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C₄ photosynthesis, atmospheric CO₂, and climate

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Abstract The objectives of this synthesis are (1) to review the factors that influence the ecological, geographical, and palaeoecological distributions of plants possessing C₄ photosynthesis and (2) to propose a hypothesis/model to explain both the distribution of C₄ plants with respect to temperature and CO₂ and why C₄ photosynthesis is relatively uncommon in dicotyledonous plants (hereafter dicots), especially in comparison with its widespread distribution in monocotyledonous species (hereafter monocots). Our goal is to stimulate discussion of the factors controlling distributions of C₄ plants today, historically, and under future elevated CO₂ environments. Understanding the distributions of C₃/C₄ plants impacts not only primary productivity, but also the distribution, evolution, and migration of both invertebrates and vertebrates that graze on these plants. Sixteen separate studies all indicate that the current distributions of C₄ monocots are tightly correlated with temperature: elevated temperatures during the growing season favor C₄ monocots. In contrast, the seven studies on C₄ dicot distributions suggest that a different environmental parameter, such as aridity (combination of temperature and evaporative potential), more closely describes their distributions. Differences in the temperature dependence of the quantum yield for CO₂ uptake (light-use efficiency) of C₃ and C₄ species relate well to observed plant distributions and light-use efficiency is

the only mechanism that has been proposed to explain distributional differences in C₃/C₄ monocots. Modeling of C₃ and C₄ light-use efficiencies under different combinations of atmospheric CO₂ and temperature predicts that C₄-dominated ecosystems should not have expanded until atmospheric CO₂ concentrations reached the lower levels that are thought to have existed beginning near the end of the Miocene. At that time, palaeocarbonate and fossil data indicate a simultaneous, global expansion of C₄-dominated grasslands. The C₄ monocots generally have a higher quantum yield than C₄ dicots and it is proposed that leaf venation patterns play a role in increasing the light-use efficiency of most C₄ monocots. The reduced quantum yield of most C₄ dicots is consistent with their rarity, and it is suggested that C₄ dicots may not have been selected until CO₂ concentrations reached their lowest levels during glacial maxima in the Quaternary. Given the intrinsic light-use efficiency advantage of C₄ monocots, C₄ dicots may have been limited in their distributions to the warmest ecosystems, saline ecosystems, and/or to highly disturbed ecosystems. All C₄ plants have a significant advantage over C₃ plants under low atmospheric CO₂ conditions and are predicted to have expanded significantly on a global scale during full-glacial periods, especially in tropical regions. Bog and lake sediment cores as well as pedogenic carbonates support the hypothesis that C₄ ecosystems were more extensive during the last glacial maximum and then decreased in abundance following deglaciation as atmospheric CO₂ levels increased.

This contribution is dedicated to Professor Harold Mooney, a pioneer in plant ecology and global ecology, on the occasion of his 65th birthday

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Introduction

Plants can be categorized photosynthetically as falling into one of three categories: C₃, C₄, and CAM. On a global basis, C₄ biota account for approximately 18% of the total global productivity, which is largely due to high

productivity of C_4 monocots in grasslands (calculated from data in Melillo et al. 1993). Most plant species globally are characterized by C_3 photosynthesis, but the C_4 and CAM pathways represent evolutionary advancements over the ancestral C_3 pathway that result in superior carbon-gaining capacities under particular environmental conditions (Osmond et al. 1982; Monson 1989; Ehleringer and Monson 1993). The performance of each pathway is significantly influenced by climatic conditions and over the past two decades attention has focused on describing those environmental parameters most closely associated with the distributional abundance of different photosynthetic pathway types.

The objectives of this synthesis are to review the factors known to influence the ecological and geographical distributions of C_4 plants and to propose a hypothesis to explain why C_4 dicotyledonous plants (hereafter dicots) are relatively uncommon, especially when compared to the widespread distributions of C_4 monocotyledonous species (hereafter monocots). What will become evident is that most previous efforts have concentrated on describing the environmental factors related to the distributions of C_4 monocots (grasses and sedges). Such a focus is expected, since approximately one-half of the 10,000 grass species have C_4 photosynthesis (Hattersley 1987; Hattersley and Watson 1992). In contrast, it appears that fewer than perhaps a thousand of the 165,000 dicots have C_4 photosynthesis. A consensus has emerged as to the environmental factors most closely associated with expansion of C_4 grasslands, but both the uncommonness of C_4 dicots as well as the environmental constraints associated with their distributions have been largely ignored.

