

Atmospheric CO₂ as a Global Change Driver Influencing Plant-Animal Interactions¹

JAMES R. EHLERINGER,² THURE E. CERLING, AND M. DENISE DEARING

Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, Utah 84112-0840

SYNOPSIS. Plants respond to changes in atmospheric carbon dioxide. To herbivores, the decreased leaf protein contents and increased C/N ratios common to all leaves under elevated atmospheric carbon dioxide imply a reduction in food quality. In addition to these fine-scale adjustments, the abundance of C₃ and C₄ plants (particularly grasses) are affected by atmospheric carbon dioxide. C₄ grasses currently predominate over C₃ grasses in warmer climates and their distributions expand as atmospheric carbon dioxide levels decreased during glacial periods. C₄ grasses are a less nutritious food resource than C₃ grasses both in terms of reduced protein content and increased C/N ratios. There is an indication that as C₄-dominated ecosystems expanded 6–8 Ma b.p., there were significant species-level changes in mammalian grazers. Today there is evidence that mammalian herbivores differ in their preference for C₃ versus C₄ food resources, although the factors contributing to these patterns are not clear. Elevated carbon dioxide levels will likely alter food quality to grazers both in terms of fine-scale (protein content, C/N ratio) and coarse-scale (C₃ versus C₄) changes.

Atmospheric gas composition plays an important role in determining many aspects of animal and plant metabolism (Körner, 2000). Do changes in atmospheric composition, particularly of CO₂ and O₂, affect plants in fundamentally different ways than they do animals? On a short-term basis, the absolute concentrations of these two gases have immediate impacts on gas exchange rates of both animal and plants with their surrounding environment. For example, the concentrations of CO₂ and O₂ will influence the degree of O₂ saturation of hemoglobin in animals and the extent of photorespiration in plants. While these responses might appear to have little in common, there is a common biochemical driver for the metabolic shifts: changes in the ratio of atmospheric CO₂/O₂. Such changes in atmospheric gas composition have occurred since the dawn of biological life several billion years ago and form the basis of different metabolic adaptations in both plants and animals.

Changes in atmospheric gas composition can also influence plant-animal interactions in fundamentally different ways. Over a longer time scale of weeks, changes in the ratio of CO₂/O₂ in the atmosphere affects plant metabolism in ways that ultimately influence the quality of leaves as a food resource for animals. In this synthesis, we focus on how historical and current global changes in atmospheric CO₂ have driven changes in plant metabolism at both a fine scale through adjustments in the relative composition of leaf-level biochemical components and at a coarse scale through shifts in the dominant photosynthetic pathway prevalent in a habitat. Both fine and coarse scale changes in leaf metabolism have direct and significant impacts on the quality of leaves as a food re-

source, thereby impacting animal performance in response to global atmospheric change.

ATMOSPHERIC CO₂

Over the past 200 million years, the atmospheric CO₂ concentrations have fluctuated, whereas on a relative basis the concentrations of atmospheric O₂ are thought to have exhibited limited changes (Berner, 1991, 1997; Petit *et al.*, 1999; Ekart and Cerling, 1999). We can divide the recent history of atmospheric CO₂ concentration into the distinct periods: 0.5–200 Ma before present, 0–420,000 yr before present, and since 1958 when high-precision and long-term CO₂ records were first continuously collected (Fig. 1). Our understanding of long-term atmospheric CO₂ is based on geochemical proxies, but there is reasonable agreement of a long-term decline in atmospheric CO₂ from ~2,000+ ppm CO₂ in the Cretaceous (about 75 million years ago) to much lower values before the Industrial Revolution began three centuries ago (Berner, 1997; Ekart and Cerling, 1999). At the moment, the fine scale estimates of atmospheric CO₂ over the past 1–30 Ma are a subject of intense interest with various proxies being considered to estimate CO₂ fluctuations over this period. Pagani *et al.* (1999a, b) used δ¹³C values of alkenones and carbonates in marine sediments to estimate atmospheric CO₂ for the last 25 million years. Their results suggest that atmospheric CO₂ had remained low (200–400 ppm) during this entire period, implying that the predicted CO₂ threshold for C₄ expansion may not have occurred. Instead Pagani and colleagues suggest that C₄ expansion was triggered by global aridity. Quite independently, Pearson and Palmer (2000) used marine boron-isotope proxies to estimate that atmospheric CO₂ levels had remained low (at or near today's levels of 370 ppm) for the past 60 Ma. However, the recent study by Lemarchand *et al.* (2000) revealed that oceanic boron isotope budgets are largely unconstrained and greatly influenced by shifts in the terrestrial inputs. Thus, one might only be

¹ From the symposium *Plant/Animal Physiology* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 3–7 January 2001, at Chicago, Illinois.

