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Atmospheric carbon dioxide is reduced to organic forms through photosynthesis. Among terrestrial and aquatic autotrophs, there are three photosynthetic pathways. Here we discuss the ecological and evolutionary aspects of C₃ and C₄ photosynthesis, the two most widely distributed pathways.

Three photosynthetic pathways exist among terrestrial plants: C₃, C₄, and *crassulacean acid metabolism* (CAM) photosynthesis. C₃ photosynthesis is the ancestral pathway for carbon fixation and occurs in all taxonomic plant groups. The term C₃ photosynthesis is based on the observation that the first product of photosynthesis is a 3-carbon molecule. In C₄ photosynthesis, the initial photosynthetic product is a 4-carbon molecule. C₄ 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 (most trees and shrubs). CAM photosynthesis, in honor of the plant family in which this pathway was first documented, occurs in many epiphytes and succulents from very arid regions. However, CAM photosynthesis is sufficiently limited in distribution that CAM plants are not an appreciable component of the global carbon cycle. This section focuses on the factors influencing the dynamics of C₃ and C₄ dominated ecosystems.

C₃ and C₄ photosynthesis are relevant to global change studies. These two photosynthetic pathways respond quite differently to changes in atmospheric carbon dioxide (CO₂) concentration and to changes in temperature. From a global change perspective, the kind of photosynthetic pathway present influences the magnitude of carbon fixation by the ecosystem, the quality of the plant food resource available to animals, and the isotopic composition of CO₂ released to the atmosphere.

C₃ photosynthesis is a multi-step process in which the carbon from CO₂ is fixed into stable organic products; it occurs in virtually all leaf mesophyll cells (Figure 1). In the first step, ribulose biphosphate (RuBP) carboxylase-oxygenase (Rubisco) combines RuBP (a 5C molecule) with CO₂ to form two molecules of phosphoglycerate (3C molecule). However, Rubisco is an enzyme capable of catalyzing two distinct reactions: one leading to the formation of two molecules of phosphoglycerate when CO₂ is the substrate and the other resulting in one molecule each of phosphoglycerate and phosphoglycolate (2C molecule) when oxygen (O₂) is the substrate. The latter oxygenase

reaction results in less net carbon fixation and eventually leads to the production of CO₂ in a process known as *photorespiration*.

The proportion of the time that Rubisco catalyzes CO₂ versus O₂ is dependent on the [CO₂]/[O₂] ratio; the reaction is also temperature dependent, with oxygenase activity increasing with temperature. This dependence of Rubisco on the [CO₂]/[O₂] ratio establishes a firm link between current atmospheric conditions and photosynthetic activity. As a consequence of Rubisco sensitivity to O₂, the efficiency of the C₃ pathway decreases as atmospheric CO₂ decreases.

C₄ photosynthesis represents a biochemical and morphological modification of C₃ photosynthesis to reduce Rubisco oxygenase activity and thereby increase photosynthetic rate in low CO₂ environments such as we have today (Figure 3). In C₄ plants, the C₃ 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, phosphoenolpyruvate (PEP) carboxylase, fixes CO₂ (but as HCO₃) into oxaloacetate, a C₄ acid. The C₄ acid diffuses to the bundle sheath cell, where it is decarboxylated and refixed in the normal C₃ pathway. As a result of the higher activity of PEP carboxylase, CO₂ is effectively concentrated in the regions where Rubisco is located and this results in a high CO₂/O₂ ratio and limited photorespiratory activity. The additional cost of C₄ photosynthesis is the adenosine triphosphate (ATP) requirement associated with the regeneration of PEP from pyruvate.

C₄ photosynthesis is advantageous under low atmospheric CO₂ and/or high temperatures. The advantages of C₄ photosynthesis occur in lower CO₂ environments and/or high temperature environments, where photorespiration rates are relatively high in C₃ plants. Under these conditions, the efficiency of C₄ photosynthesis is greater than that of C₃ photosynthesis. However, under elevated CO₂ environments or at cool temperatures, the efficiency of photosynthesis is greater in C₃ photosynthesis because photorespiration is reduced and the additional ATP cost of C₄ photosynthesis makes it less efficient. We present these trade-offs graphically in Figure 2. From these light-use efficiency model predictions, it is clear that C₄ plants are not expected in environments where atmospheric CO₂ is greater than ≈600 parts per million (ppm). As atmospheric CO₂ decreases, C₄ plants should become most common first in the warmest environments, than in progressively cooler environments as CO₂ levels then continue to decrease.

