10. The Influence of Atmospheric CO_2, Temperature, and Water on the Abundance of C_3/C_4 Taxa

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10.1 Introduction

C_3 and C_4 photosynthesis are the two most common photosynthetic pathways contributing to global primary productivity, with Crassulacean Acid Metabolism (CAM), a third pathway found in succulents, being of limited importance to global productivity (Sage and Monson 1999; Still et al. 2003). Atmospheric CO_2 is the carbon source for all three pathways; one key distinguishing feature among them, however, is that both C_4 and CAM photosynthesis involve a CO_2-concentrating mechanism to create high CO_2 concentrations at the site of photosynthetic carboxylation. In contrast, C_3 photosynthesis relies solely on diffusion of CO_2 from the outside atmosphere to the sites of photosynthetic CO_2 fixation (Fig. 10.1). Hence, it is clear that changes in the atmospheric CO_2 levels will more likely influence the photosynthetic activities of C_3 than of C_4 and CAM plants. In this chapter, we focus on how changes in atmospheric CO_2 might favor plants with C_3 versus C_4 photosynthesis and, in particular, consider how environmental and ecological factors will affect these C_3/C_4 abundance relationships.

Quite surprisingly, C_4 photosynthesis is found only among the most advanced land plants. C_4 is known to occur among the Angiosperms but has not been reported among older taxonomic groups, such as Gymnosperms (e.g., pines and other coniferous trees) or the Pteridopyhta (e.g., ferns) (Ehleringer and Monson 1993; Sage and Monson 1999; Chapter 9). Within the Angiosperms, approx

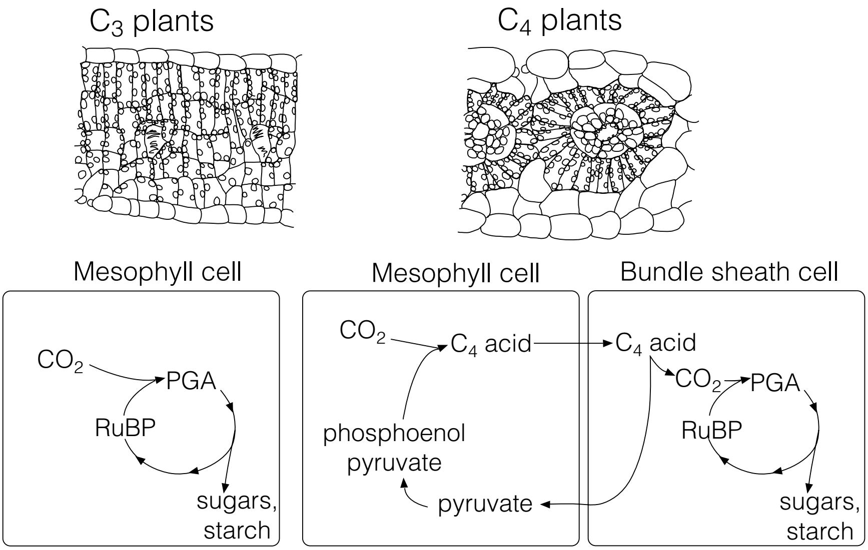

Figure 10.1. Cross-sections of leaves of C_3 and C_4 plants with the relevant features of the photosynthetic cycle for each pathway. Note that C_4 photosynthesis is essentially C_3 photosynthesis enclosed by a carbon-concentrating mechanism.

6000 of the approx 10,000 Monocotyledonae (hereafter monocots) have C_4 photosynthesis, whereas only approx 1500 of the approx 300,000 Dicotyledonae (hereafter dicots) have C_4 photosynthesis (Sage and Monson 1999). Within both monocots and dicots, C_4 photosynthesis has polyphyletic origins and appears to occur among only the most recently derived taxa, suggesting an evolutionary origin of only 10 to 15 million years ago.

Several general patterns emerge with respect to the distributions of C_3/C_4 taxa among different plant life forms (see Chapter 9). In today's world, C_4 taxa are more common among subtropical and tropical taxa; they are essentially absent from arctic and temperate taxa (Sage and Monson 1999). Furthermore, within both dicot annuals and annual/perennial monocots, C_4 taxa are typically active during the summer periods and far less common among the spring-active floras. Within the shrub life form, C_4 taxa are uncommon, but when they do occur they are largely halophytes (plants occurring on saline soils). Halophytes tend to be dicots instead of monocots, primarily in the family Chenopodiaceae. With perhaps one or two exceptions globally, C_4 photosynthesis is not found in trees. What emerges from these distribution patterns is that outside of saline soils, C_4 photosynthesis is found most commonly among herbaceous vegetation (both as annuals and as perennials). This may reflect an aspect of phylogenetic or evolutionary history, and it will certainly have ecological implications in the consideration of competition between low-stature C_4 herbaceous plants and tall C_3 trees.

The greater abundance of C_4 photosynthesis among the monocots may be a result of an anatomical pre-adaptation within this phylogenetic line. Ehleringer, Cerling, and Helliker (1997) and Sage (2001) discuss the importance of parallel venation in C_4 photosynthesis. Since the most common configuration of C_4 photosynthesis is a concentration of the C_3 cycle within the bundle sheath cells, having a parallel vein structure allows for a greater packing capacity of photosynthetic structures relative to the exposed surface area of a leaf blade. Dicots typically have a reticulate vein structure, which then results in a lower vein-packing density.