² E-mail: ehleringer@biology.utah.edu

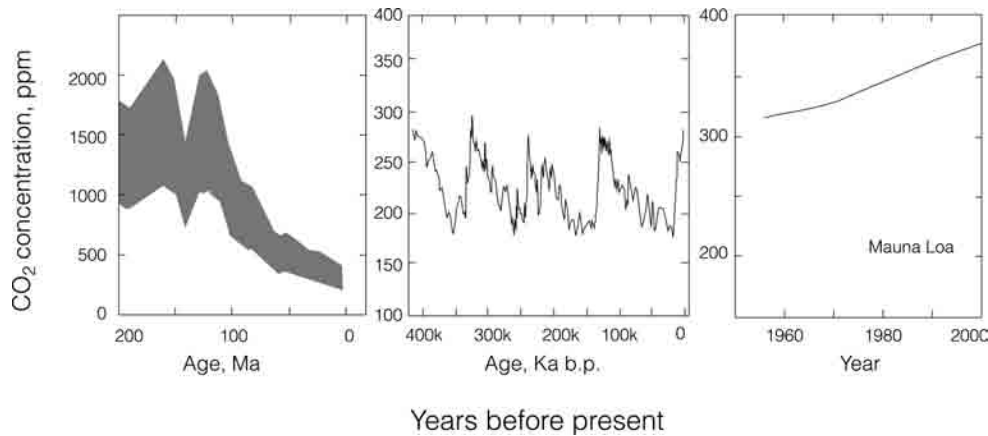


FIG. 1. Patterns of atmospheric CO₂ concentrations through time. Left plate: reconstruction of paleo CO₂ levels between 200 Ma and present; adapted from Berner (1991, 1997). Middle plate: reconstruction of atmospheric CO₂ from ice cores for the past 420,000 yr; adapted from Petit *et al.* (1999). Right plate: atmospheric CO₂ concentrations recorded at Mauna Loa, Hawaii since 1958; adapted from C. D. Keeling data at ORNL CDIAAC.

able to conclude from boron isotope studies that atmospheric CO₂ values (0–0.5 Ma b.p.) were 200–300 ppm. As will become evident shortly, knowledge of the high-resolution history of atmospheric CO₂ is important for understanding the biological mechanisms responsible for shifts in photosynthetic pathway that ultimately impact animal diets.

As a result of the Vostok ice-core studies (Fig. 1), we now know that atmospheric CO₂ values shifted between 180 and 280 ppm as the Earth oscillated between glacial and interglacial periods over the past 420,000 yr (Petit *et al.*, 1999). What constrained the global atmospheric CO₂ concentrations at these particular end points is not clear, but what is clear is both photosynthesis and the nutritional quality of leaves are particularly sensitive to changes in atmospheric CO₂ over this range (Sage and Monson, 1999). Thus, as the Earth cycled between glacial and interglacial periods, both terrestrial productivity and the quality of food available to herbivores are likely to have undergone significant swings.

Global atmospheric changes are occurring today—only this time humans are the drivers of these changes and not glacial-interglacial cycles. Today we have entered a new period in the Earth's history where humans are having a significant impact on atmospheric CO₂ values (Fig. 1). Beginning with the use of fossil fuels in the Industrial Revolution and the acceleration since the 1950s, humans now have a dominant and ever increasing impact on the Earth's atmosphere. Atmospheric CO₂ levels today exceed values recorded in the Vostok core by more than 30%. We are now entering a selective regime where CO₂ in the atmosphere exceeds the natural range under which most extant plant and animal species are thought to have evolved. This global change in the atmosphere does have direct and indirect impacts on species at the metabolic and evolutionary levels as well as on the functioning of ecosystems through impacts on both productivity and carbon cycling (Mooney *et al.*, 1999). We next examine

how global atmospheric CO₂ changes impact both plant metabolism and in turn impact the diet quality available for animals.

ATMOSPHERIC CO₂ IMPACTS DIET QUALITY

Food quality is hard to precisely define, yet there is no doubt that four parameters influencing palatability of foods include leaf protein content, soluble carbohydrate content, fiber content, and the abundance of different secondary compounds. Changes in atmospheric CO₂ will impact food quality for herbivores at both fine and coarse scales.

At a fine scale, leaves acclimate to changes in atmospheric CO₂ through adjustments in leaf protein levels, carbohydrate content, and leaf thickness (Overdieck *et al.*, 1988; Curtis and Wang, 1998; Cowling and Sage, 1998; Diaz *et al.*, 1998; Wand *et al.*, 1999). Overall, these changes result in adjustments in the C/N ratios of leaves, which in turn should impact food quality as perceived by herbivores. In response to increasing atmospheric CO₂, protein levels decrease in leaves of all species (Fig. 2). Comparisons are typically made with leaves of plants grown at 2× current ambient CO₂ (650–700 ppm), which are the anticipated levels within a century from now. The down regulation of photosynthesis results in 10–20% lower leaf nitrogen levels, since much of the soluble leaf protein is associated with RuBP carboxylase (Rubisco) (Sage, 1994; Cowling and Sage, 1998; Wand *et al.*, 1999). Even though photosynthesis is down regulated, leaves tend to accumulate greater sugar and starch levels resulting in non-structural carbohydrate levels that are 10–40% higher than levels observed in plants grown under today's CO₂ conditions. Overall, the C/N ratios of leaves increase by 20–30% under 2× elevated CO₂ conditions; these responses occur in both C₃ and C₄ photosynthetic pathway plants (Fig. 2).

Both mammalian and insect herbivores respond to leaves grown under elevated CO₂ with responses resulting in slower growth rates. In insects, these re-