Phylogenetic distribution of C_4 photosynthesis

The taxonomic distributions of plants possessing C_4 photosynthesis suggest interesting and perhaps recent evolutionary origins. C_4 photosynthesis is restricted to advanced members of the Dicotyledonae (dicots) and Monocotyledonae (monocots). The C_4 pathway has multiple evolutionary origins. It occurs within 8 of 16 superorders in the Dicotyledonae, but only within 1 of 5 superorders in the Monocotyledonae (Commelinanae) (Table 1). C_3 - C_4 intermediates are also known to occur in taxa of these superorders (Monson et al. 1984). Phylogenetically these groups are quite separated from each other (Chase et al. 1993), reinforcing the notion that the C_4 pathway must have evolved independently multiple times (see reviews in Monson 1989; Ehleringer and Monson 1993). Within the monocots, C_4 photosynthesis is quite common among grasses (Poaceae) and sedges (Cyperaceae), two closely related groups (Hattersley 1987; Hattersley and Watson 1992). Although widespread, the distribution of C_4 photosynthesis is not complete in grasses and sedges. Lineages extensive throughout tropical and subtropical regions tend to have C_4 photosynthesis, whereas those originating from

arctic or temperate regions tend to have C_3 photosynthesis (Brown 1977; Hattersley 1987). What is remarkable is that although C_4 photosynthesis is documented to occur among half of the Dicotyledonae superorders, further analysis of C_4 distributions among the dicots indicates that it occurs in only 16 of the approximately 400 families. Furthermore, within each family, it often occurs within only one to several genera and then often only within two to three species. Exceptions to this trend are in the Caryophyllales, where C_4 photosynthesis is common among genera within the Amaranthaceae and Chenopodiaceae. Thus, in C_4 dicots, we have a photosynthetic pathway whose distribution is both taxonomically uncommon and phylogenetically widely dispersed among only advanced families. Additionally, there are C_3 - C_4 intermediates in genera which at present do not have C_4 photosynthesis. This taxonomic distribution pattern is consistent with the notion that C_4 photosynthesis may have evolved recently among the dicots. Later we will suggest that C_4 photosynthesis in dicots may not have been evolutionarily favored until atmospheric CO_2 concentrations reached the low levels that characterize glacial maxima. These low atmospheric CO_2 conditions may not have occurred until the Quaternary and then for relatively brief periods of 20,000–30,000 years at a time.

Current abundances of C_4 monocots are associated with temperature

On a global basis, the greatest fraction of C_4 taxa are within the monocots, specifically the grasses (Teeri and Stowe 1976; Hattersley 1983; Teeri 1988) and the sedges (Teeri et al. 1980; Takeda et al. 1985a; Ueno and Takeda 1992). The now classic study by Teeri and Stowe (1976) first quantified the environmental characteristics associated with the distributions of C_3 and C_4 grasses in North America. They showed a correlation of $r = 0.97$ between percent C_4 grasses within a flora and the minimum growing-season temperature: the higher the temperature the more frequent C_4 photosynthesis within the grass taxa. Total precipitation was not as critical a parameter. More recently, Epstein et al. (1997) have confirmed the primary significance of temperature in association with C_3 / C_4 grass distributions in the Great Plains. Given the strong relationships between temperature and both latitude and elevation, the Teeri and Stowe (1976) study accounted for the geographic distribution of C_4 grasses across North America. In grasslands with only a spring growing season (e.g., Central Valley of California or Palouse of Washington), we find only C_3 grass species (Teeri and Stowe 1976). However, where grasslands exhibit two distinct growing seasons (winter-spring and summer), strong seasonal differences exist for the dominance of one pathway versus the other. Primary productivity in the central and northern portions of the Great Plains of North America is dominated by C_3 grasses in the spring growing season,

Table 1 Families known to contain taxa with C₄ photosynthesis. Taxonomic arrangements are according to Zomlefer (1994). Within each family, all genera possessing C₄ photosynthesis are listed. Based on data in Batanouny et al. (1991), Das and Raghavendra (1976), Das and Vats (1993), Downton (1975), Glagoleva and Chulanovskaya (1992), Imbamba and Papa (1979), Mateu (1993), Okuda and Furukawa (1990), Osmond et al. (1982), P'yankov (1994), Raghavendra and Das (1978), Sankhla and Ziegler (1975), Shomer-Ilan et al. (1981), Smith and Turner (1975), Takeda et al. (1985a, b), Welkie and Caldwell (1970), Winter (1981) and Ziegler et al. (1981). Winter et al. (1976)