The recent history of Earth has been one of decreasing atmospheric CO₂ levels. The atmospheric CO₂ levels are thought to have been higher in the Cretaceous than today (Figure 3). Some time following the Cretaceous (perhaps during the late Miocene), CO₂ levels decreased to about

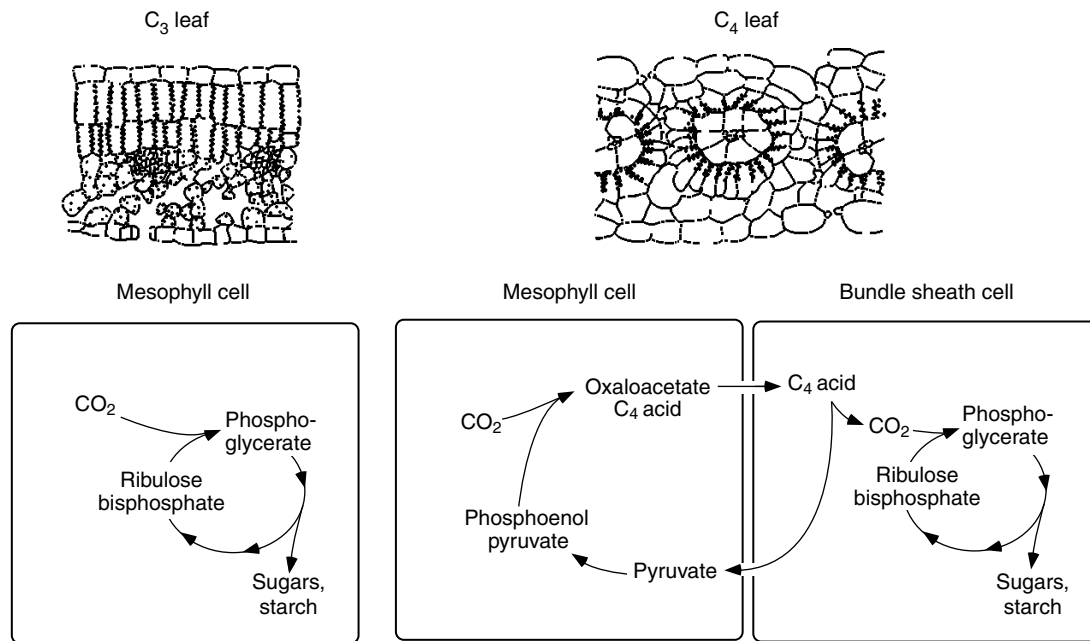


Figure 1 Leaf anatomy and basic photosynthetic biochemistry of C₃ and C₄ photosynthesis

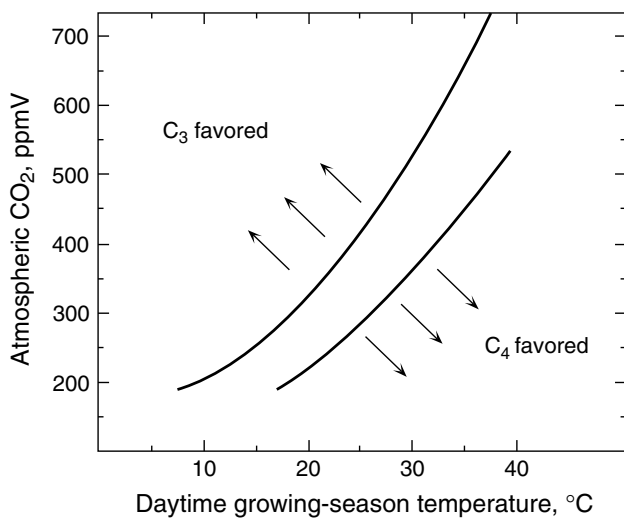


Figure 2 Modeled crossover temperatures of the photosynthetic light-use efficiency (quantum yield) for C₃ and C₄ plants as a function of atmospheric CO₂ concentrations. The crossover-temperature is defined as the temperature (for a particular atmospheric CO₂ concentration, in parts per million by volume, ppmV) at which the photosynthetic light-use efficiencies are equivalent for both the C₃ and the C₄ plant. (Figure is modified from Ehleringer *et al.*, 1997)

500 ppm. During recent glacial–interglacial cycles, atmospheric CO₂ has fluctuated between 180 and 280 ppm. Since the dawn of the Industrial Revolution, atmospheric CO₂ levels have risen and these increases have been most dramatic since the 1950s (Figure 3).