Beyond taxonomic and evolutionary inquiry, it is fair to question the value of understanding the dynamics of C_3 and C_4 taxa globally. For several key reasons, we should know the climatic and ecological factors controlling the abundances of C_4 taxa. First, in today's world, while C_4 taxa represent only approx 2% of the total species, they account for 25% to 30% of the global terrestrial primary productivity (Still et al. 2003). In a low-CO_2 world, such as during recent glacial periods, C_4 photosynthesis might have contributed an even greater proportion of global primary productivity (see Chapter 9). Second, there is ample evidence to suggest that herbivores (both insect and mammal) exhibit dietary preferences for one photosynthetic pathway over the other (summarized in Caswell et al. 1973; Ehleringer and Monson 1993; Sage and Monson 1999). Third, there is strong evidence to suggest that the relative abundances of C_3/C_4 ecosystems exhibit strong shifts over long temporal scales, such as between glacial-interglacial cycles, and that these changes may be related to atmospheric CO_2 (Talbot and Johannessen 1992; Aucour and Hillaire-Marcel 1994; Giresse, Maley, and Brenac 1994; Street-Perrott et al. 1997, 1998; Cowling and Sykes 1999; Huang et al. 1999, 2001; Boom et al. 2002; Harrison and Prentice 2003).

10.2 A Mechanistic Basis for the Advantage of C_4 Photosynthesis in a Low-CO_2 World

The enzyme Rubisco catalyzes the initial photosynthetic fixation of CO_2 in C_3 plants. Known more formally as ribulose bisphosphate carboxylase-oxygenase, Rubisco has both carboxylase and oxygenase activities:

$$\text{RuBP} + \text{CO}_2 \rightarrow 2\ \text{PGA} \tag{10.1}$$

$$\text{RuBP} + \text{O}_2 \rightarrow \text{PGA} + \text{PG} \tag{10.2}$$

where RuBP is ribulose bisphosphate, PGA is phosphoglycerate, and PG is phosphoglycolate. Subsequent oxidative metabolism of phosphoglycolate results in CO_2 loss and is known as photorespiration; the degree of oxygenase activity is a function of the atmospheric O_2/CO_2 ratio. Although Rubisco is thought to have originally evolved under anaerobic conditions, photosynthetic activity today in C_3 plants results in a relatively high photorespiration rate, simply because atmospheric CO_2 is low (~370 ppm) and atmospheric O_2 is high (~210,000 ppm). Roughly 25% to 30% of the Rubisco activity at 25°C is currently associated with oxygenase activity. Photorespiration rate is further enhanced by elevated temperature (Fig. 10.2). The photorespiratory increase with temperature occurs because Rubisco oxygenase activity is temperature sensitive, whereas carboxylase activity appears to be temperature insensitive.

The C_4 photosynthetic pathway represents a small but significant evolutionary change from C_3 photosynthesis. Biochemically, C_4 photosynthesis represents a CO_2 concentrating mechanism that achieves high CO_2 levels at the site of Rubisco activity (see Fig. 10.1). In C_3 plants, CO_2 diffuses into photosynthetic cells (resulting in lower-than-atmospheric values) and fixed by the enzyme Rubisco into phosphoglycerate (a 3C molecule). In C_4 plants, CO_2 (actually HCO_3-) is fixed more rapidly by PEP carboxylase into, initially, a 4C molecule. Since the activity of PEP carboxylase is faster than Rubisco, this leads to relatively high CO_2/O_2 levels inside bundle sheath cells, thereby eliminating photorespiration. Several C_4 photosynthetic subtypes exist (NADP-ME, NAD-ME, and PCK), with distribution following taxonomic lines (Sage and Monson 1999). The different photosynthetic subtypes represent different decarboxylation mechanisms.

The available evidence suggests that the atmospheric CO_2 levels 40 to 100 million years ago were higher than they are today (Ekart et al. 1999; see Chapter 2), and there is little likelihood that a C_4 photosynthetic carbon-concentrating

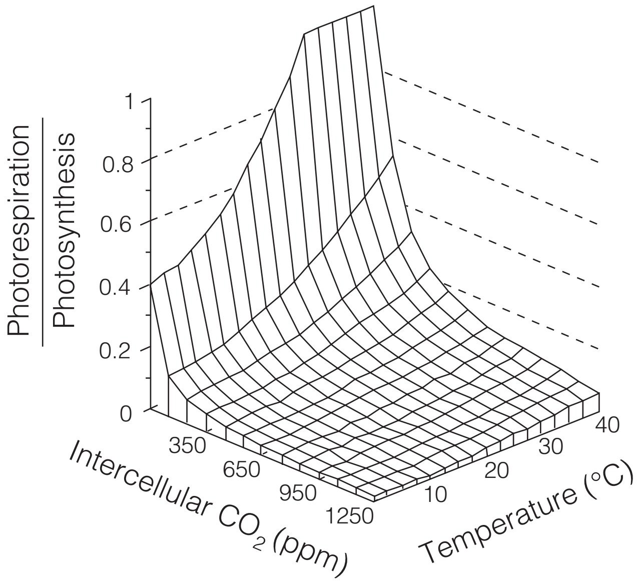

Figure 10.2. The relative proportion of photorespiration to photosynthesis in C_3 photosynthesis as a function of CO_2 and temperature. (Based on Ehleringer et al. 1991.)

mechanism would have been selectively advantageous under such conditions. Not too surprising, there is no fossil evidence to suggest that C_4 taxa were present under these high CO_2 conditions. In fact, since C_4 photosynthesis represents a CO_2 concentrating mechanism, it is likely that natural selection may not have favored the evolution of this pathway until CO_2 levels fell below some critical threshold (Ehleringer et al. 1991).