<i>Angiospermae</i> (class)	
Dicotyledonae (subclass)	
Caryophyllanae (superorder)	
Caryophylles (order)	
Aizoaceae	<i>Cypselea, Gisekia, Trianthema, Zalaeya</i>
Amaranthaceae	<i>Acanthochiton, Aerva, Alteranthera, Amaranthus, Brayulinea, Froelichia, Gomphrena, Gossypianthus, Lithophila, Tidestromia Polycarpaea</i>
Caryophyllaceae	<i>Anabis, Aellenia, Arthrophytum, Atriplex, Bassia, Bienertia, Camphorosma, Chenolea, Climacoptera, Comulaca, Cytobasis, Echinopsilon, Gamanthus, Girgensohnia, Halanthium, Halimocnemis, Halocharis, Halogeton, Halostigmara, Haloxylon, Hammada, Horaninovia, Hypocyclix, Kochia, Londezia, Noaea, Panderia, Petrosimonia, Salsola, Seidlitzia, Suaeda, Theleophyton, Traganum</i>
Chenopodiaceae	<i>Glinis, Mollugo</i>
Molluginaceae	<i>Allionia, Boerhaavia, Okenia</i>
Nyctaginaceae	<i>Portulaca</i>
Portulacaceae	
Theanae (superorder)	
Polygonales (order)	
Polygonaceae	<i>Calligonum</i>
Malvanae (superorder)	
Euphorbiales (order)	
Euphorbiaceae	<i>Chamaesyce, Euphorbia</i>
Violanae (superorder)	
Brassicales (order)	
Capparaceae	<i>Gynandropsis</i>
Geranianae (superorder)	
Linales (order)	
Zygophyllaceae	<i>Kallstroemia, Tribulus, Zygophyllum</i>
Asteranae (superorder)	
Asterales (order)	
Asteraceae	<i>Flaveria, Glossocordia, Glossogyne, Isostigma, Pectis</i>
Solananae (superorder)	
Solanales (order)	
Boraginaceae	<i>Heliotropium</i>
Convolvulaceae	<i>Evolvulus</i>
Gentiananae (superorder)	
Scrophulariales (order)	
Acanthaceae	<i>Blepharis</i>
Scrophulariaceae	<i>Anticharis</i>
Monocotyledonae (subclass)	
Commelinanae (superorder)	
Juncaceae	
Cyperaceae	<i>Ascolepis, Bulbostylis, Crosslandia, Cyperus, Eleocharis, Fimbristylis, Kyllinga, Lipocarpa, Mariscus, Pycreus, Rhynchospora</i>
Poales (order)	
Poaceae	<i>Alloteropsis, Andropogon, Arundinella, Bouteloua, Cynodon, Echinochloa, Leptochloa, Microstegium, Panicum, Paspalum, Setaria, Sorghum, Spartina, Sporobolus, Zea</i> (many more genera)

while C₄ grasses predominate during the summer growing season (Ode et al. 1980; Barnes et al. 1983; Monson et al. 1983; Boryslawski and Bentley 1985; Paruelo and Lauenroth 1996; Tieszen et al. 1997). A similar pattern occurs in the Sonoran Desert, where the winter–spring vegetation is exclusively C₃, whereas C₄ grasses dominate in the summer monsoon season (Shreve and Wiggins 1964; Mulroy and Rundel 1977).

Teeri and Stowe's initial observations lead to a series of additional grassland analyses in different global regions, from which it became clear that temperature was the dominant climatic parameter correlated with the abundance of C₄ within grass taxa (Table 2). In these

analyses, temperature has not always been quantified using the same parameter: in some cases it was minimum growing-season temperature, but in others it was day-time maximum temperature or mean temperature. Yet given the high autocorrelation between these various temperature parameters, choosing a single temperature measure may not be critical. While precipitation is obviously essential to initiate plant growth, temperature is such a dominant factor in these regression analyses that it explains more than 90% of the total C₃/C₄ distributional variation across almost all geographic regions.