C₄ photosynthesis occurs primarily within monocotyledonous plants. The flowering plants are classified as monocotyledons or dicotyledons. Approximately 6000 of the 15 000 monocotyledonous plants (primarily grasses and sedges) possess C₄ photosynthesis. In contrast, only about 1600 of the 300 000 dicotyledonous plants possess C₄ photosynthesis. In terms of taxonomic diversity, C₄ photosynthesis occurs in 401 monocotyledonous genera and 86 dicotyledonous genera.

C₄ grasslands emerged globally as an important ecosystem 6–8 Ma ago. Carbon isotope ratios are distinct and different between C₃ and C₄ plants (Figure 4). Variations in the carbon isotope ratios within a pathway reflect changes in environmental conditions and genetic differences among plants within a pathway type. The diet of animals (tissues in extant animals and tooth enamel in fossils) is reflected in their carbon isotopic composition. The offset of 14‰ between carbonate in tooth enamel and the C₃/C₄ food diet as shown in Figure 4 reflects a fractionation associated with apatite (calcium phosphate carbonate) formation in the tooth. Since animal fossils, such as teeth, are much more common in semi-arid and arid ecosystems, we can use the carbon isotopes in tooth enamel to reconstruct the presence of C₄-dominated ecosystems through time.

Between 8 and 6 Ma there was a global expansion of C₄ ecosystems (Figure 5). There is no conclusive evidence for the presence of C₄ biomass in the diets of mammals before 8 Ma, although the presence of small amounts of C₄ biomass is not excluded because of the uncertainty in the δ¹³C end member for C₃ plants. By 6 Ma there is abundant evidence for significant C₄ biomass in Asia, Africa, North

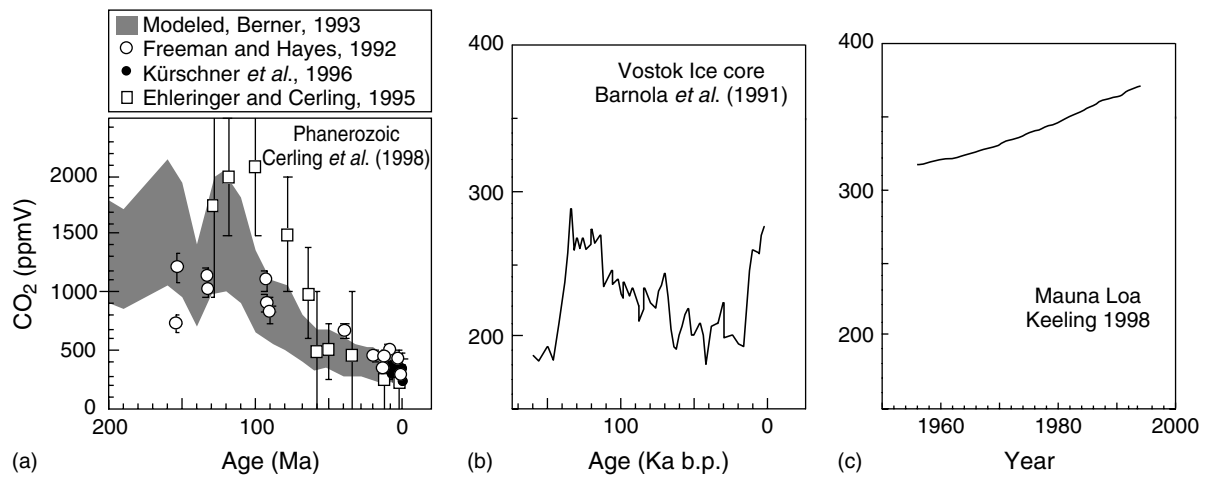


Figure 3 Patterns of atmospheric CO₂ concentrations through time. (a) Reconstruction of paleo CO₂ levels between 200 million years (Ma) ago and present; (adapted from Cerling *et al.*, 1998). (b) Reconstruction of atmospheric CO₂ from ice cores for the past 160 000 years; (adapted from Barnola *et al.*, 1991) (before present, b.p.). (c) Atmospheric CO₂ concentrations recorded at Mauna Loa, Hawaii since 1958; (adapted from Keeling and Whorf, 2000)