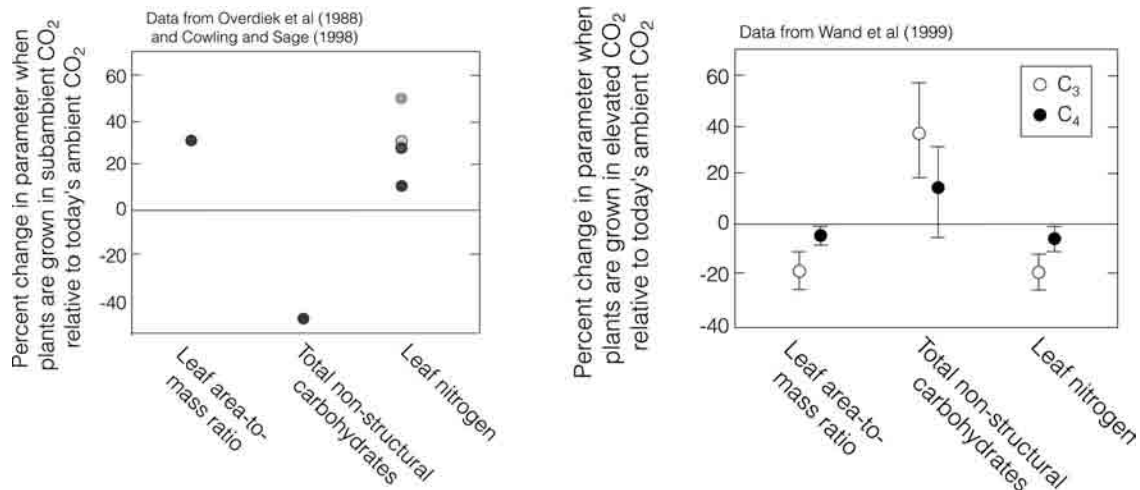


FIG. 2. Changes in the leaf thickness, soluble carbohydrate content, and leaf nitrogen (protein) content for plants grown under subambient (left) and elevated (right) atmospheric CO₂ concentrations. Adapted from data in Overdieck *et al.* (1988) and Wand *et al.* (1999).

sponses range from modified ingestion rates to longer maturation times (Arnone *et al.*, 1995; Agrell *et al.*, 2000; Körner, 2000). In cattle, there is some evidence for possible reduced growth rates of steers, particularly in spring when leaves have their highest protein contents under today's CO₂ conditions (Owensby *et al.*, 1996). Most of these responses fit into the general category of reduced digestibility and can be directly related to leaf C/N ratios. At the plant species level, plant secondary compound production will impact herbivores in species-specific ways. These secondary compounds tend to increase by as much as two-fold in defensive compounds produced via the shikimic acid pathway and little if at all in secondary compounds derived via the malvonic acid pathway (Roth *et al.*, 1998; McDonald *et al.*, 1999; Agrell *et al.*, 2000).

Fewer studies are available for understanding how plants respond to atmospheric CO₂ levels that existed during pre-Industrial periods and during glacial periods (Overdieck *et al.*, 1988; Polley *et al.*, 1992, 1993; Ward *et al.*, 1999). The pattern is opposite to that observed for leaves grown under high CO₂ (Fig. 2). In subambient CO₂, leaves have slower growth rates and as a result nonstructural carbohydrate levels are reduced. Leaf nitrogen content tends to be higher. We are aware of no studies that have examined animal feeding patterns and preferences for leaves grown under subambient CO₂ levels.

C₄ PLANTS AS A FOOD RESOURCE

It is important to distinguish fine-scale acclimation changes in food quality from the relatively large coarse-scale differences in food quality associated with leaves having C₃ *versus* C₄ photosynthesis. Historically, feeding trials and food preference studies have tended not to distinguish between leaves of plants having one photosynthetic pathway *versus* the other. Many feeding studies do distinguish between forbs and

grasses as substrate; in most cases these studies involve C₃ × C₃ comparisons and in only a few are there C₃ × C₄ comparisons. Yet as early as a quarter century ago, Caswell *et al.* (1973) hypothesized that C₄ plants were nutritionally inferior to C₃ plants. They hypothesized that animals in general avoided C₄ plants, but today we recognize that animals often exhibit distinct preferences for either C₃ or C₄ species (Ehleringer and Monson, 1993; Heckathorn *et al.*, 1999).

Although C₄ photosynthesis occurs in less than 2% of higher plant species, it accounts for 25% of today's primary productivity (Ehleringer *et al.*, 1997; Collatz *et al.*, 1998; Sage and Monson, 1999). Approximately half of the ~10,000 grass and sedge species have C₄ photosynthesis, but fewer than 2,000 of the dicotyledonous species exhibit C₄ photosynthesis. Given their disproportionate influence on global productivity, C₄ plants have attracted much attention by the ecophysiological and ecosystem communities (Sage and Monson, 1999). Yet our understanding of animal preferences for C₃ *versus* C₄ plants is still limited (Heckathorn *et al.*, 1999). Carbon isotope ratio (δ¹³C) analyses of modern mammalian herbivore teeth suggest that mammals exhibit a distinct preference for either C₃ or C₄ taxa, with limited number of species being mixed feeders (Fig. 3). McNaughton and Georgiadis (1986) and references within Heckathorn *et al.* (1999) suggest that mammals exhibit limited preference for C₃ *versus* C₄, but that the primary differences in the African savanna are tree/shrub (C₃) *versus* grass (C₄) feeding patterns. In contrast, feeding trials repeatedly show that the digestibility of C₄ plants by mammalian grazers is lower than for C₃ plants (Aiken *et al.*, 1983; Wilson and Hattersley, 1983, 1989; Wilson, 1991; Wilson *et al.*, 1991). The basis for dietary preference of C₃/C₄ grasses by mammalian grazers is not understood at the moment. Nevertheless, the available evidence suggests that C₃/C₄ dietary differences do play a role in diet selection. Since the earliest carbon-isotope insect field