Many of the previous climate-C₄ analyses allow for the calculation of the transition temperatures associated

Table 2 Studies correlating the abundance of C₃ and C₄ photosynthesis within monocot taxa from different grasslands and the relationship between C₃ or C₄ abundance and temperature. Also shown is the transition temperature, representing the thermal point above which C₄ plants predominate over C₃ grasses. The asterisk indicates that the C₃/C₄ distributional transition temperature was

estimated by Rundel (1980); the double asterisk indicates that we calculated the transition temperature based on summer-time average daytime maximum temperatures. The dashed lines indicate that no value was provided in the paper nor could it be easily calculated using the available data

Geographic location	Grouping	Relation of temperature with C ₃ /C ₄ distribution	C ₃ /C ₄ transition temperature (°C)	Author
Argentina	grass	R ² = 0.96	23°–28°	Cavagnaro (1988)
Arizona, USA	grass	–	26°	Wentworth (1983)
Central Asia	grass	r = 0.93	–	P'yankov and Mokronosov (1993)
Australia	grass	R ² = 0.94	–	Hattersley (1983)
Costa Rica	grass	–	19°–23°*	Chazdon (1978)
Europe	monocot	R ² = 0.56	–	Collins and Jones (1985)
Hawaii	grass	–	21°	Rundel (1980)
Japan	grass	r = 0.98	28°**	Takeda et al. (1985)
Japan	grass	R ² = 0.79	28°	Okuda (1987)
Japan	sedge	R ² = 0.90	28°	Ueno and Takeda (1992)
Kenya	grass	–	22°*	Tieszen et al. (1979b)
Kenya	grass	r = 0.99	–	Livingstone and Clayton (1980)
North America	grass	r = 0.97	–	Teeri and Stowe (1976)
North America	sedge	r = 0.93	–	Teeri et al. (1980)
South Africa	grass	–	25°	Vogel et al. (1978)
Wyoming, USA	grass	R ² = 0.87	26°**	Boutton et al. (1980)

Table 3 Studies correlating the abundance of C₃ and C₄ photosynthesis within dicotyledonous taxa from different ecosystems. The Doliner and Jolliffe (1979) study contained primarily dicotyledonous species, but did include monocotyledonous species as well. The data from P'yankov and Mokronosov (1993) are for

Chenopodiaceal. The dashed lines indicate that no value was provided in the paper nor could it be easily calculated using the available data. The asterisk indicates a calculated value, using data provided in the publication

Geographic location	Climatic parameter showing highest relation with C ₃ /C ₄ distribution	Maximum abundance of C ₄ dicots	Author
Arizona, USA	–	4.1%	Wentworth (1983)
Central Asia	aridity index r = 0.89*	–	P'yankov and Mokronosov (1993)
California, USA	precipitation and temperature R ² = 0.66	–	Doliner and Jolliffe (1979)
Central Europe	precipitation and temperature	–	Doliner and Jolliffe (1979)
Europe	minimum temperature and mean precipitation R ² = 0.64	0.9%	Collins and Jones (1985)
Japan	no trend	1.0% *	Okuda and Furukawa (1990)
North America	summer pan evaporation r = 0.95	4.4%	Stowe and Teeri (1978)

with a switch between C₃ dominance and C₄ dominance. Here, transition temperature was defined as the point at which C₄ abundance fell below 50%. Most of these studies calculated percent C₄ abundance on a taxonomic basis and not necessarily on a percent biomass basis. It is remarkable that these studies converge on the daytime temperature range of 20°–28°C as the temperature for the transition shift in C₃ to C₄ dominance (Table 2). This relatively narrow temperature span holds irrespective of whether the C₃/C₄ distribution analyses were based on elevational or latitudinal gradients.

There are two predominant C₄ photosynthetic subtypes (NAD-me and NADP-me), which differ from each other in terms of biochemical and morphological details (Ehleringer and Monson 1993). Field observations suggest that these C₄ subtypes also have somewhat different distributions. Within grasslands, it is interesting to note that there is a consistent transition from domination by

C₄ NAD-me-type grasses in drier regions to domination by C₄ NADP-me-type grasses in regions of increased precipitation in Central Asia, Australia, Israel, Namibia, North America, and South Africa (Vogel et al. 1978; 1986; Cowling 1983; Ellis et al. 1980; Hattersley 1983; Hattersley 1992; P'yankov and Mokronosov 1993; Schulze et al. 1996).