A common advantage of C_4 photosynthesis over C_3 photosynthesis is the lack of photorespiratory activity at the whole-leaf level. At low light levels, this difference is expressed as an enhanced photosynthetic quantum yield or light-use efficiency (Ehleringer and Björkman 1977; Ehleringer 1978; Ehleringer and Pearcy 1983; Sage 2001); at high light levels, photorespiration in today's atmosphere still results in a significant reduction in photosynthesis in C_3 plants. When individual leaves are exposed to higher light levels, the maximum quantum yield measured at low light levels may have little direct bearing on photosynthetic rate, but it is still an effective index of the relative inhibition of photosynthesis due to photorespiration (von Caemmerer 2000; Chapter 9). In this regard, the quantum yield serves a reliable indicator of the extent to which reduced CO_2 levels have resulted in lower photosynthetic rates in C_3 plants across a broad range of environmental conditions. The quantum yield of C_3 plants declined as temperatures increased (Fig. 10.3A), reflecting the negative impact of photorespiration on carbon gain.

Increasing atmospheric CO_2 levels increase quantum yield (reducing photorespiration), but the quantum yield still declines with increasing temperature. In contrast, the quantum yield of C_4 plants remains constant with temperature, since

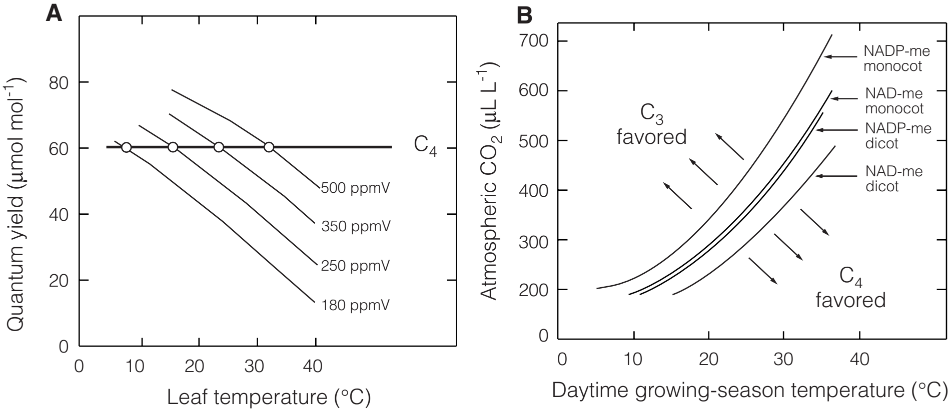

Figure 10.3. **(A)** The relationships between photosynthetic quantum yield (light-use efficiency) of C_3 and C_4 monocot taxa and temperature at several atmospheric CO_2 levels. **(B)** The prediction of where C_3 or C_4 taxa should predominate based on different combinations of atmospheric CO_2 and temperature. These curves are based on quantum yield relationships, Fig. 10.A. (Based on Ehleringer et al. 1997)

no photorespiratory activity is expressed at the leaf level. As a result of the different crossover points shown in Fig. 10.3A, we can construct a plot of those CO_2-temperature regimes where C_3 plants will have a photosynthetic advantage over C_4 plants and vice versa (Fig. 10.3B). The gap between the two central lines in the figure represents the intrinsic variations in quantum yield associated with the different C_4 subtypes.

Several distinct predictions can be made with respect to photosynthesis, temperature, and atmospheric carbon dioxide (Fig. 10.3B). First, at any point in Earth's history (and therefore at a single atmospheric CO_2 level), C_4 photosynthesis should be expected to occur largely in Earth's warmer regions with C_3 plants dominating the cooler regions. Second, as atmospheric CO_2 levels decreased in the past, the atmosphere of our planet crossed a threshold where C_4 photosynthesis became advantageous over C_3 photosynthesis, particularly at high growing-season temperatures. This necessarily implies warm temperatures during the growing season (therefore most likely a summer-wet or monsoon-type environment, but one in which grasses are not shaded out). While we cannot specify the CO_2 level at which C_4 first became advantageous, the results shown in Fig. 10.3B suggest that the crossover favoring expansion of C_4 plants occurred at atmospheric CO_2 levels that are higher than the present (i.e., >370 ppm). Atmospheric CO_2 will not be the sole factor determining a selective advantage to C_4 plants, but the differential photorespiratory responses of C_3 and C_4 photosynthetic physiologies certainly implies that C_3 plants will be sensitive to high temperature environments, particularly as atmospheric CO_2 levels decrease. Lastly, the quantum yield model predicts that C_4 photosynthesis should be expected to expand significantly under low CO_2 conditions, such as occurred during glacial periods. Under glacial CO_2 levels of 180 ppm (see Chapter 4), C_3 plants should be getting close to CO_2 starvation and photorespiration rates would be expected to be quite high (see Fig. 10.2).

