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Photosynthetic Pathways and Climate

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1. Introduction

Other chapters in this volume have explored carbon cycles within and among ecosystems, especially their response to the global changes that are occurring on earth today. In this chapter, the focus shifts from factors that influence carbon flux dynamics to the ways in which the composition of the atmosphere and thermal environment influence the type of photosynthetic system that predominates within a terrestrial ecosystem. In turn, the kind of photosynthetic system present has significant impacts on the distribution of the grazing animals that are dependent on primary productivity generated across the landscape, both in the short-term and over evolutionary time periods.

Three photosynthetic pathways exist in terrestrial plants: C_3, C_4, and CAM photosynthesis (Ehleringer and Monson, 1993). C_3 photosynthesis is the ancestral pathway for carbon fixation and occurs in all taxonomic plant groups. C_4 photosynthesis occurs in the more advanced plant taxa and is especially common among monocots, such as grasses and sedges, but not very common among dicots (Ehleringer *et al.*, 1997; Sage and Monson, 1999). CAM photosynthesis occurs in many epiphytes and succulents from very arid regions, but is sufficiently limited in distribution so that CAM plants are not an appreciable component of the global carbon cycle. Therefore, this chapter will focus on the factors influencing the dynamics of C_3- and C_4-dominated ecosystems.

Photosynthesis is a multistep process in which the C from CO_2 is fixed into stable organic products. In the first step, RuBP carboxylase-oxygenase (Rubisco) combines RuBP (a 5C molecule) with CO_2 to form two molecules of phosphoglycerate (PGA, 3C molecule). However, Rubisco is an enzyme capable of catalyzing two distinct reactions: one leading to the formation of two molecules of PGA when CO_2 is the substrate and the other resulting in one molecule each of PGA and phosphoglycolate (PG, 2C molecule) when O_2 is the substrate (Lorimer, 1981). The latter oxygenase reaction results in less net carbon fixation and eventually leads to the production of CO_2 in a process known as photorespiration:

$$\text{RuBP} + CO_2 \rightarrow \text{PGA}$$
$$\text{RuBP} + O_2 \rightarrow \text{PGA} + \text{PG}$$

The proportion of the time for which Rubisco catalyzes CO_2 versus O_2 is dependent on the $[CO_2]/[O_2]$ ratio; the reaction is also temperature-dependent, with oxygenase activity increasing with temperature. This dependence of Rubisco on the $[CO_2]/[O_2]$ ratio establishes a firm link between current atmospheric conditions and photosynthetic activity. As a consequence of Rubisco sensitivity to O_2, the efficiency of the C_3 pathway decreases as atmospheric CO_2 decreases.

C_4 photosynthesis represents a biochemical and morphological modification of C_3 photosynthesis to reduce Rubisco oxygenase activity and thereby increase the photosynthetic rate in low-CO_2 environments such as we have today (Ehleringer *et al.*, 1991; Sage and Monson, 1999). In C_4 plants, the C_3 cycle of the photosynthetic pathway is restricted to interior cells within the leaf (usually the bundle-sheath cells). Surrounding the bundle-sheath cells are mesophyll cells in which a much more active enzyme, PEP carboxylase, fixes CO_2 (but as HCO_3^-) into oxaloacetate, a C_4 acid. The C_4 acid diffuses to the bundle-sheath cell, where it is decarboxylated and refixed in the normal C_3 pathway. As a result of the higher activity of PEP carboxylase, CO_2 is effectively concentrated in the regions where Rubisco is located and this results in a high CO_2/O_2 ratio and limited photorespiratory activity.

When the focus is on ecosystem processes, an appropriate question to ask might be, "Why be concerned about the fact that different photosynthetic pathways exist?" There are several important and clear answers to this question. First, C_3 and C_4 species are capable of giving quite different photosynthetic rates and primary productivity rates, even when grown under similar environmental conditions (Sage and Monson, 1999). Second, morphological and possibly defensive-compound differences between C_3 and C_4 species lead to differences in feeding preferences among herbivores (Caswell *et al.*, 1973; Ehleringer and Monson, 1993; Sage and Monson, 1999). Third, photosynthetic pathways among intensively managed ecosystems, such as pastures and agricultural crops, differ in both productivity and water-use efficiency, exhibiting strong geographical tendencies that reflect climatic variations. Last, the natural distributions of both C_3 and C_4 species exhibit strong relationships with both atmospheric CO_2 and climate, suggesting that future plant distributions need not be similar to today's distributions.

2. A Physiological Basis for C_3/C_4 Plant Distributions

Photorespiration impacts both maximum photosynthetic rate and photosynthetic light-use efficiency (Björkman, 1966; Ehleringer and Björkman, 1977; Ehleringer and Pearcy, 1983; Sage and Monson, 1999). One consequence is that light-use efficiency or quantum yield for CO_2 uptake differ between C_3 and C_4 taxa (Ehleringer and Björkman, 1977). The quantum yield is defined as the slope of the photosynthetic light-response curve at low light levels. As the total leaf area within a canopy increases, an increasing proportion of the canopy-level carbon gain is influenced by light-use efficiency because the light level that the average leaf within the canopy is exposed to reduces with increasing total leaf area. The reduced quantum yield values in C_4 taxa are tempertature independent and reflect the additional ATP costs associated with operation of the C_4 cycle (Hatch, 1987; Kanai and Edwards, 1999). In contrast, the quantum yield values of C_3 taxa are reduced as temperatures increase, because Rubisco oxygenase activity increases with temperature. As a consequence, for any given set of atmospheric CO_2 and O_2 conditions, the light-use efficiency of C_3 plants will exceed that of C_4 plants at lower air temperatures and will fall below that of C_4 plants at higher temperatures.

Cerling *et al.* (1997) and Ehleringer *et al.* (1997) modeled the effects of variations in C_3 /C_4 quantum yields on predicted photosynthetic carbon gain under different environmental combinations of atmospheric CO_2 and temperature. They predicted that as atmospheric CO_2 levels decreased, C_4 photosynthesis should become increasingly more common because of its higher light-use efficiency (Fig. 1).This model predicts that C_3 plants predominated during periods of the earth's history when atmospheric CO_2 levels were above ~ 500 ppmV. Plants with the C_4 pathway are predicted to have a selective advantage only in the warmest ecosystems at atmospheric CO_2 levels close to 500 ppmV. However, as atmospheric CO_2 levels decrease further, the advantage of C_4 photosynthesis and C_4 dominance are predicted to drift toward cooler habitats.