Current abundances of C₄ dicots are related to aridity

C₄ dicots are far less abundant than C₄ monocots (Table 3). In contrast to C₄ monocots which might comprise well over half of the monocot taxa in a region, C₄ dicots appear not to exceed 4.4% of the flora at their maxima. In North America, C₄ dicots achieved their highest abundance in the Sonoran Desert (4.4%), a hot desert with summer precipitation (Stowe and Teeri 1978;

Wentworth 1983). With decreasing aridity, the percent C_4 dicot abundance in the flora also decreased. Thus, in subtropical regions, such as Florida (2.5%) and Texas (2.8%), C_4 dicots were a smaller percentage of the flora than they were in the Sonoran Desert. Similar patterns have been observed in Europe (Collins and Jones 1985) and Japan (Okuda and Furukawa 1990). Little information is as yet available on the factors controlling either the abundances or distributions of C_4 NADP-me and C_4 NAD-medicot plants.

There have been limited analyses of the climatic factors related to the distributions of C_4 dicots throughout the world. Stowe and Teeri (1978) conducted by far the most extensive and thorough analysis of climatic parameters that might be related to the distribution of C_4 dicots. Their analysis indicated that the percent C_4 dicots did not follow the same climatic factors as for C_4 monocots. Instead of finding strong correlations between percent C_4 dicots and temperature, the percent C_4 dicots appeared most closely related to aridity characters, such as summertime pan evaporation rates and annual dryness ratio (ratio of annual net radiation to heat required to evaporate mean annual precipitation) (Table 3). In North America, summer pan evaporation alone explained 90% of the variance in percent C_4 dicot abundance (Stowe and Teeri 1978). Similar climatic relationships have been observed for C_4 dicots within the California flora (Doliner and Jolliffe 1979), across the European continent (Collins and Jones 1985), and throughout Japan (Okuda and Furukawa 1990). In each case, the conclusion was that the distributions of C_4 monocots and dicots appear to be responding to different climatic parameters.

While C_4 dicots might be conceived as being more common than these surveys would otherwise indicate, this is undoubtedly because C_4 dicots are among the most noxious and aggressive summertime weeds in temperate and subtropical regions (Holm et al. 1977; Elmore and Paul 1983). Holm et al. (1977) noted that 14 of the 18 worst weeds globally had C_4 photosynthesis. Elmore and Paul (1983) calculated that the taxonomic fraction of C_4 weeds was 17-fold greater than would be expected based solely on a C_3/C_4 species basis. Therefore, in habitats subject to disturbance, it would appear that C_4 species are more likely than C_3 species to comprise a significant component of the invaders. Stowe and Teeri (1978) examined possible relationships between introduced C_4 dicots (weeds) and climate, but could find no climatological parameter that was significantly correlated. They concluded that perhaps similarities in the microenvironmental attributes of disturbed sites overrode climatological differences.

The quantum yield for CO_2 uptake differences among C_3 and C_4 plants relates to plant distribution

Ehleringer (1978) proposed that variations in the quantum yield for CO_2 uptake might be the mechanism

accounting for the observed geographical distribution differences of C_3 and C_4 grasses. A fundamental physiological difference between C_3 and C_4 plants is the quantum yield for CO_2 uptake, which is the leaf-level ratio of photosynthetic carbon gain to photons absorbed (Ehleringer and Björkman 1977). Sometimes referred to as light-use efficiency, the quantum yield can play an influential role in determining primary productivity rates under light-limited, canopy-level conditions, because this parameter describes the basic leaf-level conversion efficiency of the incident photon flux (Ehleringer 1978; Thornley and Johnson 1990; Ruimy et al. 1995). At the canopy level, differences in the orientation of individual leaves allow for greater light penetration into the canopy with the result that few leaves are at light saturation. As a consequence, there is often a linear relationship between incident photon flux and canopy photosynthetic rate. Thus, while the quantum yield might not be expected to play a significant role for photosynthetic rate of individual leaves at high photon flux densities, its importance comes in scaling leaf-level activities to the canopy scale (Ruimy et al. 1995). On a theoretical basis, the quantum yield is expected to be lower in C_4 than C_3 plants, because of the additional energy requirement to regenerate phosphoenolpyruvate from pyruvate in the operation of the C_4 cycle (Farquhar and von Caemmerer 1982). Yet under current atmospheric conditions, the quantum yield in C_3 plants is reduced from maximal values because of photorespiration. Since photorespiration is a temperature-dependent process, the quantum yield of C_3 plants declines with increasing temperatures.