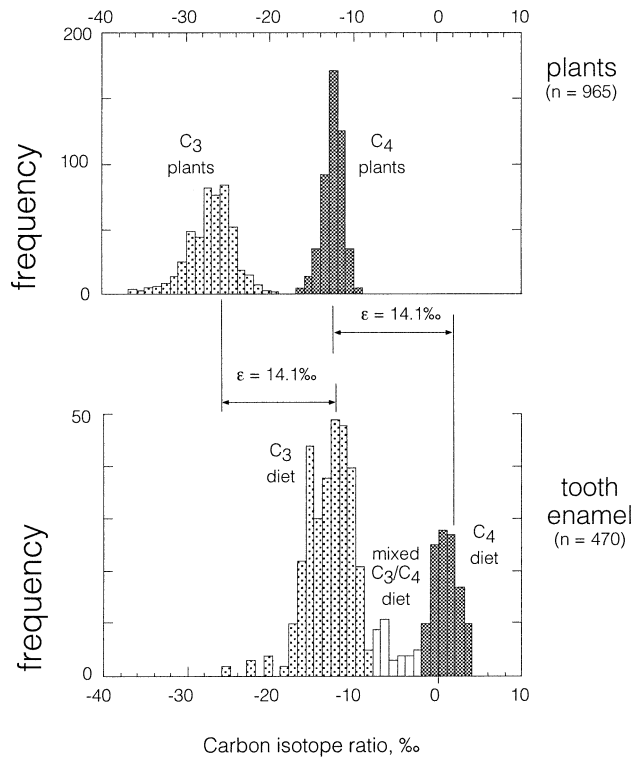


FIG. 3. Histograms of the carbon isotope ratios of modern grasses and modern tooth enamel. Adapted from Cerling *et al.* (1997).

studies, a C₃/C₄ dietary preference has been evident (Boutton *et al.*, 1978; Fry *et al.*, 1978; Heidorn and Joern, 1984). Caswell and Reed (1976) showed that when grasshoppers normally feeding on C₃ grasses were fed a C₄ grass, much of the leaf tissue passed through the crop undigested.

The dietary quality of C₃ and C₄ grasses is different. C₄ grasses maintain lower protein contents than do C₃ grasses (120–180 *versus* 200–260 mol N m⁻²) (Ehleringer and Monson, 1993). In grasses, fiber content is higher than that of dicotyledonous leaves, especially since fibers are often associated with vascular tissues and grasses tend to have a more prominent and common vascular system (when compared to dicotyledonous leaves) (Sage and Monson, 1999). In C₄ grasses, the interveinal distances are shorter than those of C₃ grasses (Kawamitsu *et al.*, 1985; Dengler *et al.*, 1994; Dengler and Nelson, 1999). As a result the C/N ratio is much higher in C₄ grasses than in C₃ grasses (Fig. 4). The C/N ratio impacts both grazing efficiency and diet selection, suggesting that C₄ plants should be a less preferred food resource.

ATMOSPHERIC CO₂ AS A DRIVER OF C₃/C₄ DISTRIBUTIONS

The initial CO₂ fixation reaction in photosynthesis involves the carboxylation of ribulose biphosphate by the enzyme Rubisco to form 2 molecules of phosphoglyceric acid, a 3-carbon molecule and hence the name C₃ photosynthesis. Under reduced CO₂ partial pressures, this enzyme also exhibits an oxygenase ac-

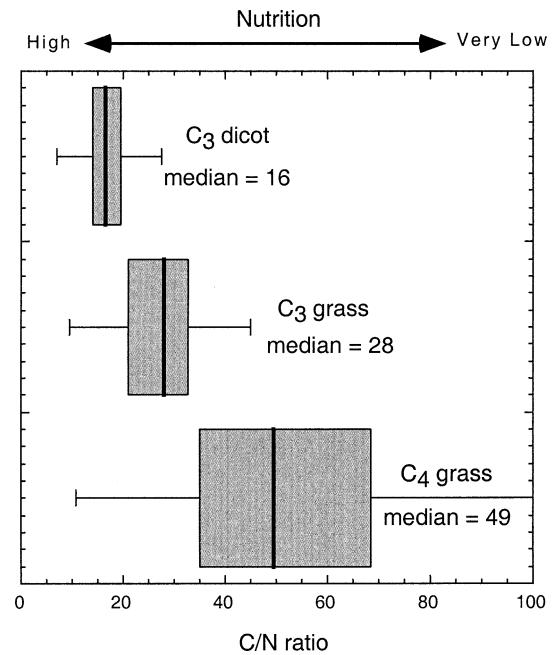


FIG. 4. The C/N ratios of C₃ dicots, C₃ grasses, and C₄ grasses. Adapted from Cerling and Ehleringer (2000).

tivity, such that at today's partial pressures, approximately 1 out of every 5 Rubisco cycles results in an oxygenase activity and not a carboxylation reaction (Kanai and Edwards, 1999). This oxygenase activity results in the evolution of CO₂ (photorespiration) and reduces the net carbon fixation into sugars by approximately 30% (Ehleringer, 1978; Ehleringer and Björkman, 1977; Sage and Monson, 1999; Sage and Percy, 2000). The rate at which the carboxylase *versus* oxygenase activity is expressed is a direct function of the atmospheric CO₂/O₂ ratio and so changes in global atmospheric composition will have a significant impact on photorespiratory rates.

One evolutionary solution to increased photorespiration under reduced atmospheric CO₂ is C₄ photosynthesis, where the normal C₃ cycle is restricted to the interior of the leaf and external to this the mesophyll cells catalyze the initial reaction: CO₂ combines with phosphoenolpyruvate to form a C₄-acid (Kanai and Edwards, 1999; Sage and Percy, 2000). This pathway appears in approximately 30 advanced Angiosperm families (see compilations in Ehleringer *et al.*, 1997; Sage and Monson, 1999) and is thought to have evolved independently at least 18 different times (Kellogg, 1999). C₄ photosynthesis is by far most common in grasses and sedges (6,000+ species) and less common in dicots (1,500+ species).