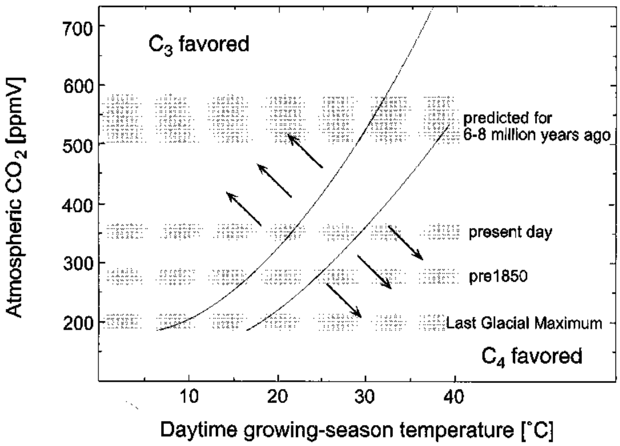

FIGURE 1 Modeled crossover temperatures of the quantum yield for CO_2 uptake for C_3 and C_4 plants as a function of atmospheric CO_2 concentrations. The boundary conditions shown are for NADP-me C_4 plants (upper boundary) and NAD-me C_4 plants (lower boundary). The crossover temperature is defined as the temperature (for a particular atmospheric CO_2 concentration) at which the quantum yields for CO_2 uptake are equivalent for both the C_3 and the C_4 plant. Figure is modified from Ehleringer *et al.* (1997).

3. A Brief History of Atmospheric Carbon Dioxide Levels

The significance of the "quantum yield" model's prediction of C_3/C_4 distributions is best viewed in the context of atmospheric CO_2 changes that have occurred over the past several hundred million years. The history of levels of atmospheric CO_2 is related to its production through volcanism relative to the losses associated with weathering, photosynthesis, and burial in the oceans (Berner, 1994, 1997). The important biogeochemical processes contributing to the change in atmospheric CO_2 are

$$CaSiO_3 + CO_2 \longrightarrow CaCO_3 + SiCO_3$$

and

$$H_2O + CO_2 \longrightarrow CH_2O + O_2,$$

where the first reaction describes weathering and the formation of carbonate sediments that are finally deposited in oceanic carbon sinks and the second reaction is an abbreviated description of the production and burial of organic matter in terrestrial sediments. The combination of these two reactions and the presence of liquid water on earth results in a long-term decline in atmospheric CO_2 values (Berner, 1991).

While there is uncertainty about the atmospheric CO_2 values prior to half a million years, most modeling and analytical approaches suggest that atmospheric CO_2 levels were substantially higher in the Cretaceous than they are today (Fig. 2, left). Modeled and experimental approaches further agree that atmospheric CO_2 levels began to decline during the late Cretaceous, eventually settling into a range of concentrations less than 500 ppmV. These

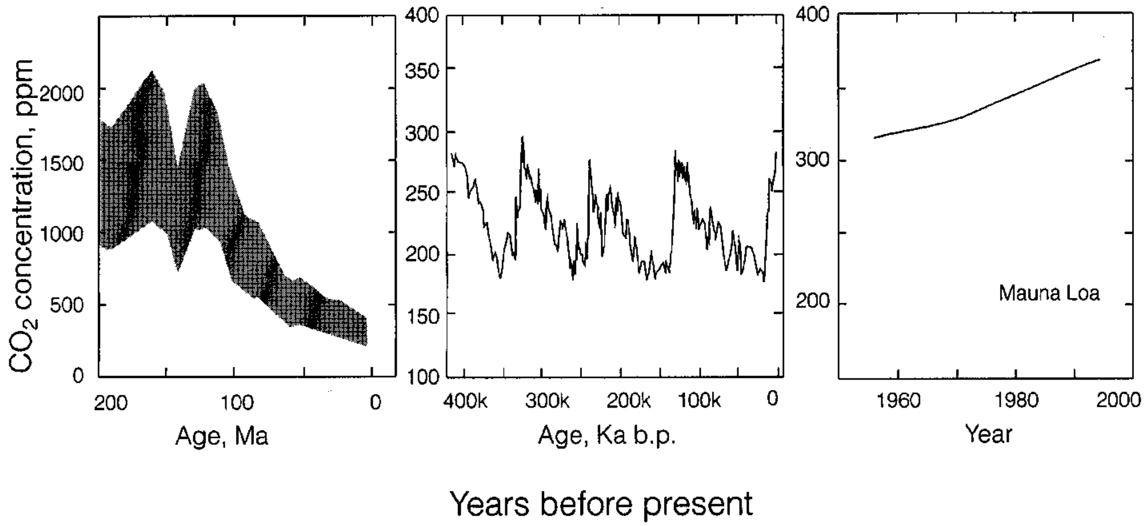

FIGURE 2 Patterns of atmospheric CO_2 concentrations through time. Left plate: reconstruction of paleo CO_2 levels between 200 Ma and present; adopted from Cerling *et al.* 1998a. Middle plate: reconstruction of atmospheric CO_2 from ice cores for the past 160,000 years; adopted from Petit *et al* (1999). Right plate: atmospheric CO_2 concentrations recorded at Mauna Loa, Hawaii since 1958; adopted from Keeling (1998). records at ORNL CDIAC

relatively low atmospheric CO_2 levels are thought to have characterized the earth's atmosphere from the late Miocene up to the dawn of the Industrial Revolution. Icecore data, particularly the lengthy Vostok ice core observations from Antarctica (Jouzel *et al.*, 1987; Petit *et al.*, 1999), indicate that over the past 420,000 years there have been oscillations in the atmospheric CO_2 from 180 to 280 ppmV, associated with glacial and interglacial periods, respectively (Fig. 2, middle). In contrast to this long-term historical pattern is an anthropogenically induced increase in atmospheric CO_2 levels, especially during the 20th century, to values well in excess of 350 ppmV in association with the continued combustion of fossil fuels (Fig. 2, right).

