wildebeest recovered from the fossil record.

Therefore $\delta^{13}C$ values characteristic of an unambiguous presence of C_4 biomass are more positive than ca. -8‰ for modern mammals, and may be as high as -7‰ for fossil mammals (the higher value is because of the uncertainty in the isotopic composition of the atmosphere, but assuming that its $\delta^{13}C$ value was similar to the pre-1850 atmosphere). Figure 3 shows the analyses of 226 mammals with ages >8 Ma from Europe, North America, South America, Asia, and Africa; all except

one sample has $\delta^{13}C < -8\text{‰}$ so that this sample suite which includes a very wide variety of large mammals (bovids, camelids, equids, notoungulates, proboscideans, rhinocerotids, suids, tapirids), does not indicate a significant (above the ' C_3 -cutoff') component of C_4 biomass in the diet for any of the animals. It is possible that some of the mammals with the more positive $\delta^{13}C$ values did have a diet including C_4 biomass, but it cannot be assumed to be so. For example, Cerling *et al.* (1997a) analysed equids from the Red Rock Canyon locality in North America (12 Ma), a site of well documented C_4 plants (Tidwell & Nambudiri 1989), but find $\delta^{13}C$ values of about -9 to -10‰ —indicating at best a minor component of C_4 biomass in the diet (and possibly no C_4 biomass).

Between 8 and 6 Ma there was a global expansion of C_4 ecosystems (Cerling *et al.* 1997b). There is no conclusive evidence for the presence of C_4 biomass in the diets of mammals before 8 Ma (figures 3 and 4) assuming a 'cutoff' of -8‰ , although the presence of C_4 biomass in diets is not excluded because of the uncertainty in the $\delta^{13}C$ endmember for C_3 plants. By 6 Ma there is abundant evidence for significant C_4 biomass in Asia (Cerling *et al.* 1993, 1997; Morgan *et al.* 1994), Africa (Morgan *et al.* 1994; Cerling *et al.* 1997), North America (Cerling 1993; MacFadden & Cerling 1996; Cerling *et al.* 1998), and South America (MacFadden *et al.* 1996; Latorre *et al.* 1997; Cerling *et al.* 1997), but not in Europe (Cerling *et al.* 1997). Figure 4 shows several different patterns of floral change as recorded in mammalian tooth enamel: Pakistan has a C_3 ecosystem that is almost completely replaced by a C_4 ecosystem; Africa has both C_3 -browsers and C_4 -grazers with only a few mixed feeders; North America has many mixed feeders, possibly because of the presence of both C_3 and C_4 grasses in regions with relatively cool growing seasons; Europe does not show any change in the fraction of C_3 biomass, remaining at virtually 100% C_3 .

Stable isotope studies of palaeosols from Pakistan and from East Africa are in good agreement with the palaeo-dietary studies. The Siwalik sequence in Pakistan has excellent exposures covering the last 20 Ma. $\delta^{13}C$ studies of palaeosol carbonates show a virtually pure C_3 ecosystem up to about 7.5 Ma, a transitional period of ecosystem change lasting 1–1.5 Ma, and then C_4 -dominated ecosystems from 6 Ma to nearly the present (Quade *et al.* 1989; Quade & Cerling 1995). Studies of fossil eggshell show that C_3 plants were present throughout the sequence, even in the last 6 Ma (Stern *et al.* 1994). Studies of palaeosols in the Turkana Basin, covering in detail the period from about 7.5 Ma to the present, show mixed C_3/C_4 ecosystems throughout this period (Cerling *et al.* 1988, 1998).

(b) *Glacial–interglacial*

The other interval when important changes in the proportion of C_4 biomass occurred is during the Pleistocene glacial–interglacial transitions. Figure 2 shows that at very low CO_2 levels C_4 photosynthesis can be favoured even at low temperatures. The oscillation between glacial and interglacial conditions reflected an oscillation between about 180 and 280 ppmv, respectively, based on the CO_2 concentrations in the Greenland and Antarctic ice cores (Jouzel *et al.* 1987; Neftel *et al.* 1988; Leuenberger *et al.* 1992). The temperature change between