The modern distribution of C₄ grasses and sedges is determined primarily by temperature during the growing season, assuming that soil moisture is available (Teeri and Stowe, 1976; Collatz *et al.*, 1998). Grasses make up important components of ecosystems where rainfall is approximately equal to potential evapotranspiration; geographically this includes the tropical sa-

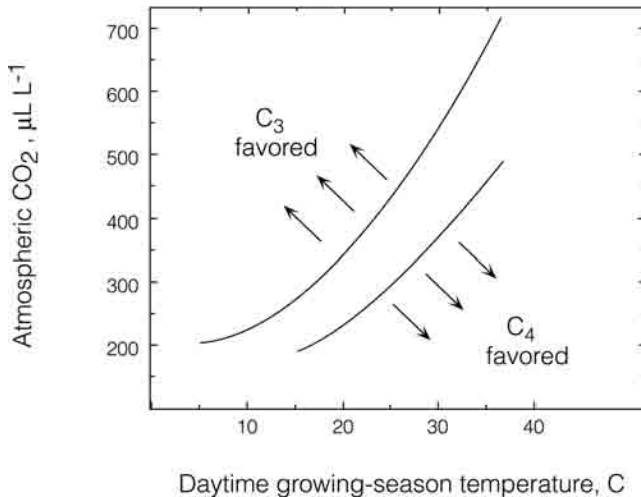


FIG. 5. Modeled crossover temperatures of the photosynthetic light-use efficiency (quantum yield) for C_3 and C_4 plants as a function of atmospheric CO_2 concentrations. The crossover temperature is defined as the temperature (for a particular atmospheric CO_2 concentration) at which the photosynthetic light-use efficiencies are equivalent for both the C_3 and the C_4 plant. Figure is modified from Ehleringer *et al.* (1997).

vannas, temperate to boreal steppes, and tropic to temperate semi-arid grasslands and deserts.

Cerling *et al.* (1997) and Ehleringer *et al.* (1997) modeled the fitness relationships between C_3 and C_4 taxa. Given similar canopies, differences in the light-use efficiencies of the two pathways result in distinct climate spaces favoring one photosynthetic pathway over the other (Fig. 5). At any given point in time, the atmospheric CO_2 value is constant, resulting in C_3 plants being more favored in cooler climates and C_4 plants in warmer climates. As the global atmospheric CO_2 values decreased, this model predicts that C_4 taxa should have first dominated in the warmest habitats and progressively expand poleward as atmospheric levels decreased (such as during glacial periods). Today's C_4 grass and sedge distributions are consistent with this model.

The quantum yield model of Figure 5 predicts that, at some time in the Earth's history, atmospheric CO_2 levels became low enough to cross a threshold which favored C_4 grasses over C_3 grasses. Cerling *et al.* (1997) reported that at 6–8 Ma b.p. there was an abrupt emergence of C_4 grasslands on a global scale. Using the $\delta^{13}C$ values of enamel in fossil teeth, there is a clear indication of the simultaneous expansion of C_4 grasslands (Fig. 6). In some locations, such as Pakistan, C_4 grasslands replaced C_3 grasslands. In other locations, such as North America, C_3 and C_4 taxa both persisted, but likely temporally or spatially separated along environmental gradients.

The expansion of C_4 photosynthesis 6–8 Ma b.p. coincides with changes in the abundances of mammalian grazers (Fig. 7). Cerling *et al.* (1998) measured the turnover of mammalian fauna through estimates of the number of new taxa added to a region and the

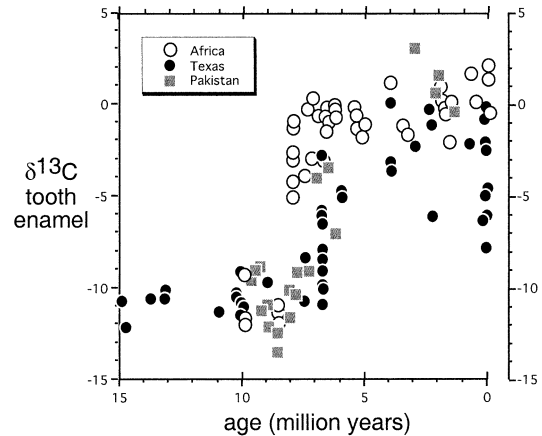


FIG. 6. $\delta^{13}C$ values for equids from North America (Texas), Pakistan (Siwaliks), and East Africa. All show an increase in $\delta^{13}C$ between about 8 and 6 million years ago, indicating a widespread increase in the global biomass of C_4 plants. Adapted from Cerling and Ehleringer (2000).

disappearance of taxa from a region over time. They showed that the period 6–8 Ma b.p. was associated with an increased turnover rate among grazing mammals. The exact causes of the emergence and loss of taxa are not established, but it is an unusual coincidence that it occurred during the same period as the global expansion of C_4 ecosystems. Diet is possibly an important consideration here. However, given the apparent selectivity of mammals for C_3 versus C_4 taxa (Fig. 3), it is possible that diet and mammalian turnover are related in more than a coincidental manner.

The quantum yield model of Figure 5 predicts a C_4 expansion during glacial periods when atmospheric CO_2 was low (~ 180 ppm) and a C_4 contraction during interglacial periods and contraction as atmospheric CO_2 increased to ~ 280 ppm. There is strong global evidence of C_4 expansion during glacial periods from a variety of sources. These data occur as $\delta^{13}C$ data from bogs, lake sediments, carbonates, and fossil bone materials from equatorial and temperate regions (Street-Perrott *et al.*, 1998; Huang *et al.*, 1999). The bog and lake sediment data are a largely continuous record of plant materials flowing into these basins, spanning 0–30 ka b.p. for lakes in Mexico and central Africa to 0–400 ka b.p. for the FUNZA II core in Colombia. Each of the cores indicate a loss of C_4 species at the end of the Last Glacial Maximum and a reversion to C_3 -dominated ecosystems. The soil carbonate data are from caliche in the arid Southwest of North America and indicate ecosystems dominated by C_4 vegetation in areas now dominated by C_3 vegetation. Based on tooth enamel studies, mammoths, camels, and equids, that lived during the last glacial in western North America contained a significant C_4 fraction in their diets (Connin *et al.*, 1998).