10.3 C_4 Photosynthesis: An Adaptation to What?

While Fig. 10.3B implies that C_4 photosynthesis should be an adaptation to warm growing-season regions of a low CO_2 world, there are other potential ecological conditions where this pathway may exhibit a competitive advantage over C_3 plants (see Chapter 9). One obviously advantageous situation is a saline environment, where plants typically have reduced transpiration rates because stomatal conductances are reduced, thus limiting the inward diffusion of CO_2 (Pearcy and Ehleringer 1984; Sage and Monson 1999). Here it appears that C_4 dicots are most abundant, especially members of the Amaranthaceae and Chenopodiaceae families, such as *Atriplex* and *Salsola* (Sage and Monson 1999; Pyankov et al. 1999, 2000). Relatively few CO_2 monocot taxa occur in saline regions, although *Distichlis* and *Spartina* are clear examples of monocots that often predominate globally in many salt marsh ecosystems.

C_4 taxa have a wide distribution, largely centered in the tropical and subtropical regions (Fig. 10.4). Here the predominance of C_4 taxa as grasses and sedges becomes most evident in the savanna and grassland biomes. Although C_4 taxa are predicted to be common in tropical regions (Collatz, Berry, and Clark 1998), their distribution is restricted to open, disturbed spaces and some aquatic regions, where competition with taller life forms is minimal. In more temperate regions, C_4 taxa are far less common, occurring largely in halophytic regions or habitats of high disturbance (Sage and Monson, 1999; Chapter 9).

Today, C_4 monocots are most abundant in summer-wet, semi-arid ecosystems, where the ratio of precipitation to evaporation approaches unity (Fig. 10.5). We find that C_4 monocots (largely grasses and sedges) are quite common in both grassland and savanna ecosystems. C_4 taxa are not common to all arid land ecosystems, and it is difficult to attribute the current primary advantage of the C_4 pathway itself as an adaptation to drought. Many of the hot, summer-dry desert ecosystems, such as the Mohave Desert of North America and the Sahara Desert of Africa, are dominated by C_3 vegetation and not by C_4 vegetation, because rains fall during the winter-spring when temperatures are cool and not in the summer when temperatures are hot (Ehleringer and Monson 1993; Sage and Monson 1999).

While some paleontological studies assume that the presence of C_4 taxa is indicative of drought environments (e.g., Huang et al., 2001), there is no evidence of C_4 dominance in today's arid land ecosystems that lack summer rain (Ehleringer and Monson 1993; Collatz, Berry, and Clark 1998; Sage and

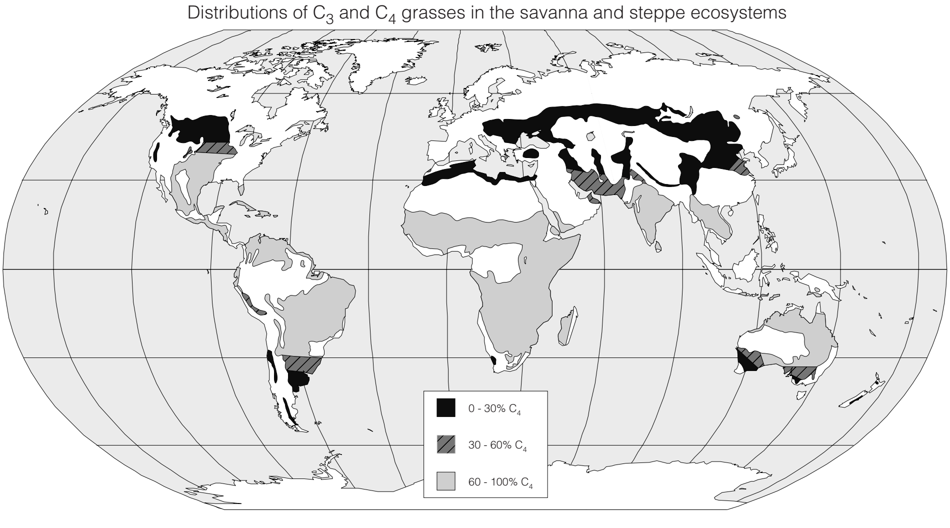

Figure 10.4. The distributions of C_3 and C_4 grasses in steppe and savanna ecosystems of the world. These are the two biomes wherein grasses are a significant fraction of the vegetation. (Adapted from Ehleringer and Cerling 2001.)

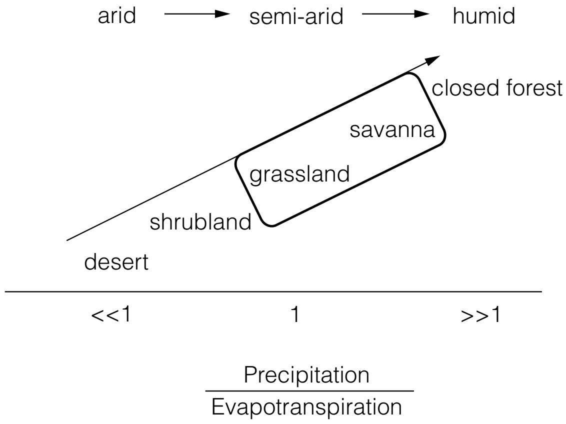

Figure 10.5. The distribution of different ecosystem types as a function of the ratio of precipitation to evapotranspiration. Circled are those ecosystems where C_4 monocot taxa are common.

Monson 1999). From a physiological perspective, there appears to be nothing inherent in the C_4 pathway that conveys a selective advantage to reduced plant water content, such as plants would typically experience during drought. Perhaps surprisingly, C_4 plants are not a large component of dry desert ecosystems where seasonal and interannual droughts are common (see Chapter 9). When they do occur in desert regions, C_4 monocots tend to be active only in the summer in regions with summer rains and then to be active only after the warm summer rains have arrived (Shreve and Wiggins 1964; Sage and Monson 1999).