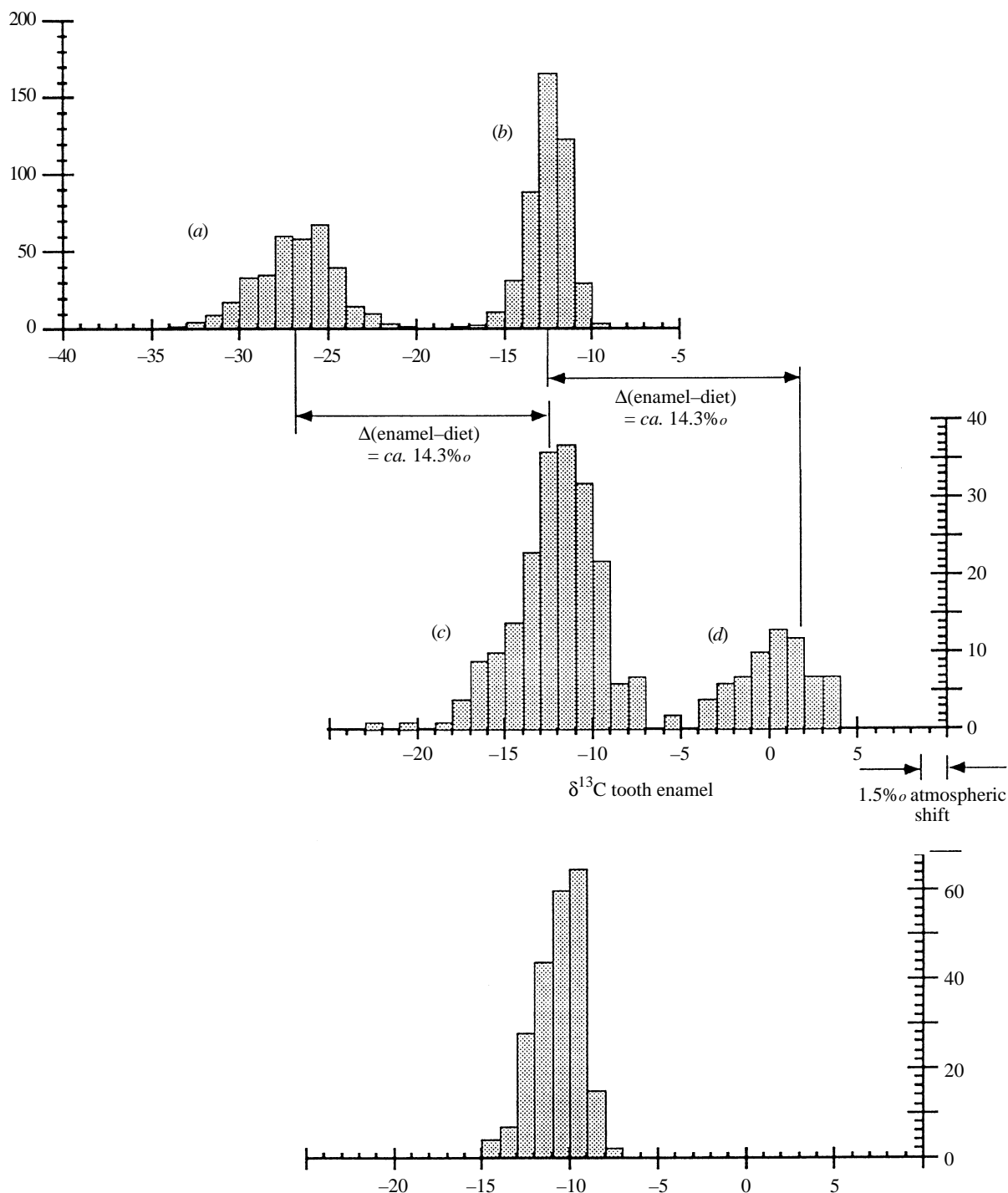


Figure 3. $\delta^{13}\text{C}$ values for: (a) modern C_3 plants ($\delta^{13}\text{C}$, $-26.7 \pm 2.7\text{‰}$, $n=370$); (b) modern C_4 plants ($\delta^{13}\text{C}$, $-12.5 \pm 1.1\text{‰}$, $n=455$); (c,d) modern mammals with a C_3 -dominated diet and C_4 -dominated diet, respectively; and (e) fossil mammals older than 8 Ma ($\delta^{13}\text{C}$, $-10.6 \pm 1.1\text{‰}$, $n=226$). (Modified from Cerling *et al.* 1997.)

the glacial and interglacial intervals varied globally, with estimate ΔT s of about 5°C in the tropics (Stute *et al.* 1995) to $>15^\circ\text{C}$ in the polar regions (Cuffey *et al.* 1995). Therefore the $\Delta\text{CO}_2/\Delta T$ gradient in the tropics was about $20\text{ ppm }^\circ\text{C}^{-1}$, compared to about $7\text{ ppm }^\circ\text{C}^{-1}$ at high latitudes. The slope of the C_3/C_4 crossover is on the order of $12\text{ ppm }^\circ\text{C}^{-1}$ (figure 2) and it is possible that in some regions more C_4 plants are to be expected in glacial conditions compared to interglacial conditions because the CO_2 starvation is more important than the temperature effect. Ehleringer *et al.* (1997) examined published reports of $\delta^{13}\text{C}$

in peat bogs and lakes from Central and East Africa and found evidence for extensive C_4 expansion during the last full glacial (figure 5). This implies extensive retreat of the African rain forest and has important implications for refugia during the Pleistocene which is discussed below.

5. IMPLICATIONS FOR MAMMALIAN EVOLUTION

Terrestrial environments on all continents (except Antarctica) underwent major changes in fauna at the end of the Miocene, an interval of major ecological change

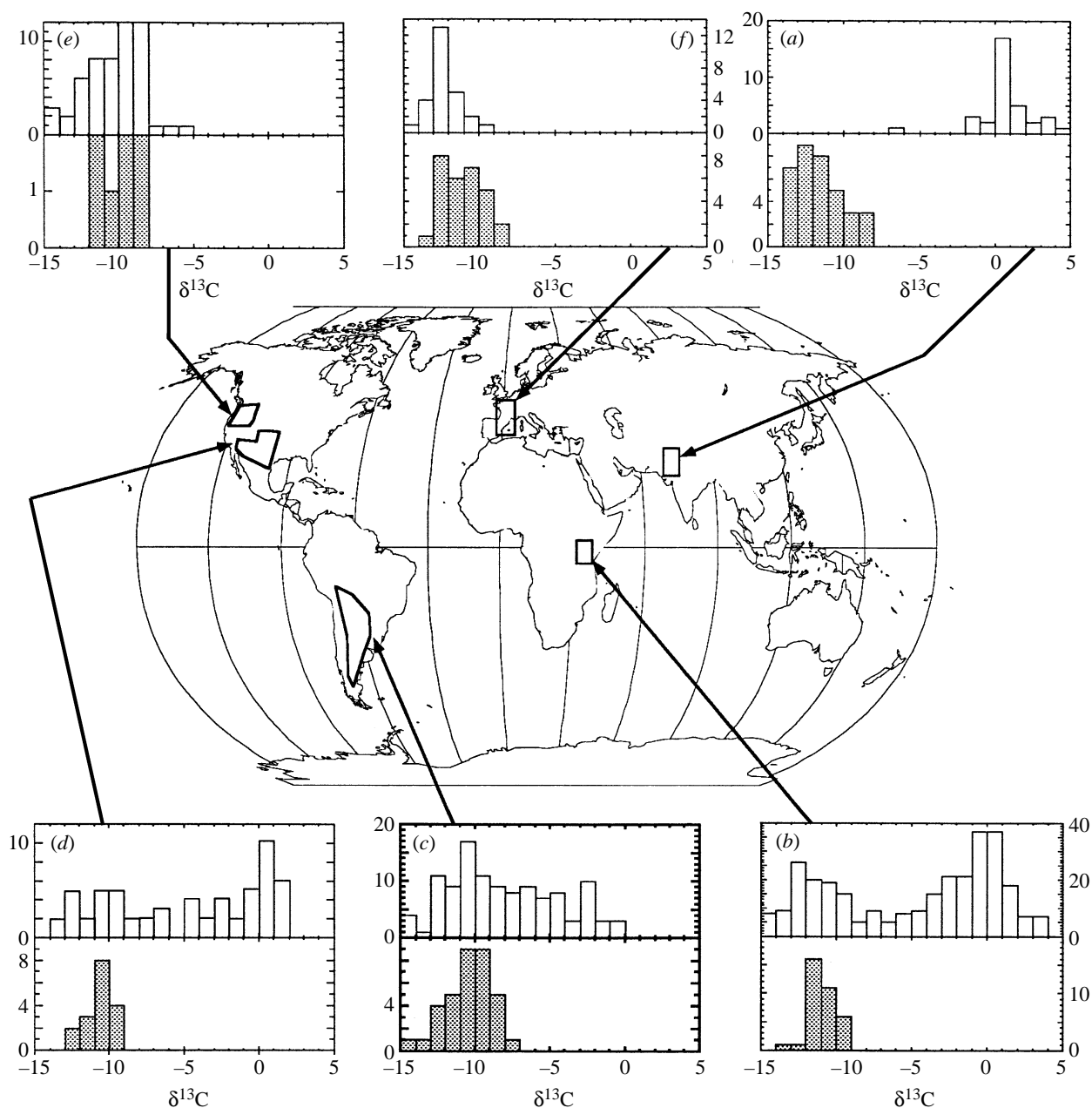


Figure 4. Histograms comparing $\delta^{13}\text{C}$ values for fossil tooth enamel older than 8 Ma (lower half of charts) with those that are younger than 6 Ma (upper half of charts) for (a) Pakistan, (b) East Africa (Kenya), (c) South America, (d) southwestern North America, (e) northwestern America, and (f) Europe. All regions have a C_3 -dominated, and perhaps exclusive C_3 diet before 8 Ma. In Pakistan the younger fauna is almost exclusively C_4 -grazers; in East Africa the younger fauna has mammals that are generally either C_3 -dominated or C_4 -dominated with a few mixed feeders; southwestern North America shows mixed feeders, as well as exclusive C_3 and C_4 -diets; in Europe and in the northwestern America the younger fauna retains a C_3 -diet: in South America both C_3 and C_4 diets are evident after 6 Ma. Data from Cerling (1997b), MacFadden *et al.* (1996), and unpublished data measured at the University of Utah.