The emergence of generalized patterns and the mechanistic basis for why animals might prefer C_3 versus C_4 diets remain to be clarified. Although there is evidence that digestion efficiencies of animals differ

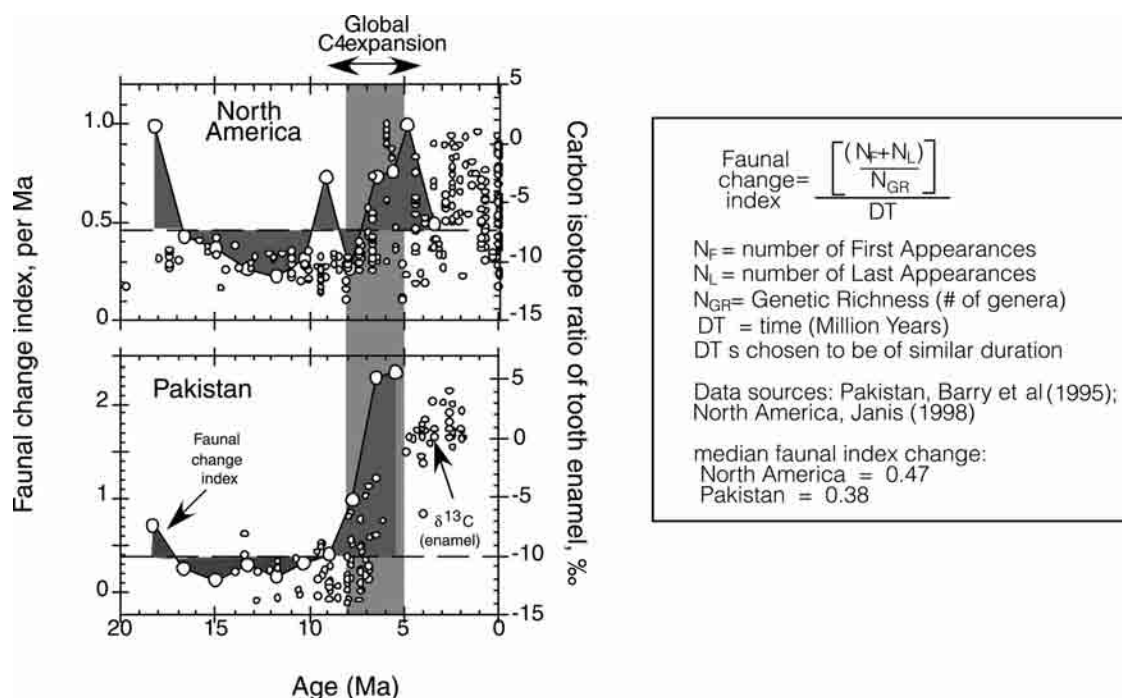


FIG. 7. The emergence of C₄ photosynthesis coincides with major changes in the abundances of mammalian grazers. Faunal Change Index from Pakistan, represented by the number of first (n_f) and last (n_l) occurrences, including only occurrences (n_o), normalized to species richness (n_s). The Faunal Change Index is normalized to 1.0 for the total data set. Adapted from Cerling *et al.* (1998) and Cerling and Ehleringer (2000).

when fed C₃ *versus* C₄ grasses (Wilson, 1991), the extent to which differences in digestion impact animal efficiency are speculative at the moment. Yet there is reason to believe that dietary efficiency and fitness should be correlated with each other.

It is anticipated that atmospheric CO₂ levels will be double the current values by the end of this century. Until mankind's thirst for fossil fuels is quenched, it is likely that atmospheric CO₂ will continue to rise beyond levels experienced in the recent history of this planet. The quantum yield model predicts that as CO₂ levels rise, the atmosphere concentrations will once again cross the CO₂-threshold where C₄ plants do not have a competitive advantage over C₃ plants from the standpoint of reduced photorespiration and enhanced light-use efficiency. Will C₄ plants disappear in the future? That answer is unclear, because other aspects of global change are occurring, which also tend to favor C₄ taxa. These additional global changes include forest to grassland conversions (particularly in the tropics), biological invasions (particularly weedy species), and the fact that many of today's most prominent crops are C₄ plants (*e.g.*, corn and sorghum). Regardless of whether or not C₄ plants are as common among subtropical and tropical ecosystems, changes in atmospheric CO₂ will have continued impacts on the quality of forage available for herbivores.

ACKNOWLEDGMENTS

The materials presented in this manuscript were supported by a grant from the Packard Foundation and participation in the symposium by NSF grant IBN-0097876.