The answer to "why should natural selection favor the emergence of a second photosynthetic pathway?" is seen in the large decreases in atmospheric CO_2 that have occurred over the past 200 million years, particularly the changes in atmospheric CO_2 levels in the past 6–8 million year, while during the same interval atmospheric O_2 levels are thought to have remained almost constant. It is the changes in the $[CO_2]/[O_2]$ ratio that result in decreased photosynthesis by C_3 plants as photorespiration rates increase, which favors the evolution and expansion of C_4 photosynthesis. The higher activity of PEP carboxylase effectively creates a "CO_2 pump," resulting in a $[CO_2]/[O_2]$ ratio inside the bundle-sheath cells of C_4 plants that is several-fold greater than observed at sites of Rubisco activity in C_3 plants. The "quantum yield" model predicts how common C_4 photosynthesis is expected to be for any global atmospheric CO_2 level. Specifically, the model predicts the temperature ranges that should have favored C_4 over C_3 as atmospheric CO_2 declined over the last 200 million years.

The decreased atmospheric CO_2 levels have had enormous consequences both for the distribution of plant communities across our planet and for animal evolution, as will be discussed below. While throughout much of history, earth had been subject to relatively high atmospheric CO_2 levels, the earth has now been in a "CO_2 -starved mode" for approximately 7 Ma with periods of exceptionally low atmospheric CO_2 levels (~180 ppmV) characterizing the atmosphere during recent glacial periods.

4. Recognizing the Presence of C_3 and C_4 Ecosystems in the Paleorecord

Carbon isotope ratios can be used to identify the presence of C_3 versus C_4 photosynthesis in the fossil records. Large differences in discrimination against $^{13}CO_2$ by the initial carboxylation reactions in C_3 (RuBP carboxylase) and C_4 (PEP carboxylase) photosynthesis result in significant differences in the carbon isotope ratios ($\delta^{13}C$) of C_3 and C_4 plants (Farquhar *et al.*, 1989). Modern C_3 plants average approximately −27‰ and C_4 plants average approximately −13‰ (Fig. 3). The observed ranges of $\delta^{13}C$ values for both C_3 and C_4 plants are the result of genetic differences among taxa as well as responses to variations in environmental conditions, including light and water stress (Farquhar *et al.*, 1989; Ehleringer *et al.*, 1993; Buchmann *et al.*, 1996). Differences among C_4 photosynthetic subtypes (NADP-me, NAD-me, and PCK) contribute as much as 1–2‰ to the range of values shown in Fig. 3 (Hattersley, 1982; 1983).

Animal tissues faithfully record the isotopic composition of their food sources (Tieszen *et al.*, 1983; Hobson, 1999), but often are not preserved in the fossil records or are subject to alteration

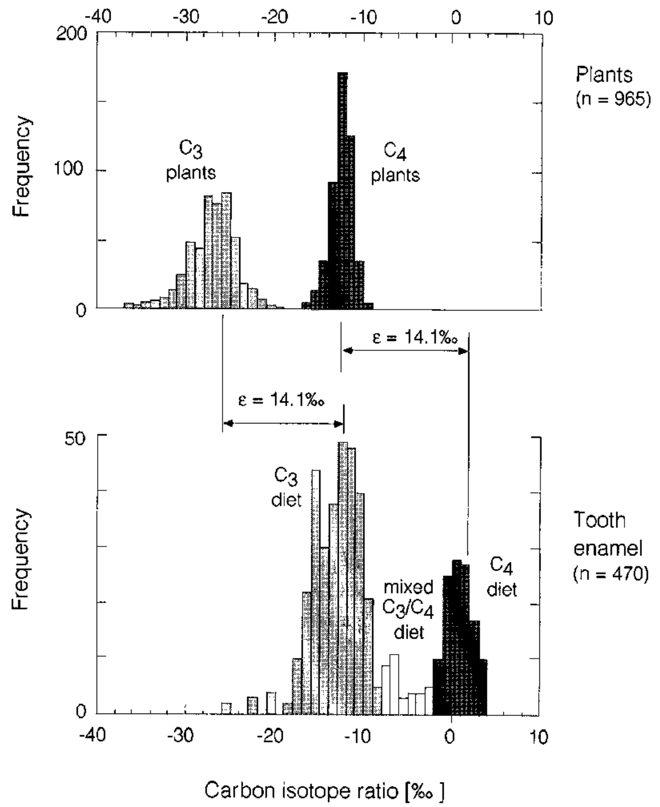

FIGURE 3 Histograms of the carbon isotope ratios of modern grasses and modern tooth enamel; adopted from Cerling *et al.* (1997).

(diagenesis) during fossilization. However, tissues such as tooth enamel are preserved without subsequent modification, thus recording the original animal diet over periods of several million years (Lee-Thorp and van der Merwe, 1987). Tooth enamel

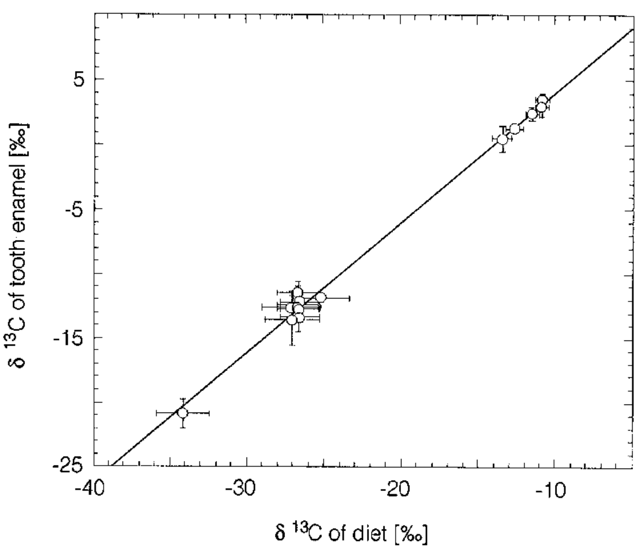

FIGURE 4 Relationship between the carbon isotope ratio values of estimated diet and measured tooth enamel for ungulate mammals; adopted from Cerling and Harris (1999).