Table 4 A comparison of the quantum yield for CO_2 uptake ($\mu\text{mol mol}^{-1}$) among the different photosynthetic subtypes. All data were collected under conditions of approximately 30°C leaf temperature and 320–340 ppmV CO_2 . Studies were selected that focused on quantum yield measurements over a photon flux range of 0–0.15 $\text{mmol m}^{-2} \text{s}^{-1}$, rather than those that derived a quantum yield estimate from a much broader photon flux range. This is because nonlinearity in the photosynthetic light response curve over a broad photon flux range inevitably leads to an inaccurate, reduced estimate of the true quantum yield for CO_2 uptake. The quantum yield values are statistically different from each other if followed by a different letter. Data are from Baruch et al. (1985), Ehleringer and Björkman (1977), Ehleringer and Pearcy (1983), Hunt et al. (1985), Kirschbaum and Farquhar (1987), Ku and Edwards (1978), Leverenz and Öquist (1987), Monson et al. (1982), Monson et al. (1986), Monson et al. (1987), Myers et al. (1990), Osborne and Garrett (1983), Pearcy et al. (1982), Pearcy and Francheschi (1986), Robichaux and Pearcy (1980), Schwarz and Redmann (1989), Sharp et al. (1984), Valle et al. (1985) and Wang (1996).

Photo-synthetic pathway	Grouping	Subtype	N	Quantum yield for CO_2 uptake ($\mu\text{mol mol}^{-1}$)
C_3	Dicotyledonae	–	34	51.5 ± 2.5^a
C_3	Monocotyledonae	–	23	51.7 ± 2.6^a
C_4	Dicotyledonae	NAD-me	12	52.6 ± 1.6^a
C_4	Monocotyledonae	NAD-me	6	59.7 ± 1.9^b
C_4	Dicotyledonae	NADP-me	11	60.4 ± 2.1^b
C_4	Monocotyledonae	NADP-me	11	64.5 ± 3.6^c

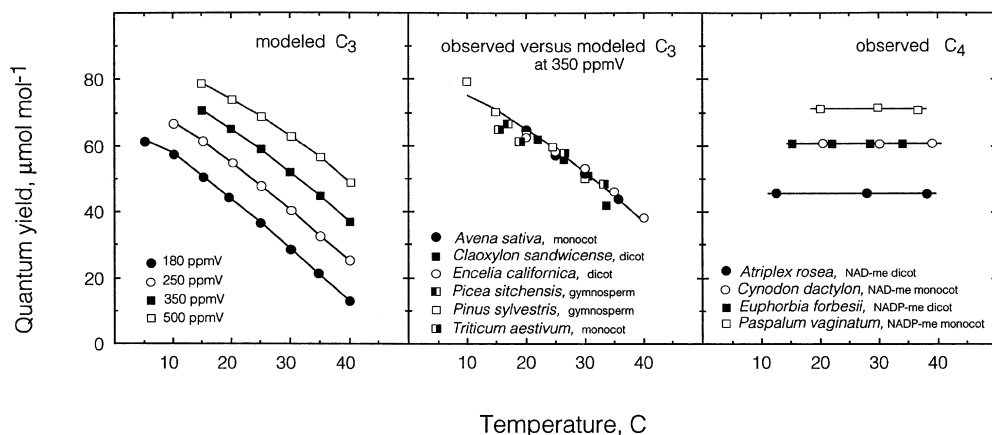


Fig. 1 Modeled and observed values of the quantum yield for CO_2 uptake of C_3 and C_4 plants. **LEFT PLATE.** Modeled values of the quantum yield for CO_2 uptake of C_3 plants as a function of temperature and atmospheric CO_2 concentrations. Changes in the quantum yield for CO_2 uptake are largely driven by changes in photorespiration. The model is based on equations from Farquhar and von Caemmerer (1982) with enzymatic data from Jordan and Ogren (1984). **MIDDLE PLATE.** Comparison of modeled and observed values of the quantum yield for CO_2 uptake of C_3 plants as a function of temperature and 350 ppmV atmospheric CO_2 . Data are from Ehleringer and Björkman (1977), Ku and Edwards (1978), Leverenz and Jarvis (1979), Robichaux and Pearcy (1980), Ehleringer and Pearcy (1983), Öquist and Strand (1986), and Wang (1996). **RIGHT PLATE.** Observed values of the quantum yield for CO_2 uptake of C_4 plants as a function of temperature and 320–340 ppmV atmospheric CO_2 . Data are from Ehleringer and Björkman (1977), Robichaux and Pearcy (1980), and Ehleringer and Pearcy (1983)