that is most clearly expressed by a global increase in C_4 biomass. The traditional explanation for most of these faunal changes involves a component of aridity or global drought, mainly based on the occurrence of mammals adapted to open habitats (e.g. Janis 1993; Avery 1995; Webb *et al.* 1995), or the recognition of the expansion of grasslands (e.g. Axelrod 1985). We suggest in this paper that the drought was a 'CO₂ drought' which caused global changes in flora and, subsequently, in fauna. Changes in precipitation may have accompanied some of these changes, but the primary driver for floral change was gradually decreasing CO₂ levels in the atmosphere. It is

plausible that changes in the chemistry of the atmosphere would affect all continents, but it is hard to see why most parts of the world would undergo a trend to aridity at about the same time.

(a) *Differential herbivory in mammals*

Differential herbivory in mammals, insects, and other animal groups is likely to be an important factor in the coevolution of plants and their herbivores leading to the evolution of entire ecosystems (Ehleringer & Monsoon 1993). Such transition in habitats is not simply a matter of substituting C_3 biomass for C_4 biomass because leaf protein

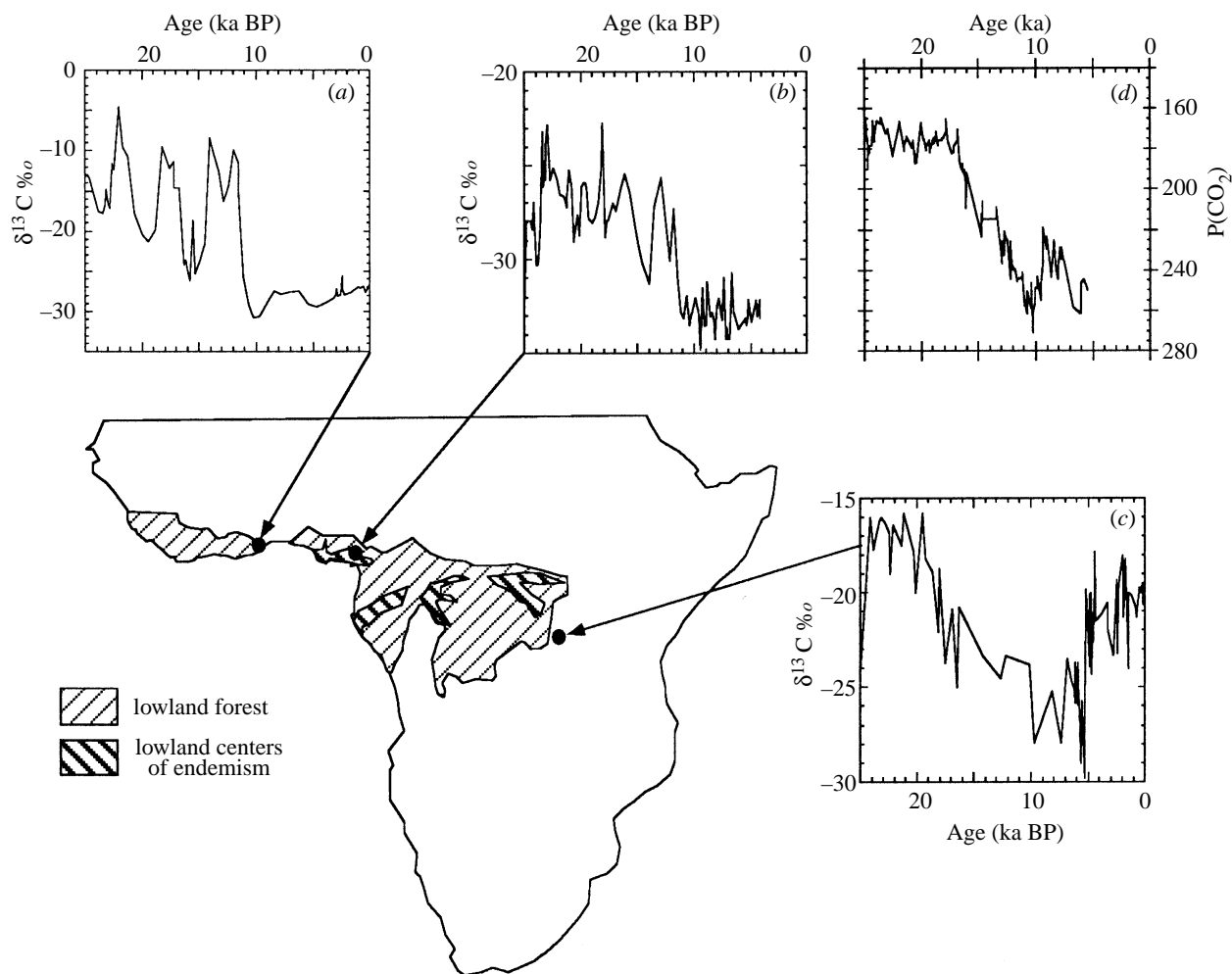


Figure 5. Chronological profiles of $\delta^{13}\text{C}$ of organic matter in (a) Lake Bosumtwi (Ghana; Talbot & Johannessen 1992), (b) Lake Barombi Mbo (Cameroon; Giresse *et al.* 1994), and (c) the Kashiri peat bog (Burundi; Aucour *et al.* 1994). These are near the edge of the lowland forest region, which had four main centres of endemism in the late Quaternary (Kingdon 1989). These three areas all had more extensive C_4 biomass during full glacial conditions (30 000 to 20 000 years ago), than during the Holocene (10 000 years ago to the present). (d) CO_2 concentrations from Antarctic ice cores (Byrd) are shown (data from Neftel *et al.* 1985). The scale is reversed to show the similarity in timing of the CO_2 decrease and C_3 expansion from 18 to 12 thousand years ago.

in C_4 plants tends to be concentrated in the bundle sheath cells which have thicker cell walls than mesophyll cells, thereby protecting the leaf protein and making the bundle sheath cells less digestible than mesophyll cells. Within the C_4 plants NAD-me plants have short and cubical bundle sheath cells, whereas those of the NADP-me plants are long and rectangular (Brown 1974), making the NADP-me bundle sheath cells more easily crushed. Furthermore, C_3 plants and NADP-me C_4 plants often contain toxic secondary metabolites, whereas NAD-me plants rarely contain toxic secondary metabolites. Preferential herbivory of $\text{C}_3 > \text{NADP-me} > \text{NAD-me}$, or the opposite, has been observed probably due to the factors mentioned above (Ehleringer & Monsoon 1993).