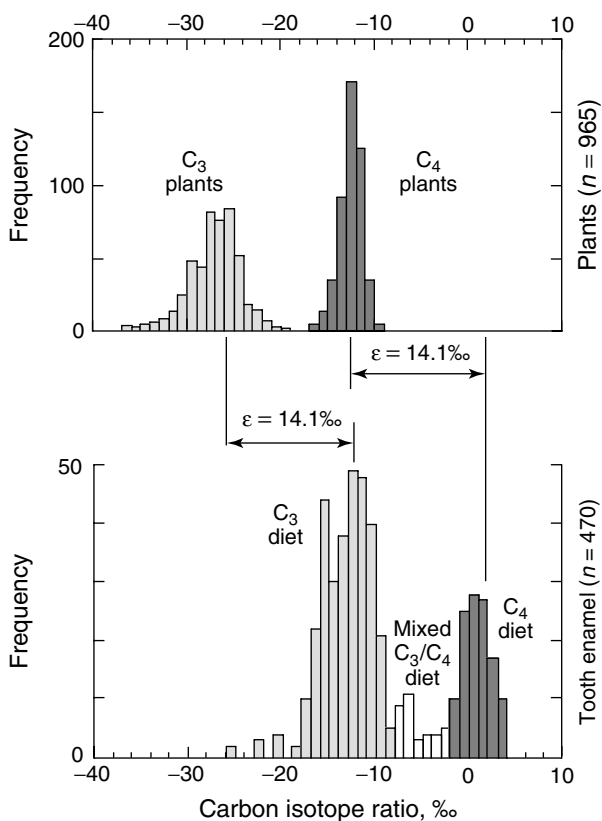


Figure 4 Histograms of the carbon isotope ratios of modern grasses and modern tooth enamel; (adapted from Cerling *et al.*, 1997)

America, and South America, but not in Europe. 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 C₃ ecosystems earlier in the Miocene, the C₃ Pakistani ecosystem was almost completely replaced by a C₄ ecosystem; African, North American, and South American ecosystems retained both C₃ and C₄ components. European and northern portions of North American ecosystems did not show any change in the fraction of C₃ biomass, remaining at virtually 100% C₃ ecosystems. The mixture of both C₃ and C₄ components within a grazing ecosystem can be achieved in one of two ways: a temporal separation with C₃ grasses active in winter–spring and C₄ grasses active in summer or by a monsoonal system with C₄ grasses and C₃ woody vegetation.

The isotopic evidence in tooth enamel indicates clearly that the expansion of C₄ ecosystems was a global phenomenon, persisting until today. The C₃/C₄ changes were accompanied by significant faunal changes in many parts of the world. It is unlikely that the global expansion of C₄ biomass in the late Miocene was due solely to higher temperatures or to the development of arid regions. There have always been regions of Earth with hot, dry climates. To explain the simultaneous global expansion of C₄ plants requires a global process. The light-use efficiency model (Figure 2) suggests that changes in atmospheric CO₂ are a strong possibility for this global mechanism. The supporting evidence indicates that the global expansion of C₄ 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 abundance of C₄ photosynthesis in moving from warm equatorial to cooler temperate latitudes.