In the current atmospheric environment (350 ppmV CO_2 , 21% O_2), the higher photon requirement of C_4 plants and the photorespiration impact on quantum yield in C_3 plants offset each other in the temperature range of 22°–30°C (Ehleringer and Björkman 1977; Ku and Edwards 1978; Monson et al. 1982; Ehleringer and Pearcy 1983; Osborne and Garrett 1983). There are basically no differences in the quantum yields of C_3 monocots and C_3 dicots (Table 4). Nor are there any differences in the temperature dependence of the quantum yields of C_3 monocots and C_3 dicots (or of C_3 gymnosperms for that matter) (Fig. 1). Both C_3 monocots and C_3 dicots show a tendency for sharp reductions in quantum yield with increasing temperatures and the responses of these two groups are indistinguishable from each other.

Differences in the quantum yield for CO_2 uptake between C_4 monocots and C_4 dicots are critical to determining the C_3/C_4 crossover temperatures where one photosynthetic pathway becomes superior to the other (Table 4). Here we define crossover temperature as that temperature at which the quantum yields of C_3 and C_4 plants are similar. For reasons that will be explored shortly, the quantum yields of C_4 monocots are consistently higher than values for C_4 dicots. This is particularly evident when comparing quantum yields of specific C_4 photosynthetic subtypes, where it is clear that the C_4

NADP-me monocot subtypes are on average 7% higher than C_4 NADP-me dicot subtypes and C_4 NAD-me monocot subtypes are on average 13% higher than C_4 NAD-me dicot subtypes. The average quantum yield for CO_2 uptake in NADP-me monocots is lower than might be expected, because the analysis includes observations of domesticated *Zea* and *Sorghum* species, which have lower quantum yield values than wild species. Were we to exclude the quantum yield values of these two domesticated taxa, then the average quantum yield of C_4 NADP-me monocots would increase from 64.5 to 66.9 $\mu\text{mol mol}^{-1}$. The consequence of differences in quantum yields among C_4 photosynthetic subtypes is that the crossover temperature for C_3/C_4 superiority is lower in C_4 monocots than in C_4 dicots and lower in C_4 NADP-me plants than in C_4 NAD-me plants.

The temperature-dependent decline in quantum yield leads to several predictions, given a quantum yield model with its assumptions of equivalent canopy structures and otherwise similar photosynthetic characteristics between a C_3 and a C_4 plant. C_4 grass canopies should have higher rates of overall carbon gain than C_3 grass canopies under warm temperatures. Under cool temperatures, C_3 grass canopies should have higher rates of carbon gain than C_4 grass canopies. If these differences in canopy-level carbon gain translate into a competitive advantage, then C_3 grass canopies should predominate in environments where daytime growing-season temperatures are less than 22°C and C_4 grass canopies should predominate when growing season temperatures exceed 30°C (assuming soil moisture is adequate). These differences in quantum yield and therefore implications for primary productivity allowed Ehleringer (1978) to predict latitudinal gradients in the distributions of C_3 and C_4 grasses in the Great Plains of North America which were consistent with the observed percent C_4 distributions. Ehleringer (1978) calculated canopy-level CO_2 uptake rates, assuming identical C_3 and C_4 canopies, except for differences in their quantum yields. CO_2 uptake calculations for C_3/C_4 grasses in the Great Plains lead Ehleringer (1978) to predict a C_3/C_4 crossover latitude of 45° N, instead of the approximately 38°N predicted by Teeri and Stowe (1976) on the basis

of taxonomic abundance. Recently, Epstein et al. (1997) have used field observations to calculate C_3/C_4 primary productivity patterns; they conclude that the crossover latitude is about 43°N. Tieszen et al. (1997) have evaluated the C_3/C_4 crossover latitude based on both primary productivity observations and carbon isotope ratios of the organic soil matter in the upper soil layers, which should integrate over an extended multi-decadal time period. Their conclusions are that the C_3/C_4 crossover latitude is around 43–45°N. Both studies are in solid agreement with predictions based on a physiological model that uses only differences in the quantum yield to estimate the overall success of one photosynthetic pathway over the other.