As a consequence of their low stature, C_4 monocots can predominate only in open ecosystems where trees do not shade them out. This makes it particularly difficult in a historical sense to distinguish C_3/C_4 shifts that are associated with C_3/C_4 monocot changes (such as would occur in grasslands) from C_3/C_4 shifts associated with the gaps between tree canopies opening and closing, such as those that would occur in savannas in response to fire or grazing pressures (see Chapter 9). Bond, Midgley, and Woodward (2003) have recently modeled C_3 tree and C_4 grass responses to fire, a major disturbance of African grassland and savanna ecosystems. They found that the slow recovery of trees under a low-CO_2 environment favored the expansion of grasslands. This is similar to the conclusion of Cerling, Ehleringer, and Harris (1998) that C_3 taxa tend to approach CO_2 starvation under the low CO_2 levels of glacial periods. Thus, it is easier to interpret and understand the contributing factors impacting historical changes in local-to-regional C_3/C_4 abundances when comparisons are made within a single life form (grass-grass) rather than across life forms (tree-grass).

10.4 The Interactions Between Atmospheric CO_2, Temperature, and Precipitation: How They Affect C_4 Monocot Distribution

At any given atmospheric CO_2 level, the Ehleringer et al. (1997) model predicts that C_4 taxa should be most likely to occur in those habitats having a warmer growing season. Implicit in this model is that growing-season temperatures are distinguished from non–growing-season temperatures. Plants experiencing a cool winter-precipitation regime followed by a hot, dry summer (such as all Mediterranean climates) would not be considered warm-temperature ecosystems. Thus, Mediterranean climate and monsoonal climates would be distinct from each other, even though summertime temperatures in both climates might be similar. Teeri and Stowe (1976) were the first to show that C_4 grass distributions across the Great Plains of North America were linearly related to growing-season temperature. Ehleringer (1978) modeled current C_4 grass distributions under several ecological situations (geographic gradients in the Great Plains and biseasonal precipitation regimes) and showed that C_4 grass distributions followed the predicted temperature relationships shown in Fig. 10.3B. Recently, Ehleringer, Cerling, and Helliker (1997) reviewed more than 20 C_4 monocot studies and showed that in each case, % C_4 abundance was a linear function of growing-season temperature. Sage and Monson (1999) showed that % C_4 abundance on islands followed latitudinal gradients, with C_4 plants most common in warm regions. Collatz, Berry, and Clark (1998) predicted global C_4 abundances using the quantum yield model. Their results were constrained to consider only growing-season temperatures (i.e., monthly periods during which precipitation exceeded a threshold). In each of these studies, the regional and global C_3/C_4 distributions are consistent with predictions shown in Fig. 10.3B.

The quantum yield model predicts that at some time in Earth's recent history the atmospheric CO_2 declined to a point where a threshold was crossed and C_4 plants would be favored globally in the warmest growing-season habitats. Cerling et al. (1997) provided convincing evidence for a global expansion of C_4-dominated ecosystems approximately 6 to 8 million years ago during the late Miocene. At that time, C_4 ecosystems appeared nearly simultaneously in North and South America, Africa, and Asia. In each case, C_4 ecosystems appeared in warmer, lower latitudes and not in higher, cooler latitudes. Just exactly what that threshold CO_2 level was is unclear, but the threshold CO_2 would clearly have depended on the growing-season temperature (Fig. 10.3B). It is likely that the CO_2 level was somewhere in the range of 350 to 500 ppm. Firm estimates of the atmospheric CO_2 levels during the late Miocene are not well constrained. Some CO_2 proxies suggest that atmospheric CO_2 levels have been at near current levels since the Eocene (Pagani, Freeman, and Arthur 1999; Freeman and Colarusso 2001; see Chapter 3). Oxygen isotope ratio data suggest that increased monsoonal activity in southern Asia and the Indian subcontinent preceded the expansion of C_4 ecosystems by 1 to 2 million years (Quade, Cerling, and Bowman 1989). Such activity would have increased weathering of Himalayan uplift and could have been a driver for reducing atmospheric CO_2 levels (Ruddiman

1990). Until we have a clear high-resolution time course of CO_2 for the past 40 to 60 million years, the exact threshold that precipitated the expansion of C_4 ecosystems will remain unclear.

10.5 Was Atmospheric CO_2 a Driver for C_4 Expansion During Glacial Periods?

The changes in atmospheric CO_2 levels between 180 and 280 ppm over the past 420,000 years (Petit et al., 1999; see Chapter 4) should have impacted the abundances of C_3/C_4 taxa. The quantum yield model predicts that in ecosystems with warm growing-season temperatures the potential abundances of C_3/C_4 taxa fluctuated as CO_2 rose and declined between glacial and interglacial periods. There is now ample evidence from ecosystems in North America, South America, Central America, and Africa showing that C_4 taxa replaced C_3 taxa during glacial periods and that C_4 taxa often decreased in abundance following the last glacial maximum (e.g., Talbot and Johannessen, 1992; Aucour and Hillaire-Marcel 1994; Giresse, Maley, and Brenac 1994; Street-Perrott et al. 1997, 1998; Huang et al. 1999, 2001). Three depth-time profiles from different tropical regions clearly demonstrate a carbon isotopic shift in the historical record between glacial and interglacial periods (Fig. 10.6).