(bioapatite) is enriched 14.1‰ relative to a grazing mammal's diet (Fig. 4), resulting in a straightforward means of recording long-term feeding patterns by mammalian grazers (Cerling and Harris, 1999). The lower histograms in Figure 3 illustrate this offset between animals and their food sources, based on an accumulation of observations of $\delta^{13}C$ values of apatite from a wide variety of grazing species (Cerling *et al.*, 1997; Cerling and Harris, 1999). It is important to note that the variation in plant $\delta^{13}C$ values is similar in magnitude to the variation in tooth-enamel $\delta^{13}C$ values. Thus, small variations in tooth-enamel $\delta^{13}C$ values on the order of 1–2‰ are just as likely to represent variations in food quality associated with changing environmental conditions as variations in the abundances of C_3 and C_4 plants in the animal's diet or the changing carbon isotope ratio of the atmosphere.

5. Global Expansion of C_4 Ecosystems

Figure 5 shows that between 8 and 6 Ma there was a global expansion of C_4 ecosystems (Cerling *et al.*, 1997, 1998a). There is no conclusive evidence for the presence of C_4 biomass in the diets of mammals before 8 Ma (Cerling *et al.*, 1997; 1998a), although the presence of small amounts 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, *et al* 1993; MacFadden and Cerling, 1999; Cerling *et al.*, 1999), and South America (MacFadden *et al.*, 1996; Cerling *et al.*, 1997), but not in Europe (Cerling *et al.*, 1997). Figure 5 documents several different ecosystem type changes as recorded in mammalian tooth enamel. While each of these regions appears to have been dominated by C_3 ecosystems earlier in the Miocene, the C_3 Pakistani ecosystem was almost completely replaced by a C_4 ecosystem; African, North American, and South American ecosystems retained both C_3 and C_4 components; European and northern portions of North American ecosystems did not show any change in the fraction of C_3 biomass, remaining at virtually 100% C_3 ecosystems. The mixture of C_3 and C_4 components within a grazing ecosystem can be achieved by one of two ways: a temporal separation with C_3 grasses active in winter–spring and C_4 grasses active in summer or a monsoonal system with C_4 grasses and C_3 woody vegetation. Without fine-scale analyses of the seasonal dynamics with tooth enamel, the isotopic record is silent as to which pattern existed.

The isotopic evidence is clear that the expansion of C_4 ecosystems was a global phenomenon, persisting until today. It was accompanied by significant faunal changes in many parts of the world. It is unlikely that the global expansion of C_4 biomass in the late Miocene was due solely to higher temperatures or to the development of arid regions. There have always been regions on earth with hot, dry climates. To explain the simultaneous global expansion of C_4 plants requires a global phenomenon. Changes in