Within C_4 grasses, the subtype NADP-me (which tend to be the tall grasses) is more sensitive to aridity than the NAD-me subtype (the short grasses) which predominate in the more arid regions (Hattersley 1992). The distribution and availability of the different C_4 subtypes according to climate, coupled with herbivory preferences for C_3 or for the different C_4 plants, may be an important

factor in the evolutionary trends of mammals. The fossil record is notably silent on the history of the C_4 -subpathway differentiation, but the trends noted here provide food for thought about the well preserved mammalian fossil record.

(b) Faunal changes in the late Miocene and Pliocene

In southern Asia, middle to late Miocene floras were predominantly moist woodlands, and were replaced by dryland forests by 7.5 Ma (Prasad 1993). The best dated and studied faunal sequence of the Siwaliks is in Pakistan where woodland-adapted mammals were replaced by more open habitat representatives between 8 and 7 Ma (Barry 1995; Barry & Flynn 1990). Tragulids are replaced by hypsodont artiodactyls, and true giraffes appear in the post-7.5 Ma assemblages, along with hippopotamid species. After 7.4 Ma, local assemblages are dominated by hypsodont ungulates. Among the primates, cercopithecoids become dominant, replacing *Sivapithecus* (a large bodied hominoid) and lorisids. Late Miocene changes among the small mammals include extinction of dormice,

and the appearance of more open-adapted advanced rhyzomyids and hares (Barry & Flynn 1990). These faunal changes are considered to be consistent with a global episode of cooling and increasing aridity (Barry 1995). An intriguing aspect of the faunal change in the Pakistan Siwalik sequence is that the mammalian herbivore assemblage changes from a C₃-dominated to a C₄-dominated diet, apparently reflecting total replacement of the prevailing vegetation (figure 4). In North and South America and East Africa a substantial proportion of the herbivorous assemblages retain a C₃ or mixed diet after the radiation of the C₄ biomass (figure 4).

North American faunas and floras undergo considerable change in the late Neogene. The change to the North American Steppe is traditionally thought to be related to increasing aridity (Axelrod 1985; Wolfe 1985). Equids reach their maximum diversity in the Middle Miocene, and undergo a diversity crash at the end of the Miocene (MacFadden 1992). 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 over the Miocene. The early Hemphillian was characterized by an invasion of migratory forms from Eurasia and South America, many of which perished in a mid-Hemphillian extinction episode (Tedford *et al.* 1987). Equids first exploited C₄ vegetation in the late Hemphillian, although Kranz structure has been documented in fossil plants of Clarendonian age (Tidwell & Nambudiri 1989). The terminal Hemphillian episode of extinction was the most severe documented in the record of North American land mammal genera (Webb *et al.* 1995). Once again, the 'usual suspect' is blamed: widespread aridity and deteriorating climate conditions.

East African mammal faunas exhibit a marked shift in their community structure during the Neogene. Early Miocene mammalian faunas in East Africa had a tropical forest character and local assemblages were characterized by hominoids, hyraxes, suids, rhinos, and proboscideans (Andrews & Van Couvering 1975). During the terminal Miocene, open wooded grassland habitats replaced the earlier less seasonal woodland-forest habitats and were exploited by an entirely new suite of mammals that included the ancestors of the extant mammalian assemblages. Grazing antelopes and hippos replaced chevrotains and anthracotheres as the dominant artiodactyls. Among the perissodactyls, three-toed equids replaced the browsing rhinos. Elephantids with high crowned teeth replaced bunodont long-jawed gomphotheres. Monkeys underwent a major radiation, with cercopithecoids replacing the diverse early and middle Miocene hominoid assemblage. The premise that the history of the Hominidae is bound up with the development of savanna vegetation in Africa is gaining acceptance (Avery 1995), and indeed a few rare and fragmentary specimens from late Miocene deposits at Lothagam and Lukeino hint at the emergence of our own family. The Pliocene witnessed a sharp increase in seasonality with the faunas evolving a savanna-mosaic character and it is from early Pliocene localities in Ethiopia and northern Kenya respectively that the oldest recognizably human representatives *Ardipithecus ramidus* and *Australopithecus anamensis* have been recovered (White *et al.* 1994; Leakey *et al.* 1995). Figure 6

shows the ranges of some of the significant taxa in East African assemblages over the last 20 Ma, and shows that the modern assemblage was essentially in place by about 5 Ma.

It is interesting that the East African grazers did not exploit the C₄ biomass simultaneously but sequentially. There seems to be evidence from the Lothagam and Samburu Hills sequences, for example, that perissodactyls were the first to exploit the C₄ biomass, followed by the proboscideans, suids and bovids (Harris & Cerling 1996). In figure 6 the three most ¹³C-depleted hipparions are from Nakali (*ca.* 10 Ma) and all younger ones have significantly higher δ¹³C values; *Nyanzachoerus* records a change from a C₃-dominated diet to a C₄-dominated diet in the Lothagam and Omo-group sediments; the oldest *Stegatrabelodon* are more depleted in ¹³C than younger ones.

Although we have not yet sampled Australian faunas, we note that one of the major intervals of faunal turnover was between 8 and 5 Ma and that forests were replaced by open woodlands and arid habitats (Archer *et al.* 1995). Archer *et al.* (1995) note that 'the events that tugged bipedal humans out of the forests and into the African savanna and bipedal kangaroos into the Australian savanna may well have been driven by the same global engine of climatic change'. These authors also noted that a major innovative phase of what they interpreted as xeric-adapted lineages started or accelerated some time between 6 and 4.5 Ma. The Australian landscape is thought to have gradually changed from a forested habitat to an arid habitat, with widespread aridity appearing about 2 Ma. This is compatible with a decrease in atmospheric CO₂ levels, where the C₄ plants (which in Australia includes grasses, sedges, and some C₄ dicots) expanded their respective ranges throughout the late Neogene.

In each of these widely separated parts of the world there is a notable change from more forested conditions to more open habitat at the end of the Miocene. Although in many cases drought has been implicated there is little evidence for drought conditions *per se*. However, there is now evidence for widespread expansion of C₄ biomass at the end of the Miocene. It is known that the competition between C₃ and C₄ plants depends very much on atmospheric CO₂ levels. We suggest therefore that the conditions that led to a fundamental change in global ecology were CO₂ starvation of the terrestrial biosphere, brought on in large part by the complex interaction of sea-floor spreading, silicate weathering, and sediment burial (Berner 1991, 1994), and compounded by the increased weathering due to the uplift of the Himalayas (Raymo & Ruddiman 1992).

Ten years ago, Hill (1987) noted 'it is hard to justify global climate change as the sole explanation of observed faunal shifts... As yet there is no convincing demonstration of synchronicity in faunal turnover. Evidence of a simple shift from forest conditions to grasslands, an event that has been correlated with the origins of hominid bipedalism, is hard to detect'. Ten years prior to that, Bishop (1976) concluded that 'cold water must be poured on the notion of Pliocene aridity'. There is now a great accumulation of evidence pointing to global ecological change in the late Miocene, driven by gradual CO₂ starvation of C₃ plants and their replacement by C₄ plants.