REFERENCES

- Agrell, J., E. P. McDonald, and R. L. Lindroth. 2000. Effects of CO₂ and light on tree phytochemistry and insect performance. *Oikos* 88:259–272.
- Aiken, D. E., J. R. Wilson, and W. R. Windham. 1983. Site and rate of tissue digestion in leaves of C₄, C₃, and intermediate *Panicum* species. *Crop Sci.* 23:155–157.
- Arnold, J. A., III, J. G. Zaller, C. Ziegler, H. Zandt, and Ch. Körner. 1995. Leaf quality and insect herbivory in model tropical plant communities after long-term exposure to elevated atmospheric CO₂. *Oecologia* 104:72–78.
- Berner, R. A. 1991. A model for atmospheric CO₂ over Phanerozoic time. *Am. J. Sci.* 291:339–376.
- Berner, R. A. 1997. The rise of plants and their effect on weathering and atmospheric CO₂. *Science* 276:544–546.
- Boutton, T. W., G. N. Cameron, and B. N. Smith. 1978. Insect herbivory on C₃ and C₄ grasses. *Oecologia* 36:21–32.
- Caswell, H. and F. Reed. 1976. Plant-herbivore interactions: The indigestibility of C₄ bundle sheath cells by grasshoppers. *Oecologia* 26:151–156.
- Caswell, H., F. Reed, S. N. Stephenson, and P. A. Werner. 1973. Photosynthetic pathways and selective herbivory: A hypothesis. *Am. Nat.* 107:465–479.
- Cerling, T. E. and J. R. Ehleringer. 2000. Welcome to the C₄-world. *In* R. A. Gastaldo and W. M. DiMichele (eds.), *Phanerozoic terrestrial ecosystems*. The Paleontology Society Papers 6:273–286.
- Cerling, T. E., J. M. Harris, B. J. MacFadden, M. G. Leakey, J. Quade, V. Eisenmann, and J. R. Ehleringer. 1997. Global vegetation change through the Miocene-Pliocene boundary. *Nature* 389:153–158.
- Cerling, T. E., J. M. Harris, B. J. MacFadden, J. Quade, M. G. Leakey, V. Eisenmann, and J. R. Ehleringer. 1998. Miocene-Pliocene shift: One step or several? *Nature* 393:127.
- Collatz, G. J., J. A. Berry, and J. S. Clark. 1998. Effects of climate and atmospheric CO₂ partial pressure on the global distribution of C₄ grasses: Present, past, and future. *Oecologia* 114:441–454.
- Connin, S. L., J. Betancourt, and J. Quade. 1998. Late Pleistocene