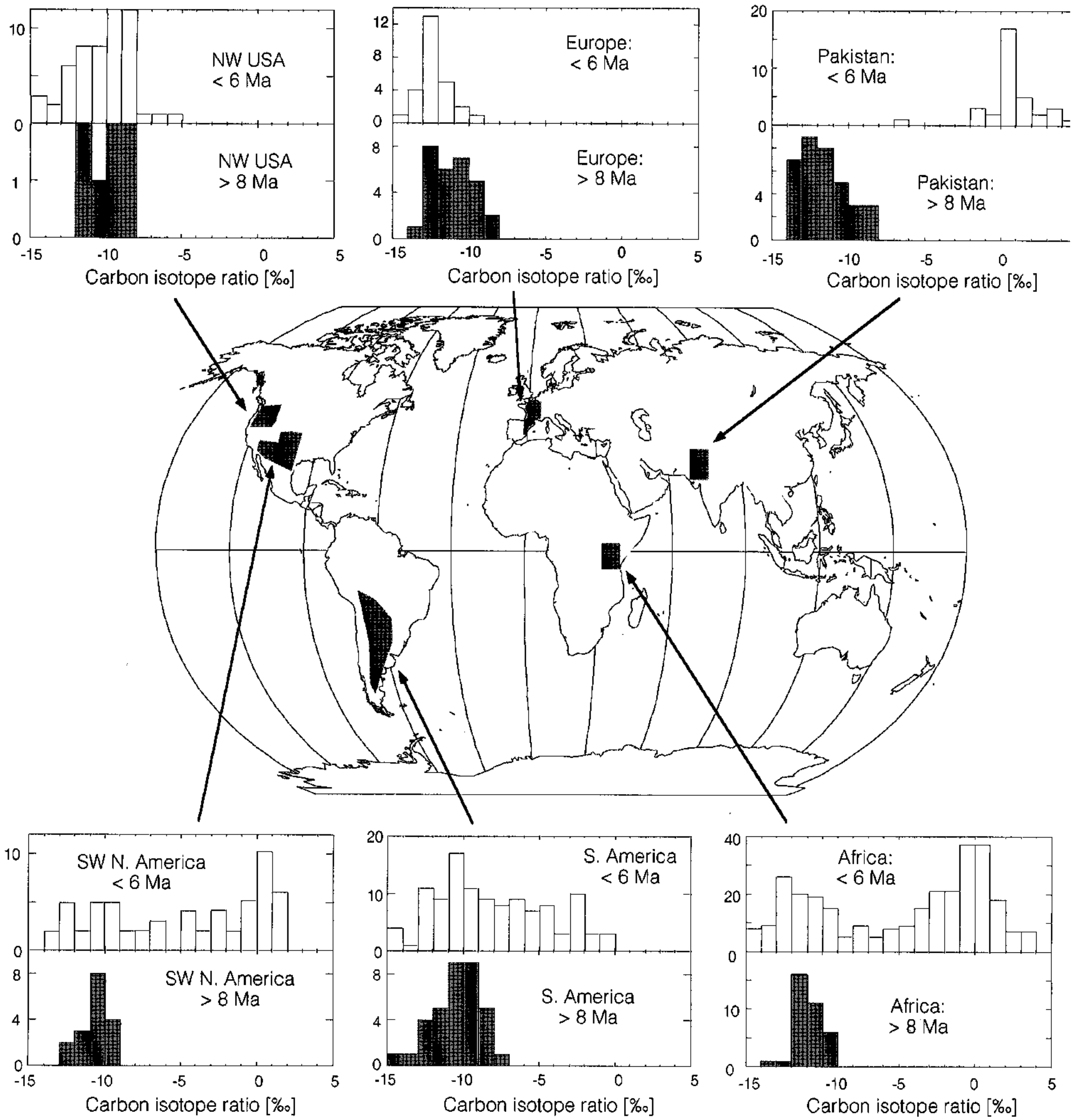

FIGURE 5 Histograms comparing the carbon isotope ratio values for fossil tooth enamel older than 8 Ma (lower charts) with those that are younger than 6 Ma for six regions of earth; adopted from Cerling *et al.* (1998a).

atmospheric CO_2 as predicted by the quantum-yield model are a strong possibility for this global mechanism. Supporting evidence indicates that the global expansion of C_4 ecosystems appears to have originated in warmer, equatorial regions and then spread to cooler regions, consistent with the temperature-sensitivity predictions of the quantum-yield model. Cerling *et al.* (1997) documented that within both modern and fossil horses (equids), the distributions of isotope ratios strongly support a decrease in the importance of C_4 photosynthesis in moving from warm equatorial to cooler temperate latitudes.

Stable-isotope studies of paleosols from Pakistan and East Africa are in good agreement with the paleodietary studies. The Siwalik sequence in Pakistan has excellent exposures covering the last 20 Ma. $\delta^{13}C$ studies of paleosol carbonates show a virtually pure C_3 ecosystem up to about 7.5 Ma ago, a transitional period of ecosystem change lasting 1–1.5 Ma, and then C_4-dominated ecosystems from 6 Ma ago to nearly the present (Quade *et al.*, 1989; Quade and 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 paleosols in the Turkana Basin in Africa, 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.*, 1993; 1997).

6. C_3/C_4 Dynamics during Glacial-Interglacial Periods

The quantum-yield model predicts that important changes in the global proportions of C_4 biomass occurred during the Pleistocene glacial–interglacial transitions. Figure 1 shows that at very low atmospheric CO_2 levels, C_4 plants can be favored even at moderately low temperatures. The oscillation between glacial and interglacial conditions reflected an oscillation between about 180 and 280 ppmV (Fig. 2, middle), respectively, based on the CO_2 concentrations in the Antarctic ice cores (Petit *et al.*, 1999). The temperature change between the glacial and interglacial intervals varied globally, with estimated changes in temperature from about 5°C in the tropics (Stute *et al.*, 1995) to >15°C in the polar regions (Cuffey *et al.*, 1995). Therefore, the dCO_2/dT gradient in the tropics was about 20 ppm/°C, compared to about 7 ppm/°C at high latitudes. Based on the slope of the C_3/C_4 crossover at low atmospheric CO_2 levels (Fig. 1), it is possible that in some regions greater C_4 abundance would be expected in glacial conditions relative to interglacial conditions, because the "CO_2 starvation" effect would be more decisive than the "temperature" effect.