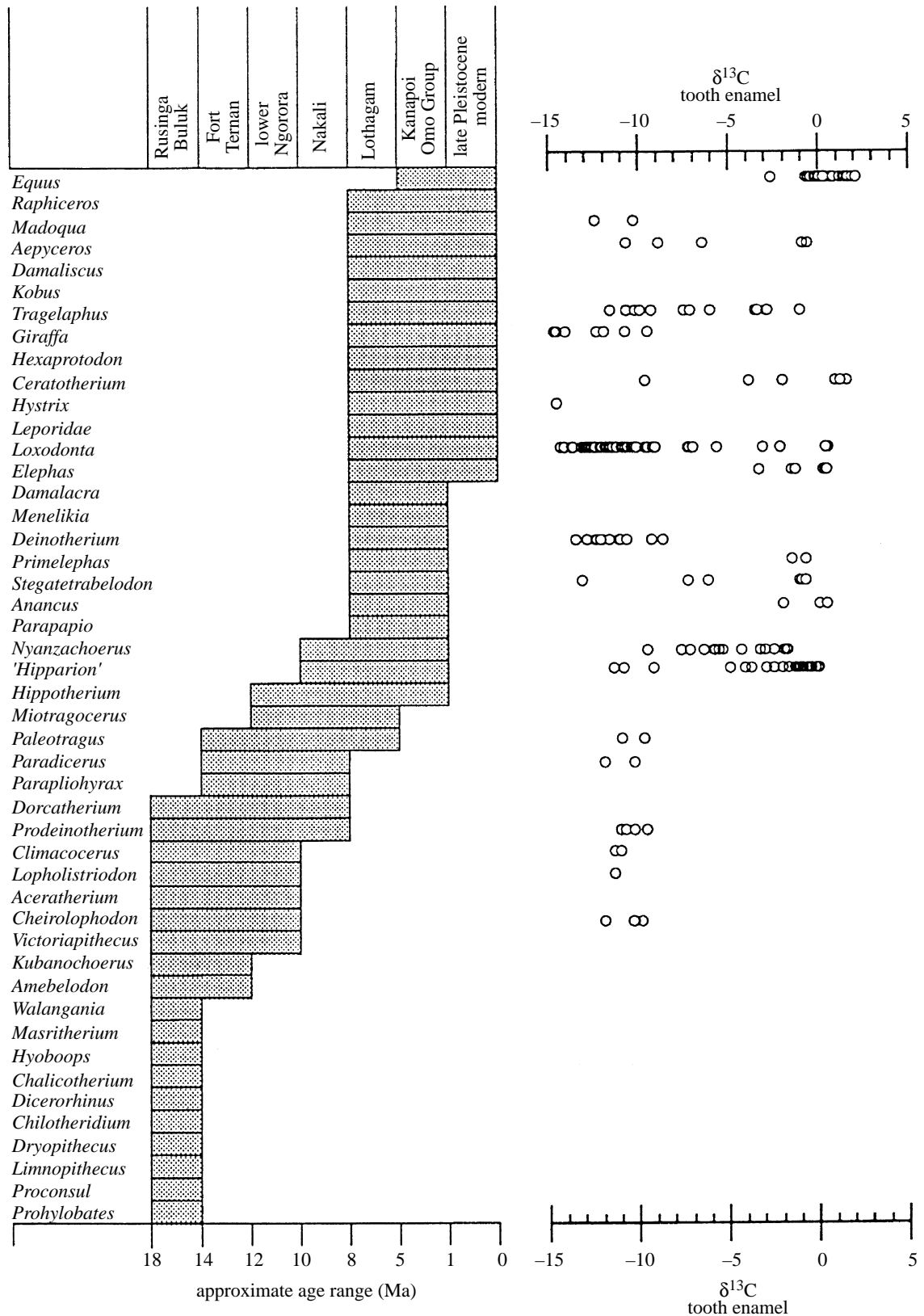


Figure 6. First and or last appearances of some significant taxa in East Africa from about 20 Ma to the present (modified from Leakey *et al.* 1996) and $\delta^{13}\text{C}$ values for tooth enamel for African mammals. Samples older than 8 Ma have $\delta^{13}\text{C}$ values characteristic of a pure C_3 -diet, whereas the assemblage after 8 Ma shows that the herbivores had diets generally close to the C_3 end member (*ca.* -8 to -15‰) or close to the C_4 end member (*ca.* -1 to $+4$). Many (but not all) of the transitional $\delta^{13}\text{C}$ values are between 6 and 8 Ma.

Although evidence for a change from 'forest' to 'grassland' is equivocal and it is difficult to make a strong case for global aridity based on the geological evidence, the evidence for replacement of C₃ biomass by C₄ biomass over vast areas of low and intermediate latitudes is overwhelming. Global ecological changes in the same direction can be recognized over a very limited time span, and essentially 'modern' faunas are found by the latest Miocene to early Pliocene in many parts of the world (Janis 1993). We contend that the modern 'C₄-world', where C₄ plants make up a significant part of the global biomass and where ungulate grazers make up a major part of faunal assemblages, may be a result of the 'CO₂ starvation' of C₃ plants.

(c) *Refugia in the tropics and other Pleistocene problems*

The tropical rainforest of Zaire is thought to be presently much larger than many times in the past, where it shrunk to the extent that it split into several different refugia. Kingdon (1989) recognizes at least three major lowland refugia in the Zaire basin and three major highlands on the margins of the Basin. The restriction of the tropical rainforest previously has been attributed to aridity. However, we explore the idea that CO₂ starvation of C₃ plants during glacial intervals could be a major cause of the contraction of the rainforest. However, because of globally lower temperatures and reduced evaporation from the oceans during these glacial maxima, it is possible that reduced rainfall accompanied these episodes.

Figure 5 shows δ¹³C profiles from lakes or bogs from three regions of equatorial Africa that are now forested but had a significant C₄ biomass during full glacial conditions: these are in lowland Ghana, lowland Cameroon and highland Burundi. The glacial–interglacial temperature change in equatorial regions is estimated to be about 5 °C (Stute *et al.* 1995). The ΔCO₂/ΔT gradient in the tropics then is estimated to be 100 ppm 5 °C⁻¹ which is a low enough gradient that in some environments there would be a 'crossover' in the quantum yields for C₄ grasses versus C₃ plants (see figure 2; Ehleringer *et al.* 1997). Thus, in full glacial conditions C₄ grasslands are expected to expand in the tropics at high and low elevations in response to changing CO₂ levels. Therefore the isolation leading to refugia may be directly linked to atmospheric CO₂ levels and the CO₂ starvation of C₃ dicots and monocots. Decreased rainfall in the full glacial maxima, due to decreased sea surface temperatures, may have accompanied the change further favouring C₄ grasses adapted to water stressed conditions.