- C₄ plant dominance and summer rainfall in the southwestern United States from isotopic study of herbivore teeth. *Quaternary Res.* 50:179–193.
- Cowling, S. A. and R. F. Sage. 1998. Interactive effects of low atmospheric CO₂ and elevated temperature on growth, photosynthesis and respiration in *Phaseolus vulgaris*. *Plant Cell Environ.* 21:427–435.
- Curtis, P. S. and X. Wang. 1998. A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* 113:299–313.
- Dengler, N. G. and T. Nelson. 1999. Leaf structure and development in C₄ plants. In R. F. Sage and R. K. Monson (eds.), *C₄ plant biology*, pp. 133–172. Academic Press, San Diego.
- Dengler, N. G., R. E. Dengler, P. M. Donnelly, and P. W. Hattersley. 1994. Quantitative leaf anatomy of C₃ and C₄ grasses (Poaceae): Bundle sheath and mesophyll surface area relationships. *Ann. Bot.* 73:241–255.
- Diaz, S., L. H. Fraser, J. P. Grime, and V. Falczuk. 1998. The impact of elevated CO₂ on plant-herbivore interactions: Experimental evidence of moderating effects at the community level. *Oecologia* 117:177–186.
- Ehleringer, J. R. 1978. Implications of quantum yield differences on the distribution of C₃ and C₄ grasses. *Oecologia* 31:255–267.
- Ehleringer, J. R. and O. Björkman. 1977. Quantum yields for CO₂ uptake in C₃ and C₄ plants: Dependence on temperature, CO₂ and O₂ concentration. *Plant Physiol.* 59:86–90.
- Ehleringer, J. R., T. E. Cerling, and B. R. Helliker. 1997. C₄ photosynthesis, atmospheric CO₂, and climate. *Oecologia* 112:285–299.
- Ehleringer, J. R. and R. K. Monson. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Ann. Rev. Ecol. Syst.* 24:411–439.
- Ekart, D. D. and T. E. Cerling. 1999. A 400 million year carbon isotope record of pedogenic carbonate: Implications for atmospheric carbon dioxide. *Am. J. Sci.* 299:805–817.
- Fry, B., A. Joern, and P. L. Parker. 1978. Grasshopper food web analysis: Use of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. *Ecology* 59:498–506.
- Heckathorn, S. A., S. J. McNaughton, and J. S. Coleman. 1999. C₄ plants and herbivory. In R. F. Sage and R. K. Monson (eds.), *C₄ plant biology*, pp. 285–312. Academic Press, San Diego.
- Heidorn, T. and A. Joern. 1984. Differential herbivory on C₃ versus C₄ grasses by the grasshopper *Ageneotrix deorum* (Orthoptera: Acridae). *Oecologia* 65:19–25.
- Huang, Y., K. H. Freeman, T. I. Eglinton, and F. A. Street-Perrott. 1999. δ¹³C analysis of individual lignin phenols in Quaternary lake sediments: A novel proxy for deciphering past terrestrial vegetation changes. *Geology* 27:471–474.
- Kanai, R. and G. E. Edwards. 1999. The biochemistry of C₄ photosynthesis. In R. F. Sage and R. K. Monson (eds.), *C₄ plant biology*, pp. 49–87. Academic Press, San Diego.
- Kawamitsu, Y., S. Hahoyama, S. Agata, and T. Takeda. 1985. Leaf interveinal distances corresponding to anatomical types in grasses. *Plant Cell Physiol.* 26:589–593.
- Kellogg, E. A. 1999. Phylogenetic aspects of the evolution of C₄ photosynthesis. In R. F. Sage and R. K. Monson (eds.), *C₄ plant biology*, pp. 411–444. Academic Press, San Diego.
- Körner, C. 2000. Biosphere responses to CO₂ enrichment. *Ecol. Appl.* 10:1590–1619.
- Lemarchand, D., J. Gaillardet, É. Lewin, and C. J. Allègre. 2000. The influence of rivers on marine boron isotopes and implications for reconstructing past ocean pH. *Nature* 408:951–954.
- McDonald, E. P., J. Agrell, and R. L. Lindroth. 1999. CO₂ and light effects on deciduous trees: Growth, foliar chemistry, and insect performance. *Oecologia* 119:389–399.
- McNaughton, S. J. and N. J. Georgiadis. 1986. Ecology of African grazing and browsing mammals. *Ann. Rev. Ecol. Syst.* 17:39–65.
- Mooney, H. A., J. Canadell, F. S. Chapin, III, J. R. Ehleringer, Ch. Körner, R. E. McMurtrie, W. J. Parton, L. F. Pitelka, and E.-D. Schulze. 1999. Ecosystem physiology responses to global change. In B. H. Walker, W. Steffen, J. Canadell, and J. Ingram (eds.), *The terrestrial biosphere and global change: Implications for natural and managed ecosystems*, pp. 141–189. Cambridge Univ. Press, Cambridge.
- Overdieck, D., C. Reid, and B. R. Strain. 1988. The effects of pre-industrial and future CO₂ concentrations on growth, dry matter production and the C/N relationship in plants at low nutrient supply: *Vigna unguiculata* (cowpea), *Abelmoschus esculentus* (okra), and *Raphanus sativus* (radish). *Angew. Botanik* 62:119–134.
- Owensby, C. E., R. C. Cochran, and L. M. Auen. 1996. Effects of elevated carbon dioxide on forage quality for ruminants. In C. Körner and F. A. Bazzaz (eds.), *Carbon dioxide, populations, and communities*, pp. 363–371. Academic Press, San Diego.
- Pagani, M., M. A. Arthur, and K. H. Freeman. 1999a. Miocene evolution of atmospheric carbon dioxide. *Paleoceanography* 14: 273–292.
- Pagani, M., K. H. Freeman, and M. A. Arthur. 1999b. Late Miocene atmospheric CO₂ concentrations and the expansion of C₄ grasses. *Science* 285:876–879.
- Pearson, P. N. and M. R. Palmer. 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* 406:695–699.
- Petit, J. R., J. Jouzel, D. Raynaud, N. I. Barkov, J.-M. Barnola, I. Basile, M. Benders, J. Chappellaz, M. Davis, G. Delaygue, M. Delmotte, V. M. Kotlyakov, M. Legrand, V. Y. Lipenkov, C. Lorius, L. Pépin, C. Ritz, E. Saltzman, and M. Stievenard. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429–436.
- Polley, H. W., H. B. Johnson, B. D. Marino, and H. S. Mayeux. 1993. Increase in C₃ plant water-use efficiency and biomass over glacial to present CO₂ concentrations. *Nature* 361:61–64.
- Polley, H. W., H. B. Johnson, and H. S. Mayeux. 1992. Carbon dioxide and water fluxes of C₃ annuals and C₃ and C₄ perennials at subambient CO₂ concentrations. *Funct. Ecol.* 6:693–703.
- Roth, S., R. L. Lindroth, J. C. Volin, and E. L. Kruger. 1998. Enriched atmospheric CO₂ and defoliation: Effects on tree chemistry and insect performance. *Global Change Biol.* 4:419–430.
- Sage, R. F. 1994. Acclimation of photosynthesis to increasing atmospheric CO₂: The gas exchange perspective. *Photosynth. Res.* 39:351–368.
- Sage, R. F. and R. K. Monson. 1999. *C₄ plant biology*. Academic Press, San Diego.
- Sage, R. F. and R. W. Pearcy. 2000. The physiological ecology of C₄ photosynthesis. In R. C. Leegood, T. D. Sharkey, and S. von Caemmerer (eds.), *Photosynthesis: Physiology and metabolism*, pp. 497–532. Kluwer Academic Publishers, Amsterdam.
- Street-Perrott, F. A., Y. Huang, R. A. Perrott, and G. Eglinton. 1998. Carbon isotopes in lake sediments and peats of last glacial age: Implications for the global carbon cycle. In H. Griffiths (ed.), *Stable isotopes*, pp. 381–396. BIOS Scientific Publishers Ltd.
- Teeri, J. A. and L. G. Stowe. 1976. Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia* 23:1–12.
- Ward, S. J. E., G. F. Midgley, and M. H. Jones. 1999. Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentrations: A meta-analytic test of current theories and perceptions. *Global Change Biol.* 5:723–741.
- Ward, J. K., D. T. Tissue, R. B. Thomas, and B. R. Strain. 1999. Comparative responses of model C₃ and C₄ plants to drought in low and elevated CO₂. *Global Change Biol.* 5:857–867.
- Wilson, J. R. 1991. Plant structures: Their digestive and physical breakdown. *Recent Adv. Nutr. Herbivores* 10:207–215.
- Wilson, J. R., B. Deinum, and F. M. Engles. 1991. Temperature effects on anatomy and digestibility of leaf and stem of tropical and temperate forage species. *Nether. J. Agricult.* 39:31–38.
- Wilson, J. R. and P. W. Hattersley. 1983. *In vitro* digestibility of bundle sheath cells in rumen fluid and its relation to the suberized lamella and C₄ photosynthetic type in *Panicum* species. *Grass Forage Science* 38:219–223.
- Wilson, J. R. and P. W. Hattersley. 1989. Anatomical characteristics and digestibility of leaves of *Panicum* and other grass genera with C₃ and different types of C₄ photosynthetic pathway. *Austral. J. Agricult. Res.* 40:125–136.