In each of these cases, the trends are consistent with increased C_4 abundance during the Last Glacial Maximum (LGM), followed by a decrease in the abundance of C_4 photosynthesis following deglaciation and the correlated increase in atmospheric CO_2. Recently, Boom et al. (2002) showed that the transition between C_3 and C_4 dominated ecosystems in the Bogota basin, Colombia, has repeatedly followed glacial-interglacial cycles for the past 400,000 years. During

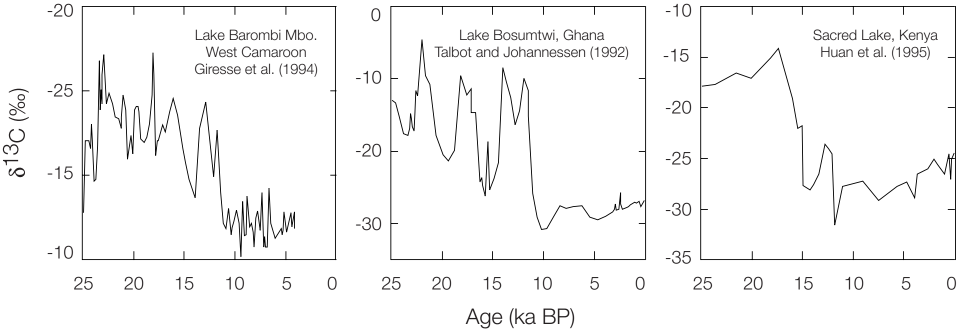

Figure 10.6. Chronological profiles of the carbon isotope ratio values of organic matter in *left* Lake Barombi Mbo, Cameroon (Giresse et al., 1994), *middle* Lake Bosumtwi, Ghana (Talbot and Johannessen (1992), and *right* Sacred Lake, Kenya (Huang et al., 1995).

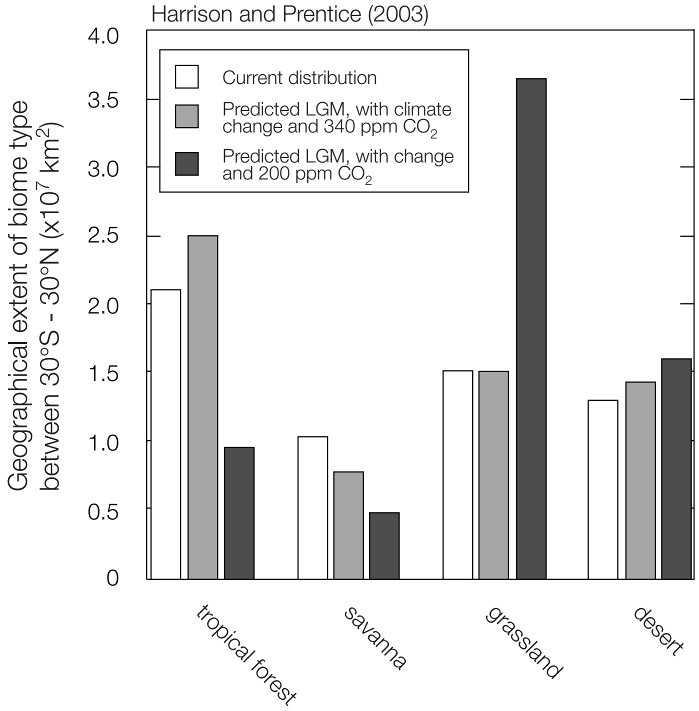

Figure 10.7. A comparison of the current geographic extent of tropical forest, savanna, grassland, and desert biomes between latitudes 30°S and 30°N to the geographical extent predicted from BIOME4 for these biomes types during the last glacial maximum under two environmental scenarios: (a) the last glacial maximum climate and today's atmospheric CO_2 level and (b) the last glacial maximum climate and a reduced CO_2 level of 200 ppm. Bars indicate the average geographic extent predicted based on 17 different climate simulations. (Based on data presented in Harrison and Prentice 2003.)

each glacial period (low CO_2), C_4 taxa expanded, whereas during interglacial periods, C_3 taxa predominated. Whether these C_3/C_4 shifts are associated with changes in the abundances of C_3/C_4 monocots or changes in the abundances of C_3 trees versus C_4 monocots is not always clear. Pollen evidence (when available) often indicates that the latter possibility is more likely. Other paleontological evidence indicates shifts in C_3/C_4 abundances that are correlated with the changes in atmospheric CO_2. In regions of western North America now dominated by C_3 taxa, tooth analyses of several extinct grazers (e.g., mastadonts, bison, and camels) indicate that C_4 species were a major dietary component (see Chapters 12 and 13 and Connin, Betancourt, and Quade 1998 for interpretation of tooth data). At the landscape scale, caliche carbonate analyses indicate that some portions of Arizona and New Mexico had a significant C_4 component even though these sites are C_3 dominated today (Cole and Monger 1994).

Recently, Harrison and Prentice (2003) have examined the extent to which the changes in global vegetation between the last glacial maximum and present have been driven by (a) changes in climate (temperature and precipitation) alone or (b) changes in both climate and atmospheric CO_2. They examined predictions of a global vegetation model driven by 17 different simulations of the paleoclimate at the LGM. Of considerable interest is that simulations with and without the direct consideration of atmospheric CO_2 on photosynthesis yielded quite different predictions (Fig. 10.7).