It is tempting to describe some of the faunal features ascribed to the refugia hypothesis to CO₂ starvation in glacial conditions. This may provide an explanation for the distribution of some of the tropical faunas such as the two chimpanzees, *Pan troglodytes* and *Pan paniscus* which are separated by the Zaire River. On the other hand, some apparent reversals must be considered: in Africa some of the giant artiodactyl grazers became extinct in the Pleistocene and *Loxodonta* and *Diceros* (bush/forest types) replaced *Elephas* and *Ceratotherium* (plains grazing types). Having sampled the fossil record, we find that the fossil *Loxodonta* was predominantly a grazer but that the modern *Loxodonta* is primarily a browser (Harris &

Cerling 1996); could the return to browsing by *Loxodonta* be due to competition from overwhelming numbers of efficient grazing bovinds?

In North America the great extinction affecting large mammals (including *Equus*, *Mammot*, *Mammuthus*) at the end of the Pleistocene has been variously attributed to human overkill (e.g. Martin 1990) or increased seasonality. The vegetation changes observed during the Pleistocene and discussed elsewhere in this paper raise the possibility of a different mechanism: ecological change due to CO₂ stress.

The expansion and contraction of tropical forests due to CO₂ forcing through the glacial and interglacial intervals can be tested once suitable sediment accumulations are located in other tropical regions outside of Africa. Other localities where glacial–interglacial temperature changes were small may also exhibit a similar ecological trend to that of tropical Africa. A number of different studies have been initiated to document changes in diets and in palaeoecology using stable isotopes in well dated sequences—the key to their success will be the quality of the geological record and the ability to date the samples accurately.

6. CONCLUDING REMARKS

Geological evidence and arguments indicate that atmospheric CO₂ levels have been generally declining over the last 65 Ma or longer from values more than 1000 ppmv at the end of the Cretaceous to glacial and interglacial levels between about 200 and 300 ppmv, respectively, in the last 1 Ma. Physiological studies of plants show that C₃ plants become increasingly less efficient under low atmospheric CO₂ levels, especially when accompanied by high temperatures, leading to conditions where C₄ plants have a higher efficiency than C₃ plants. Stable isotope studies of mammalian diets show that there was a global increase of C₄ biomass in the latest Miocene to earliest Pliocene (8 to 5 Ma), a time when faunas similar to the modern type replaced faunas adapted to more closed habitats in many parts of the world. Stable carbon isotope studies of lake sediments and bogs from tropical regions show that in some tropical environments C₄ plants were more abundant under the cooler glacial conditions than under warmer interglacial conditions. Previously, the changes noted in faunas and floras at the end of the Miocene and between glacial and interglacial intervals have been attributed to aridity changes. However, these observations are also consistent with a model of CO₂ starvation of C₃ biomass in the late Cenozoic up to the present day.

Although the CO₂-starvation hypothesis is attractive, much needs to be done to study the interaction between the atmosphere, biosphere, and geosphere. Detailed studies of the chronology of faunal dietary change are needed to establish the details of timing in different parts of the world. These should be accompanied by morphological studies of mammals to understand adaptive changes made to accommodate new dietary and habitat possibilities during the transition from C₃-dominated to C₄-dominated ecosystems. Palaeobarometers of atmospheric CO₂, with longer preservation potential than ice cores, must be developed for levels below 1000 ppmv CO₂.