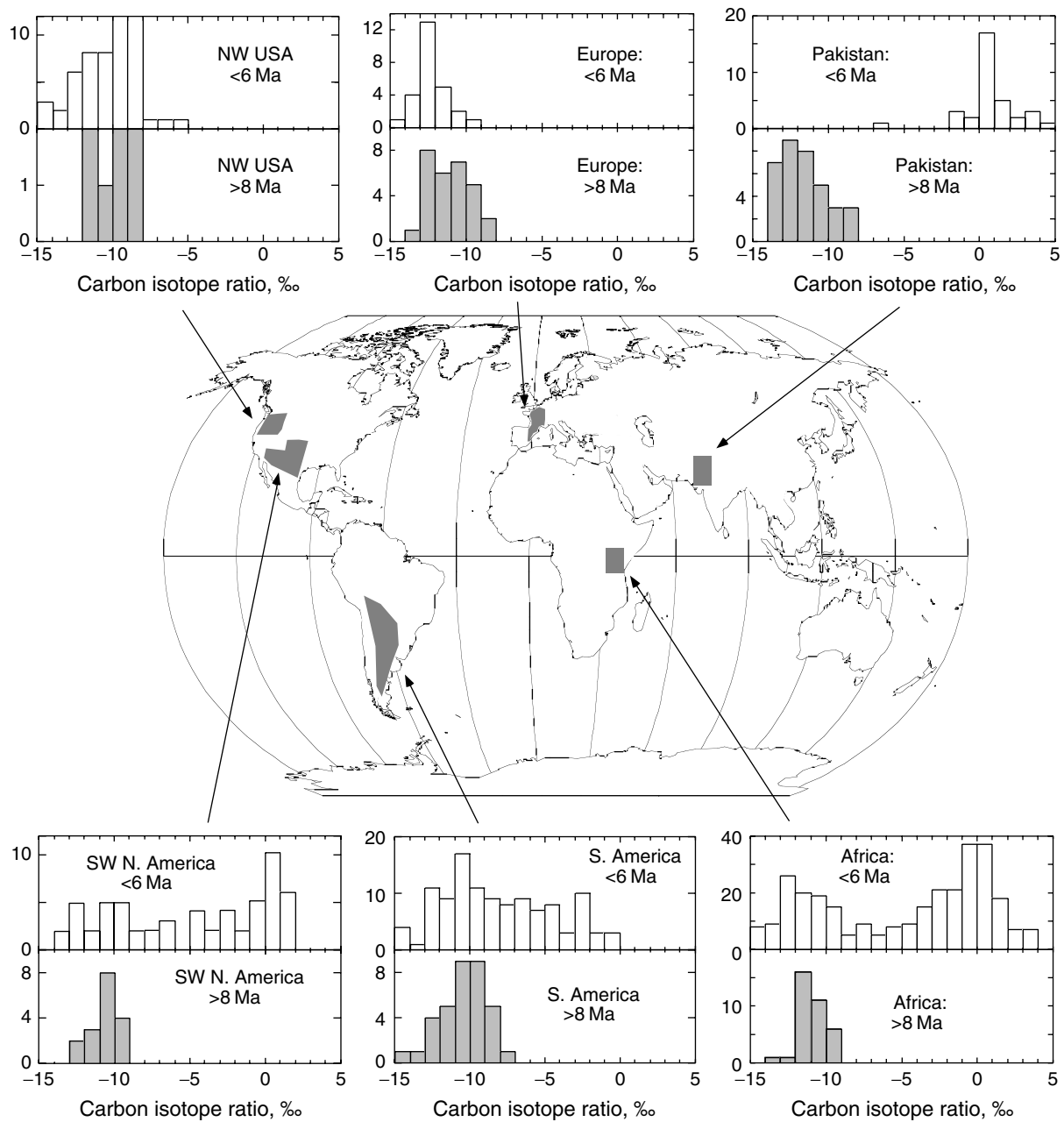


Figure 5 Histograms comparing the carbon isotope ratio values for fossil tooth enamel older than 8 Ma (lower charts) with those that are younger than 6 Ma for six regions of Earth; (adapted from Cerling *et al.*, 1998)

C_4 grasslands are thought to have a wider distribution during glacial periods than they do today. The model in Figure 2 predicts greater global proportions of C_4 biomass during Pleistocene glacial, than interglacial periods. The published literature of organic $\delta^{13}C$ values in peat bogs and lakes from Central and Eastern Africa in regions (areas currently dominated by rain forest ecosystems) strongly suggest extensive C_4 expansion during the last full glacial period. Within western portions of North American, soil carbonate data also indicate that C_4 ecosystems were

more extensive during the last glacial period than they are today. The model in Figure 2 suggests that mechanically C_4 grasses were much more common during the glacial period when C_3 vegetation would have been CO_2 starved. Following deglaciation, the decline in C_4 abundances appears to be correlated with increases in atmospheric CO_2 levels.

What of the future? It is anticipated that atmospheric CO_2 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, but it appears that they will not have a competitive advantage. Certainly humans will continue to plant C₄ crops since 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 distributions of C₄ taxa.

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