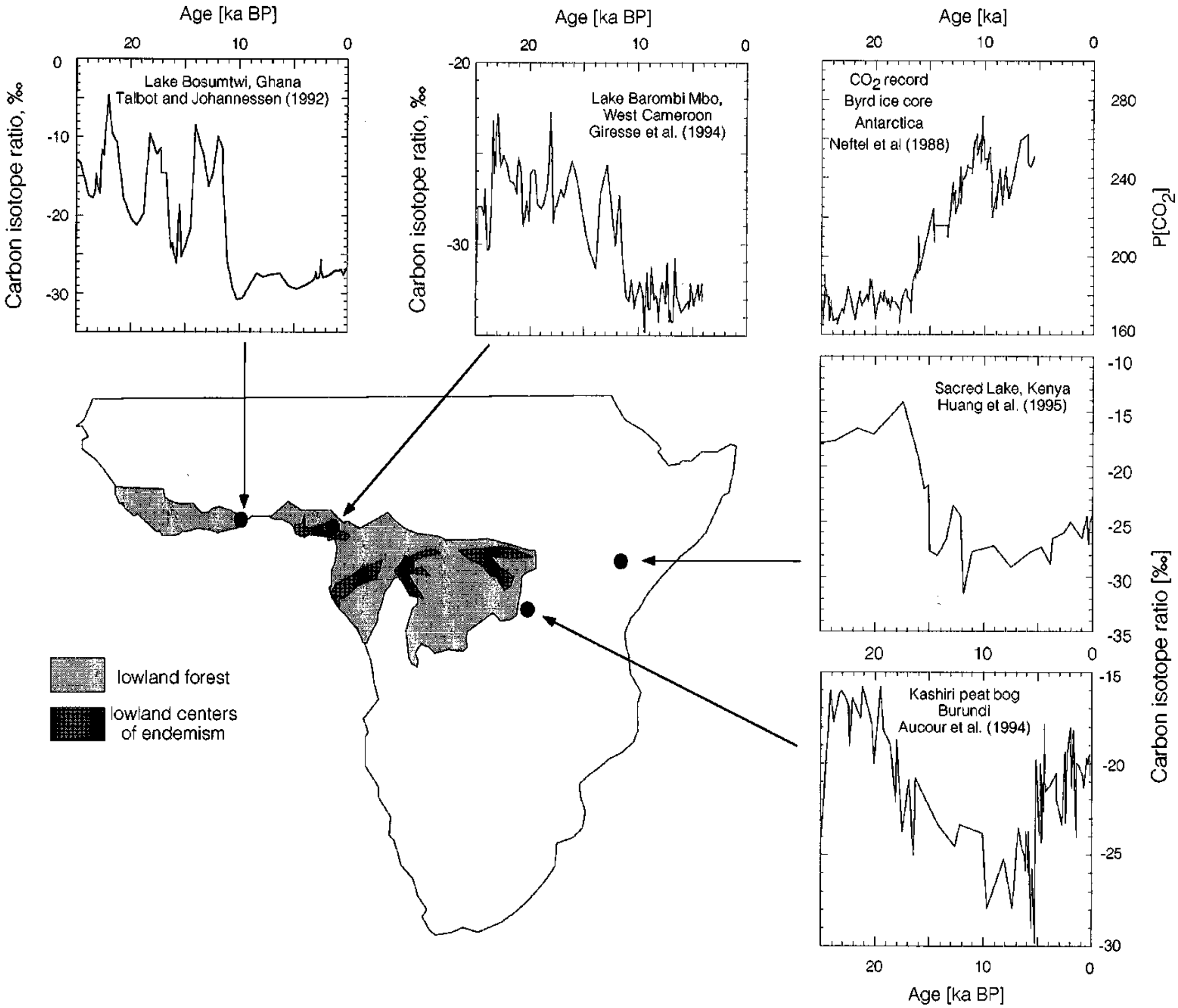

FIGURE 6 Chronological profiles of the carbon isotope ratio values of organic matter from lake sediments and bogs in central Africa. The data indicate that these areas all had more extensive C_4 biomass during the last glacial maximum (30–20 ka B.P. than during the Holocene (10 ka B.P. to present). Data are from Talbot and Johannessen (1992), Giresse *et al.* (1994) Aucour *et al.* (1994), and Neftel *et al.* (1988). Adopted from Cerling *et al.* (1998a).

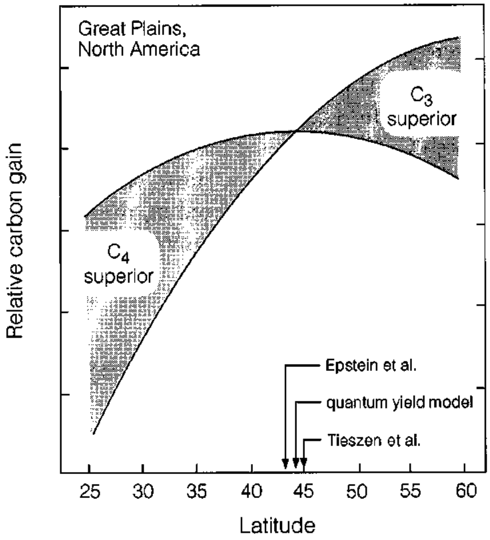

FIGURE 7 Predicted relative carbon gain by the quantum-yield model and therefore predicted competitive success by C_3- and C_4-grass canopies across the Great Plains of North America under today's atmospheric carbon dioxide levels. Noted are the predicted cross-over points from C_3- to C_4-dominance based on the quantum-yield model and the observations for soil organic matter (Tieszen *et al.*, 1997) and for aboveground harvests (Epstein *et al.*, 1997). Adopted from Ehleringer (1978).

Ehleringer *et al.* (1997) examined published reports of $\delta^{13}C$ in peat bogs and lakes from Central Africa in regions that are currently dominated by rain-forest ecosystems. The available data strongly support the hypothesis of extensive C_4 expansion during the last full glacial (Aocour *et al.*, 1993; Hillaire *et al.*, 1989)(Fig. 6). This implies extensive retreat of the African rain-forest ecosystems and has important implications for refugia during the Pleistocene which are discussed below. Farther east in Africa, sedimentary data from Sacred Lake in Kenya also show that C_4 grasses were much more common during the glacial period when C_3 vegetation would have been "CO_2 starved" (Street-Perrott *et al.*, 1995; 1997; Huang *et al.*, 1995; 1999). Following deglaciation, the C_4 abundances in the Sacred Lake region exhibited a dramatic decline correlated with the increases in atmospheric CO_2 levels.

Within North American ecosystems, there is also evidence that C_4 ecosystems were more extensive during the last glacial period than they are today. Soil carbonates from the southwestern portions of North America show that C_4 plants dominated the landscape during glacial periods, but are less abundant in these aridland ecosystems today (Cole and Monger, 1994; Liu *et al.*, 1996; Monger *et al.*, 1998). Dietary analyses of fossil herbivores from western North America also provide convincing evidence of widespread C_4 abundance in regions that have a near absence of C_4 grasses today (Connin *et al.*, 1998). While the mechanisms for the observed decline in C_4 abundance in North America require further study, the dramatic decrease in C_4 plants is correlated with the transition out of the glacial and the abrupt increases in atmospheric CO_2 levels.