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REFERENCES

- Andrews, P. & Van Couvering, J. A. H. 1975 Palaeoenvironments in the East African Miocene. In *Approaches to primate palaeobiology* (ed. F. Szalay), pp. 62–103. Basel: Karger.
- Archer, M., Hand, S. J. & Godthelp, H. 1995 Tertiary environmental and biotic change in Australia. In *Paleoclimate and evolution, with emphasis on human origins* (ed. E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle), pp. 77–90. New Haven, CT: Yale University Press.
- Avery, D. M. 1995 Micromammalian studies; information from the past of relevance to the future. *Trans. R. Soc. S. Afr.* **50**, 41–47.
- Aucour, A.-M. & Hillaire-Marcel, C. 1993 A 30 000 year record of ^{13}C and ^{18}O changes in organic matter from an equatorial bog. *Am. Geophys. Monogr.* **78**, 343–351.
- Axelrod, D. I. 1985 Rise of the grassland biome, Central North America. *Bot. Rev.* **51**, 163–201.
- Barron, E. J., Hay, W. W. & Thompson, S. 1989 The hydrologic cycle: a major variable during Earth history. *Palaeo. Palaeo. Palaeo.* **75**, 157–174.
- Barron, E. J., Fawcett, P. J., Pollard, D. & Thompson, S. 1993 Model simulations of Cretaceous climates: the role of geography and carbon dioxide. *Phil. Trans. R. Soc. Lond. B* **341**, 307–316.
- Barry, J. C. 1995 Faunal turnover and diversity in the terrestrial Neogene of Pakistan. In *Paleoclimate and evolution, with emphasis on human origins* (ed. E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle), pp. 115–134. New Haven, CT: Yale University Press.
- Barry, J. C. & Flynn, L. J. 1990 Key biostratigraphic events in the Siwalik sequence. In *European neogene mammal chronology* (ed. E. H. Lindsay, V. Fahlbasch, & P. Mein), pp. 557–571. New York: Plenum.
- Bender, M. M. 1971 Variations in the $^{13}\text{C}/^{12}\text{C}$ ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. *Phytochemistry* **10**, 1239–1245.
- Berner, R. A. 1991 A model for atmospheric CO_2 over Phanerozoic time. *Am. J. Sci.* **291**, 339–376.
- Berner, R. A. 1994 GEOCARB II; a revised model of atmospheric CO_2 over Phanerozoic time. *Am. J. Sci.* **294**, 56–91.
- Berner, R. A. 1997 The rise of plants and their effect on weathering and atmospheric CO_2 . *Science* **276**, 544–545.
- Bishop, W. W. 1976 Pliocene problems relating to human evolution. In *Human origins* (ed. G. Ll. Isaac & E. R. McCown), pp. 139–153. Menlo Park, CA: W. A. Benjamin.
- Brown, W. V. 1974 Another cytological difference among the Kranz subfamilies of the Graminae. *Bull. Torrey Bot. Club* **101**, 120–124.
- Cerling, T. E. 1991 Carbon dioxide in the atmosphere: evidence from Cenozoic and Mesozoic paleosols. *Am. J. Sci.* **291**, 377–400.
- Cerling, T. E. 1997a Late Cenozoic vegetation change, atmospheric CO_2 , and tectonics. In *Tectonic uplift and climate change* (ed. W. F. Ruddiman), Plenum. (In the press.)
- Cerling, T. E. 1997b Stable carbon isotopes in paleosol carbonates. In *Palaeoweathering, palaeosurfaces, and related continental deposits* (ed. M. Thiry & R. Simon-Coinçon). Int. Assoc. of Sedimentologists, Spec. Publ. (In the press.)
- Cerling, T. E., Bowman, J. R. & O'Neil, J. R. 1988 An isotopic study of a fluvial-lacustrine sequence: the Plio-Pleistocene Koobi Fora sequence, East Africa. *Palaeo. Palaeo. Palaeo.* **63**, 335–356.
- Cerling, T. E., Wang, Y. & Quade, J. 1993 Expansion of C_4 ecosystems as an indicator of global ecological change in the late Miocene. *Nature* **361**, 344–345.
- Cerling, T. E., Harris, J. M. & MacFadden, B. J. 1997a Carbon isotopes, diets of North American equids, and the evolution of North American C_4 grasslands. In *Stable isotopes and the integration of biological, ecological, and geochemical process* (ed. H. Griffiths, D. Robinson & P. Van Gardingen). Oxford: Bios Scientific. (In the press.)
- Cerling, T. E., Harris, J. M., MacFadden, B. J., Leakey, M. G., Quade, J., Eisenmann, V. & Ehleringer, J. R. 1997b Global change through the Miocene/Pliocene boundary. *Nature* **389**, 153–158.
- Cuffey, K. M., Clow, G. D., Alley, R. B., Stuiver, M., Waddington, E. D. & Saltus, R. W. 1995 Large Arctic temperature change at the Wisconsin-Holocene glacial transition. *Science* **270**, 455–458.
- Deines, P. 1980 The isotopic composition of reduced organic carbon. In *Handbook of environmental isotope geochemistry. I. The terrestrial environment*, A (ed. P. Fritz & J. C. Fontes), pp. 329–406. Amsterdam: Elsevier.
- DeMenocal, P. B. 1995 Plio-Pleistocene African climate. *Science* **270**, 53–59.
- Ehleringer, J. R. & Cerling, T. E. 1995 Atmospheric CO_2 and the ratio of intercellular to ambient CO_2 concentrations in plants. *Tree Physiol.* **15**, 105–111.
- Ehleringer, J. R. & Monsoon, R. K. 1993 Evolutionary and ecological aspects of photosynthetic pathway variation. *A. Rev. Ecol. Syst.* **24**, 411–439.
- Ehleringer, J. R., Sage, R. F., Flanagan, L. B. & Pearcy, R. W. 1991 Climate change and the evolution of C_4 photosynthesis. *Trends Ecol. Evol.* **6**, 95–99.
- Ehleringer, J. R., Hall, A. E. & Farquhar, G. D. (eds) 1993 *Stable isotopes and plant/carbon/water relations*. San Diego, CA: Academic.
- Ehleringer, J. R., Cerling, T. E. & Helliker, B. R. 1997 C_4 photosynthesis, atmospheric CO_2 , and climate. *Oecologia* **112**, 285–299.
- Farquhar, G. D. & Van Caemmerer, S. 1982 Modeling of photosynthetic response to environmental conditions. *Encycl. Plant Physiol.* **D12**, 549–587.
- Farquhar, G. D., Ehleringer, J. R. & Hubrick, K. T. 1989 Carbon isotopic discrimination and photosynthesis. *A. Rev. Plant Physiol. Molec. Biol.* **40**, 503–537.
- Freeman, K. H. & Hayes, J. M. 1992 Fractionation of carbon isotopes by phytoplankton and estimates of ancient CO_2 levels. *Global Biogeochem. Cycl.* **6**, 185–198.
- Friedli, H., Lotscher, H., Oeschger, H., Siegenthaler, U. & Stauffer, B. 1986 Ice core record of the $^{13}\text{C}/^{12}\text{C}$ ratio of atmospheric CO_2 in the past two centuries. *Nature* **324**, 237–238.
- Giresse, P., Maley, J. & Brenac, P. 1994 Late Quaternary palaeoenvironments in Lake Barombi Mbo (West Cameroon) deduced from pollen and carbon isotopes in organic matter. *Palaeo. Palaeo. Palaeo.* **107**, 65–78.
- Harris, J. M. & Cerling, T. E. 1996 Isotopic changes in the diet of African Proboscideans. *J. Vert. Paleol.* **16**, 40A.
- Hattersley, P. W. 1982 ^{13}C values of C_4 types in grasses. *Aust. J. Plant Physiol.* **9**, 139–154.
- Hattersley, P. W. 1992 C_4 photosynthetic pathway variation in grasses (Poaceae): its significance for arid and semi-arid lands. In *Desertified grasslands: their biology and management*, pp. 181–212. The Linnean Society of London.
- Hill, A. 1987 Causes of perceived faunal change in the Neogene of East Africa. *J. Hum. Evol.* **16**, 583–596.
- Janis, C. M. 1993 Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *A. Rev. Ecol. Syst.* **24**, 467–500.
- Jordan, D. B. & Ogren, W. L. 1984 The CO_2/O_2 specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase. *Planta* **161**, 308–313.
- Jouzel, J., Lorius, C., Petit, J. R., Genthon, C., Barkov, N. I., Kotlyakov, V. M. & Petrov, V. M. 1987 Vostok ice core: a