When compared to the present-day aerial extent of major biomes, the model predicted that with climate change alone (temperature and precipitation), there would be little change in the global extent of forest, savanna, and grassland vegetation. That predicted pattern is not consistent with the available pollen record. However, when the change in atmospheric CO_2 was also included with climate change in the model, then there were large predicted reductions in both the extent of tropical forest and savanna biomes (Fig. 10.7). This direct effect of CO_2 on biome-scale photosynthesis and hence on productivity and plant distribution is consistent with the predictions of the quantum yield model. C_4 grasslands apparently expanded as C_3 forests retreated during glacial periods. In effect, the C_3 forests in warm climates became much more CO_2 starved under the 180 to 190 ppm CO_2 of glacial periods.

10.6 Seasonality's Impact on When Plants Can Grow

Seasonality is an important ecological factor that is often difficult to extract from paleo-observations. When reconstructing C_3/C_4 abundance relationships, it is essential to recognize that changes in ocean circulation patterns can lead to changes in the seasonality of precipitation. For example, pack rat midden data indicate that the extent of summer rains in the western United States retreated southward over the past several thousand years (Betancourt et al. 1990). Bristlecone pine tree ring isotope data from the southern Sierra Nevada Range support the notion of the loss of summer rains in the western United States and suggest that some of these precipitation shifts could have been abrupt during the last millennium (Yapp and Epstein 1982). This possibility is also supported by lake-level increase indicating more winter precipitation in the area over the past 700 years (Stine 1994). In such cases, atmospheric CO_2 levels need not have decreased to favor expansion or contraction of C_4 monocots in the semi-arid western United States. Based on the quantum yield model, the critical factor would be the temperature during the growing season. In the absence of a summer growing season, the vegetation would likely be C_3 since temperatures are cool during the late winter and spring growing conditions.

Extending this analogy to present-day subtropical latitudes such as found in southwestern and western North America, winter precipitation regimes will favor C_3 monocots, whereas summer precipitation will favor C_4 monocots (Mulroy and Rundel 1977; Ehleringer, Cerling, and Helliker 1997; Sage and Monson

1999). This should also have been the case in the past, such as during glacial periods, although some regions could have been warm enough to favor C_4 monocots even during winter-spring periods. Huang et al. (2001) have attributed both seasonality and CO_2 as drivers in the C_3/C_4 shifts in Central American ecosystems, as predicted by the quantum yield model. In that study, Huang et al. hypothesized that shifts between summer monsoonal and winter frontal precipitation patterns likely contributed to an absence of C_4 taxa in northern Mexico (Chihuahua region) during the last glacial maximum, whereas C_4 taxa were quite common in a Guatemalan ecosystem. Ultimately, other factors could have contributed to the absence of C_4 taxa in this Chihuahuan ecosystem, since C_3 monocots are common there today (Shreve and Wiggins 1964; Huang et al. 2001) and since regions to the north were known to have been C_4 dominated during the last glacial maximum (cited above).

To illustrate the importance of seasonality favoring one photosynthetic pathway over another, consider the abundances of C_3/C_4 monocots in southern California and Florida today. Even though both locations are at similar latitudes, the C_4 abundance is high in Florida and low in southern California (Sage and Monson 1999). This is because the precipitation in California comes during the spring cool season, whereas the predominant precipitation in Florida is in the warm summer season. Accordingly, there is a high proportion of C_4 plants in Florida but not in southern California (Teeri and Stowe 1976; Sage and Monson 1999), as predicted by the quantum yield model shown in Fig. 10.3B. Similarly, in the southern United States and in northwestern Mexico where biseasonal precipitation patterns are common today, we see the same C_3/C_4 separations, with C_4 taxa active during the warm, wet summer periods (Shreve and Wiggins 1964; Mulroy and Rundel 1977). Today in these biseasonal precipitation ecosystems, C_3 grasses dominate the winter growing season, while C_4 grasses dominate the summer growing season. In order for C_4 grasses to have had a competitive advantage over C_3 grasses, the quantum yield model predicts that if current wintertime temperatures were maintained, the CO_2 level would have had to decrease substantially before C_4 grasses would be favored throughout the year. Thus, the seasonality of the precipitation event has a significant impact, influencing C_4 abundance because of temperature differences between winter and summer in temperate regions.

10.7 Ecological Factors Further Limit the Abundances of C_4 Monocot Taxa

Both climatic and nonclimatic factors will influence the abundances of C_4 taxa. Among the climatic factors already considered are atmospheric CO_2 and O_2 levels, temperature, and seasonality of precipitation (Fig. 10.8).

Yet consideration must also be given to nonclimatic drivers that will influence the abundances of C_3/C_4 taxa. Primary among these ecological considerations are factors that tend to open a C_3 forest and to allow expansion of the understory

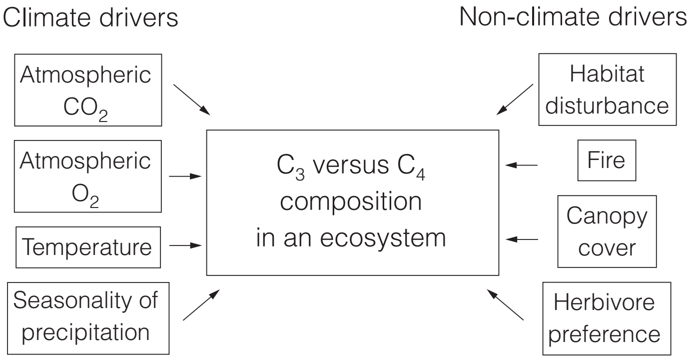

Figure 10.8. Climatic and nonclimatic drivers for changes in the abundances of C_3 and C_4 taxa in an ecosystem.