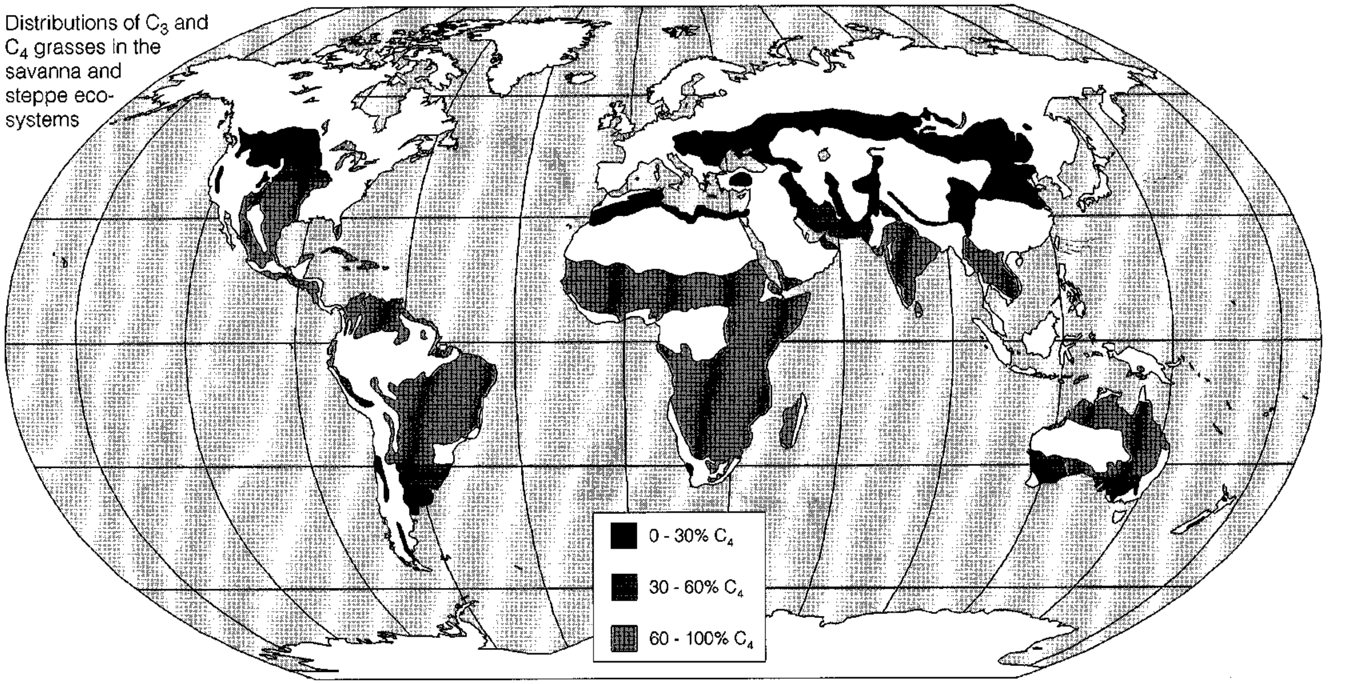

FIGURE 8 Predicted distributions of C_3 and C_4 grasses in steppe and savanna ecosystems of the world. These are the only two ecological regions where grasses are a significant fraction of the vegetation. Distribution of ecological regions is based on Bailey (1998) and the partitioning of photosynthetic pathways is based on the synthesis in Sage and Monson (1999).

7. Photosynthetic Pathway Distribution in the Modern World

The current distributions of C_4 plants within grassland ecosystems at an atmospheric CO_2 level of 350 ppmV are well predicted by the quantum-yield model (Fig. 1). Across the Great Plains of North America, the crossover between C_3- and C_4-dominated grasslands is predicted to occur at a latitude of approximately 45°N (Figure 7). Both long-term aboveground harvest studies (Epstein *et al.*, 1997) and belowground soil organic carbon studies (Tieszen *et al.*, 1997) independently indicate a C_3/C_4 transition near 45°N. In the case of C_3/C_4 grasses from the Great Plains as well as all other monocot studies, the relationships between C_3 and C_4 grass abundances were all very highly correlated with temperature (Ehleringer *et al.*, 1997). In most of these studies, >90% of the variance in C_3 /C_4 abundance in today's ecosystems is explained by temperature alone.

Collatz *et al.* (1998) extended predictions of the quantum-yield model to the global scale (Fig. 8). Their model predicted that C_4 abundances are expected in all geographical regions where the monthly mean temperature exceeds 22°C (the crossover temperature) and where precipitation exceeds 25 mm (i.e., the soil must be wet for plants to grow). This model predicts a much broader distributional range for C_4 taxa than is observed for undisturbed ecosystems, with C_4 taxa extending into currently forested regions of tropical and subtropical latitudes. However, when the competitive advantage of tree height is factored in, the Collatz *et al.* extrapolation correctly predicts the observed C_3/C_4-grass abundances on a global basis (Fig. 8).

8. Photosynthetic Pathway Impacts Herbivores

Megafaunal changes are correlated with a shift between C_3- and C_4-dominated ecosystems. Several lines of evidence suggest relationships between turnover of mammalian grazing taxa and the shifts between C_3/C_4 vegetation types. Cerling *et al.* (1998a) reported abrupt changes in mammalian lineages in East Africa asso-

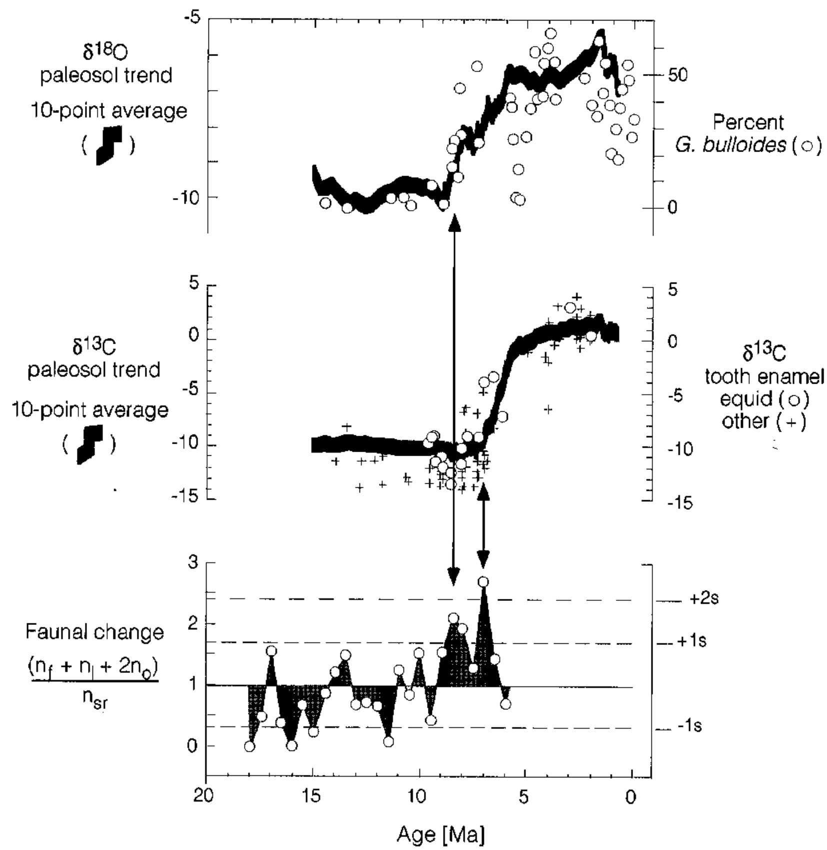

FIGURE 9 Faunal Change Index from the Pakistan, represented by the number of first (n_f) and last (n_l) occurrences, including only occurrences (n_o), normalized to species richness (n_{sr}). The Faunal Change Index is normalized to 1.0 for the total data set. Adopted from Cerling *et al.* (1998b).