- continuous isotope temperature record over the last climate cycle (160 000 years). *Nature* **329**, 403–408.
- Kingdon, J. 1989 *Island Africa: the evolution of Africa's rare animals and plants*. Princeton, NJ: Princeton University Press.
- Kurschner, W. M., Van der Burgh, J., Visscher, H. & Dilcher, D. L. 1996 Oak leaves as biosensors of late Neogene and early Pleistocene paleoatmospheric CO₂ concentrations. *Marine Micropaleontol.* **27**, 299–312.
- Latorre, C., Quade, J. & McIntosh, W. C. 1997 The expansion of C₄ grasses and global change in the late Miocene: stable isotope evidence from the Americas. *Earth Planet. Sci. Lett.* **146**, 83–96.
- Leakey, M. G., Feibel, C. S., McDougall, I. & Walker, A. 1995 New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* **376**, 565–571.
- Leakey, M. G., Feibel, C. S., Bernor, R. L., Harris, J. M., Cerling, T. E., Stewart, K. M., Stoops, G. W., Walker, A., Werdelin, L. & Winkler, A. J. 1996 Lothagam: a record of faunal change in the Late Miocene of East Africa. *J. Vert. Paleol.* **16**, 556–570.
- Leuenberger, M., Siegenthaler, U. & Langway, C. C. 1992 Carbon isotope composition of atmospheric CO₂ during the last ice age from an Antarctic ice core. *Nature* **357**, 488–490.
- MacFadden, B. J. 1992 *Fossil horses: systematic, paleobiology and evolution of the family Equidae*. New York: Cambridge University Press.
- MacFadden, B. J. & Cerling, T. E. 1996 Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10 million-year sequence from the Neogene of Florida. *J. Vert. Paleol.* **16**, 103–115.
- MacFadden, B. J., Cerling, T. E. & Prado, J. 1996 Cenozoic terrestrial ecosystem evolution in Argentina: evidence from carbon isotopes of fossil mammal teeth. *Palaio* **11**, 319–327.
- Marino, B. D. & McElroy, M. B. 1991 Isotopic composition of atmospheric CO₂ inferred from carbon in C₄ plant cellulose. *Nature* **349**, 127–131.
- Martin, P. S. 1990 Who or what destroyed our mammoths? In *Megafauna & man; discovery of America's heartland* (ed. L. D. Agenbroad, J. I. Mead & L. W. Nelson), pp. 109–117. Flagstaff, AZ: North Arizona University Press.
- Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B. III, Vorosmarty, C. J. & Schloss, A. L. 1993 Global climate change and terrestrial net primary production. *Nature* **363**, 234–240.
- Morgan, M. E., Kingston, J. D. & Marino, B. D. 1994 Carbon isotope evidence for the emergence of C₄ plants in the Neogene from Pakistan and Kenya. *Nature* **367**, 162–165.
- Neftel, A., Oeschger, H., Staffelback, T. & Stauffer, B. 1988 CO₂ record in the Byrd ice core 50 000–5000 years BP. *Nature* **331**, 609–611.
- Prasad, M. 1993 Siwalik (Middle Miocene) woods from the Kalgargh area in the Himalayan foothills and their bearing on paleoclimate and phytogeology. *Rev. Paleobot. Palynol.* **76**, 49–82.
- Quade, J. & Cerling, T. E. 1995 Expansion of C₄ grasses in the late Miocene of northern Pakistan: evidence from stable isotopes in paleosols. *Palaeo. Palaeo. Palaeo.* **115**, 91–116.
- Quade, J., Cerling, T. E. & Bowman, J. R. 1989 Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature* **342**, 163–166.
- Raymo, M. E. & Ruddiman, W. F. 1992 Tectonic forcing of late Cenozoic climate. *Nature* **359**, 117–122.
- Stern, L. A., Johnson, G. D. & Chamberlain, C. P. 1994 Carbon isotope signature of environmental change found in fossil ratite eggshells from a South Asian Neogene sequence. *Geology* **22**, 419–422.
- Stute, M., Forster, M., Frischkorn, H., Serejo, A., Clark, J. F., Schlosser, P., Broecker, W. S. & Bonani, G. 1995 Cooling of tropical Brazil (5 °C) during the last glacial maximum. *Science* **269**, 379–383.
- Talbot, M. R. & Johannessen, T. 1992 A high resolution palaeoclimatic record for the last 27 500 years in tropical west Africa from the carbon and nitrogen isotopic composition of lacustrine organic matter. *Earth Planet. Sci. Lett.* **110**, 23–37.
- Tedford, R. H., Skinner, M. F., Fields, R. W., Rensberger, J. S., Whistler, D. P., Galusha, T., Tayler, B. E., Macdonald, J. R. & Webb, S. D. 1987 Faunal succession and biochronology of the Arikarean through Hemphillian interval (Late Oligocene through earliest Pliocene epochs) in North America. In *Cenozoic mammals of North America* (ed. M. D. Woodburne), pp. 153–210. Berkeley: University of California Press.
- Tidwell, W. D. & Nambudiri, E. M. V. 1989 *Tomlinsonia thomasonii*, gen. et sp. nov., a permineralized grass from the upper Miocene Ricardo Formation, California. *Rev. Paleobot. Palynol.* **60**, 165–177.
- Van der Merwe, N. J. & Medina, E. 1989 Photosynthesis and ¹³C/¹²C ratios in Amazon rain forests. *Geochim. Cosmochim. Acta* **53**, 1091–1094.
- Vrba, E. S. 1995 The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In *Paleoclimate and evolution, with emphasis on human origins* (ed. E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle), pp. 385–424. New Haven, CT: Yale University Press.
- Vrba, E. S., Denton, G. H., Partridge, T. C. & Burckle, L. H. (eds) 1995 *Paleoclimate and evolution, with emphasis on human origins*. New Haven, CT: Yale University Press.
- Webb, S. D., Hulbert, R. C. & Lambert, W. D. 1995 Climatic implications of large-herbivore distributions in the Miocene of North America. In *Paleoclimate and evolution, with emphasis on human origins* (ed. E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle), pp. 91–108. New Haven, CT: Yale University Press.
- White, T. D., Suwa, G. & Asfaw, B. 1994 *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* **371**, 306–312.
- Wolfe, J. A. 1985 Distribution of major vegetational types in the Tertiary. *Am. Geophys. Union Monogr.* **32**, 357–375.

Discussion

D. J. BEERLING (*Department of Animal and Plant Sciences, University of Sheffield, UK*). You suggest that the switch from C₃- to C₄-dominated ecosystems is due to the decline of atmospheric CO₂ over the past 10 Ma. This concerns me in two ways. First, the evidence for a dramatic drop in CO₂ is not as clear as suggested, and second, the absolute values are also unclear and could range from 1500–500 ppm. Over this CO₂ range the photosynthetic systems of both C₄ and C₃ plants are largely saturated. Furthermore, experiments exposing naturally occurring C₃ and C₄ species to CO₂ enrichment have shown, contrary to expectations, that C₄ plants did better than C₃ plants (Owensby *et al.* 1993). These considerations, therefore, point more towards some other explanation for the isotopic changes documented—aridity being the most likely. To what extent are you able to exclude this possibility?

T. E. CERLING. We are not arguing for a dramatic drop in atmospheric CO₂ between 8 and 6 Ma, but rather for CO₂ falling below a threshold that is important to C₃ plants. We suspect that this threshold is between 400 and 600 ppmv CO₂ for the modern atmosphere having 21% O₂.

The Owensby (1993) experiment was conducted on a water-stressed system and does not represent all conditions globally. Other studies (reviewed by Poorter *et al.* 1996)

find that in general, but not always, C₃ plants respond better than C₄ plants to increased CO₂. On a global scale, it may be important to consider how the relationship between water use efficiency and atmospheric CO₂ levels affects the ability of C₃ or C₄ plants to adapt to arid climates and to displace other plants.

We argue against aridity being the primary cause of the expansion of C₄ ecosystems for several reasons. First, there have always been places on Earth that have been arid and sometimes there has been widespread aridity. Yet during periods when the geological evidence of aridity is compelling (e.g. the Triassic), there is no evidence for C₄ plants. Second, much of the evidence for aridity is based on evidence for open habitat or for the presence of grasses. We have shown that grasses, and hence open habitats, can be caused by CO₂ changes so that aridity is not necessarily the primary driver in the expansion of C₄ ecosystems. Third, an abrupt expansion of C₄ biomass is seen at about the same time in Africa, Asia, North America, and South America. If the aridity is the primary reason then

presumably it must have been a rapid change to more arid conditions in these widespread parts of the world. Fourth, preliminary evidence suggests that the C₄ expansion occurred in the tropics slightly before the higher latitudes. This is compatible with gradually declining levels of CO₂ so that the 'crossover' favouring C₄ monocots occurs first in the tropics and is followed by the cooler temperate latitudes. There is no model that suggests that a sudden change to more arid conditions should occur in Asia, North America, South America, and Africa and that it should follow such a pattern.

- Owensby, C. E., Coyne, P. I., Ham, J. M., Auen, L. M. & Knapp, A. K. 1993 Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO₂. *Ecol. Applic.* **3**, 644–653.
- Poorter, H., Roumet, C. & Campbell, B. D. 1996 Interspecific variation in the growth response of plants to elevated CO₂: a search for functional types. In *Carbon dioxide, populations and communities* (ed. C. Körner & F. A. Bazzaz), pp. 375–412. San Diego: Academic.