C_4 monocot components. These include habitat disturbance, fire, and herbivory, each of which affects the extent of tree canopy cover (Fig. 10.9).

In recent historical times, man is known to be a causal agent for such change as extensive deforestation, which leads to grass expansion. Consider four broad examples. First, forest destruction associated with the expansion of the Mayan civilization in Central America (Huang et al. 2001) and expansions in Ethiopia (Eshetu and Högberg 2000; Eshetu 2002) resulted in large changes in carbon isotope ratios of soil organic matter and lake sediments, allowing a time course reconstruction of the C_3/C_4 shifts. Second, recent conversions of tropical rainforests to pastures also result in profound shifts in the carbon isotope ratios of tropical soils (e.g., Neill et al. 1996). Third, large herbivores, such as elephants, are known to prefer C_3 trees and can have a profound effect on opening canopies (Cerling and Harris 1999). Fourth, fire will open forest canopies, allowing a C_3-to-C_4 shift (e.g., Bond 2000). In general, increased disturbance will make ecosystems appear more C_4-like, since C_3 trees are more likely to be impacted by disturbances such as fire and herbivory than are the C_4 grasses. Recovery from disturbance in these C_3/C_4 ecosystems will lead to a C_3 conversion as trees overtop and shade out the C_4 grasses (Bond 2000). If fine-scale paleontological isotope data were the only information available for recent time periods, it would be possible misinterpret the C_3/C_4 shifts as being climatically driven when, in fact, the C_3/C_4 shifts could have been driven by nonclimatic factors.

In Fig. 10.9 the climatic and nonclimatic drivers of change in C_3/C_4 ecosystems are integrated into a simple but mechanistically based model. Each of these ecosystems is semi-arid, with precipitation to evaporation ratios near unity. Shifts in C_3/C_4 abundances in tree-grass ecosystems are driven by both climatic (e.g., CO_2, temperature, precipitation) and nonclimatic factors (fire, disturbance). Within these C_3/C_4 shifts, C_4 NAD-ME grasses should occur on the drier sites, since these grasses have the lowest quantum yield values and may not out-

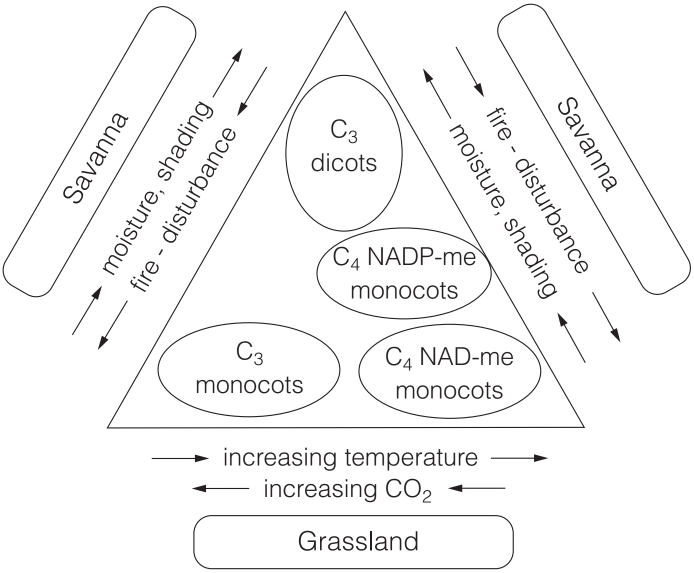

Figure 10.9. A plot of the environmental and ecological factors that govern shifts in the abundances of C_3 monocots and C_4 dicots within grassland and savanna ecosystems.

compete the more efficient NADP-ME grasses. In contrast, C_4 NADP-ME grasses are predicted to be more common on wetter sites than those occupied by NAD-ME plants. As moisture levels increase along this geographic cline, support of a higher leaf-area tree life form ultimately becomes possible. These predictions are consistent with observed temperate ecosystem distributions globally, such as the savannas, tall-grass prairie (NADP-ME dominated), and short-grass prairie (NAD-ME dominated) of North America. Similarly, in subtropical ecosystems globally, disturbance levels determine the shifts between open C_4 grass-dominated savanna and closed C_3 savanna forests in wet regions, while the C_3/C_4 savanna to C_4 grassland distributions are determined by precipitation levels. The second class of C_3/C_4 shifts occurs in grassland ecosystems, where life form remains constant but the growing-season temperatures dictate the extent to which photorespiratory costs favor the C_3 or C_4 photosynthetic pathway.

10.8 Summary

The abundance of plants having C_3 versus C_4 photosynthesis is strongly coupled to two environmental factors: atmospheric CO_2 and growing-season temperature. The mechanistic quantum yield predicts the combinations of CO_2 and temperature that result in photorespiratory changes that favor C_4 taxa over C_3 taxa. Warm temperatures and low atmospheric CO_2 levels favor C_4 taxa over C_3 taxa.

The abundance of C_4-dominated ecosystems is of only recent origin, with C_4-dominated ecosystems having expanded globally about 6 to 8 million years ago. Seasonality and disturbance regimes are important ecological considerations, which can contribute to the C_3/C_4 dominance in transition climate regimes under a constant atmospheric CO_2. Future increases in atmospheric CO_2 are likely to favor the expansion of C_3-dominated ecosystems over C_4-dominated ecosystems.

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