ciated with the transition from C_3-dominated to C_3/C_4-dominated ecosystems. During the same time period, Cerling *et al.* (1998b) showed that abrupt changes in faunal diversity of Pakistani mammals occurred at the same time as the emergence of C_4-dominated ecosystems in Pakistan (Fig. 9). Evolutionary relationships between C_3/C_4 and horses appear to be somewhat different (MacFadden and Cerling, 1996; MacFadden *et al.*, 1996). Evolution of the modern horse is associated with the transition from "browsing" to "grazing" horses, which is typically marked by the lengthening of the M1 molar, creating the high-crowned tooth (Fig. 10). However, the evolution of the M1 tooth and the increased diversity of horse taxa was not associated with the global expansion of C_4 ecosystems, because these changes occurred in a C_3 world. However, the crash in biological diversity of horses at 6 Ma is associated with the expansion of C_4-dominated ecosystems into regions that once contained only C_3 plants (Fig. 10).

Modern mammalian herbivores exhibit strong preferences for C_3 versus C_4 diets (Fig. 11), with only limited numbers of examples of mixed C_3 /C_4 feeding (Figure 3). While it may be difficult to quantify the exact percentages of C_3/C_4 within the diets of some mammals, it is possible to classify the extreme grazers and browsers: hypergrazers with nearly 100% C_4 grass and hyperbrowsers with nearly 100 % C_3 browse. It is remarkable that the herbivore mammals of the savannahs and grasslands of Africa falls into such distinct C_3/C_4 dietary categories, with extreme hypergrazers such as the wildebeest standing distinct from grazers such as the oryx and zebra (Fig. 11). The modern African elephant

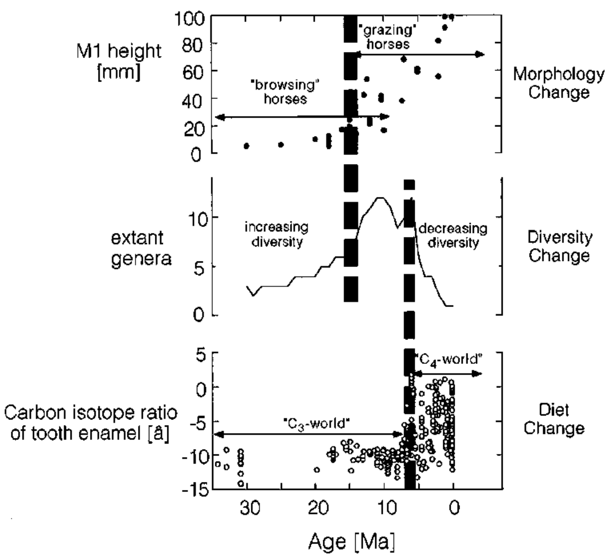

FIGURE 10 A chronology of horse evolution. Top plate: morphological changes in the height of the M1 tooth. Middle plate: diversity changes as recorded by the number of extant genera. Bottom plate: carbon isotope ratios of tooth enamel illustrating that the transition from browsing horses to grazing horses was not associated with expansion of C_4 ecosystems, but that the loss of genera was correlated in time with C_4 expansion. Adopted from Cerling (1999).

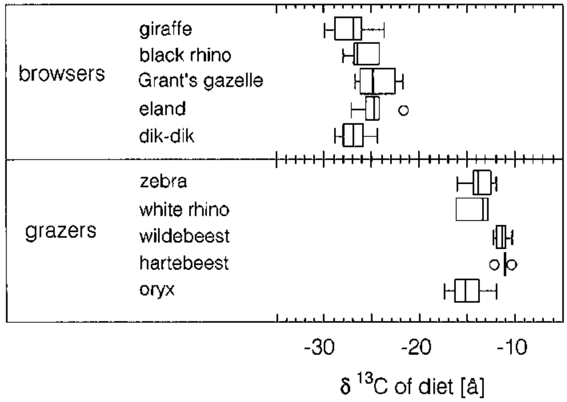

FIGURE 11 Ranges in the carbon isotope ratios of diets for African browsers and grazers. Adopted from Cerling *et al.* (1999).

(*Loxodonta*) is often regarded as a grazing animal, yet its isotopic composition strongly shows that these animals are distinctly C_3 browsers (Cerling *et al.*, 1999). In contrast, a million years ago elephants were distinctly grazers.

The selective basis for differential C_3/C_4 herbivory may be related to the differential distributions of leaf protein within C_3 and C_4 leaves (Ehleringer and Monson, 1993). In C_3 plants, relatively high protein levels are found in most mesophyll cells. These cells have relatively thin cell walls, especially when compared to the much thicker bundle-sheath cell walls (Brown, 1977). In contrast, there is relatively more protein within bundle-sheath cells of C_4 leaves than in mesophyll cells. Thus, tooth morphology in mammalian grazers would be expected to play a role in determining whether or not animals were able to extract sufficient protein from their C_3/C_4 diet. Insects such as grasshoppers show a strong preference for C_3 or C_4 food sources, but typically not for both (Isely, 1946; Caswell *et al.*, 1973; Boutton *et al.*, 1978; Ehleringer and Monson, 1993). Here it is known that there are significant differences in mandible morphology correlated with C_3/C_4 dietary preference.

9. Summary

The current distribution of C_3 and C_4 photosynthetic pathways in today's ecosystems is a strong function of temperature. Changing atmospheric CO_2 levels modify this geographical distribution. The global emergence of C_4-dominated ecosystems in the late Miocene suggests that atmospheric CO_2 levels decreased across a threshold of ~500 ppmV favoring C_4 photosynthesis over C_3 photosynthesis in warm ecosystems. More recently during glacial periods when atmospheric CO_2 levels decreased to 180 ppmV, C_4 taxa were apparently more abundant than they are today. These changes in C_3/C_4 abundances have had enormous impacts on both evolution and distribution of mammalian grazers. The mechanistic basis for this impact on mammal herbivory may be feeding preferences associated with differential digestibility of C_3 versus C_4 grasses.

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