Variation in the quantum yields of C_3 and C_4 species is the only physiological mechanism proposed which can account for the observed geographic, biseasonal, and sun-shade distribution differences of C_3/C_4 grasses. Numerous studies from grasslands throughout the world, including the Great Plains, have confirmed the C_3/C_4 transition in grassland composition correlated with temperature along a geographic gradient (Table 2) or on an interseasonal basis (Ode et al. 1980; Barnes et al. 1983; Monson et al. 1983; Boryslawski and Bentley 1985) as predicted by the quantum yield model. It is unlikely that the strong agreements between predictions of C_3/C_4 monocot transition based on quantum yield modeling analysis and field observations are fortuitous. More likely, these tight correlations between quantum yield crossover temperatures and observed C_3/C_4 transition distributions indicate that competitive interactions in these grasslands are strong and that light-use efficiency plays a role in determining the competitive outcome of these interactions. The differential distribution patterns of NADP-me and NAD-me grasses are consistent with the higher quantum yield of C_4 NADP-me grasses providing a competitive advantage over C_4 NAD-me grasses in ecosystems with higher productivity and higher leaf area index canopies.

Anatomical differences may contribute to a higher quantum yield in C_4 monocots

What is the basis for the relatively higher quantum yields among C_4 monocots? While that question is largely unresolved, one factor could be leaf venation patterns, since the quantum yield reflects the ratio of photosynthetic CO_2 capture relative to photon capture – with both parameters expressed on a projected surface area basis. In C_4 photosynthesis, photon capture is not evenly distributed, making relative photosynthetic cell arrangements important. This arises because the photosynthetic carbon assimilation (PCA) cycle in C_4 photosynthesis occurs in mesophyll cells containing limited if any chlorophyll (Hatch 1987), especially in NAD-me plants. Therefore, little reducing power is generated in mesophyll cells that can be translocated to the bundle sheath to offset the increased ATP cost of the

C_4 cycle. At the same time, the photosynthetic carbon reduction (PCR) cycle occurs in the bundle sheath cells (containing chlorophyll) surrounding the veins. Given this, decreasing the number of mesophyll cells in the interveinal spaces across a leaf should have the effect of increasing the quantum yield because these cells would contribute little to photon capture when the activities of all cells are scaled to the leaf level and expressed on a projected area basis. Hattersley (1984) analyzed the morphology of a large number of C_3 and C_4 grasses and concluded that the PCA area per vein differed in the following order: $C_3 > C_4$ NAD-me $> C_4$ NADP-me, which is consistent with the argument presented above. He speculated that differences in the architectural construction of grass leaves were likely to be functionally significant and may be related to known differences in the carbon isotope ratios among C_4 subtypes.

There is ample evidence to suggest that interveinal distances differ in grass leaves (Hattersley and Watson 1975; Kawamitsu et al. 1985; Ohsugi and Murata 1986; Dengler et al. 1994). In comparisons of C_3 and C_4 grass leaves, interveinal distances were closer in C_4 grasses ($\bar{x} = 124 \mu\text{m}$) than in C_3 grasses ($\bar{x} = 304 \mu\text{m}$) (Kawamitsu et al. 1985). Moreover, among C_4 grasses, interveinal distances in C_4 NADP-me grasses ($\bar{x} = 89 \mu\text{m}$) were shorter than C_4 NAD-me grasses ($\bar{x} = 142 \mu\text{m}$). In addition, NADP-me grasses have suberized lamella that prevent apoplastic bundle sheath CO_2 leakage out of the PCR cells, whereas NAD-me grasses do not (Hattersley 1987, 1992). Together, the possibility of greater CO_2 retention within PCR cells (which influences net CO_2 uptake) and a shorter interveinal distance (which influences effective photon capture) should contribute to a higher quantum yield (light-use efficiency) in C_4 NADP-me over C_4 NAD-me grass leaves.

A major difference in the anatomy of dicots and monocots is the general tendency for tight parallel venation in monocots versus a reticulate, multi-branched venation pattern in dicots. Unfortunately, we are unaware of any studies that have quantified interveinal spacing or PCA area per vein (PCR tissue) in dicot species, and so a direct comparison of monocots and dicots is not possible at this time. However, intuitively, the reticulate packing of veins within dicot leaves should increase the fraction of the projected leaf area that is occupied by PCA tissues, if PCR activities occur only in bundle sheath cells surrounding veins. We hypothesize that this structural difference contributes to the reduced light-use efficiency of C_4 NAD-me dicots relative to C_4 NAD-me monocots and of C_4 NADP-me dicots relative to C_4 NADP-me monocots.

Based upon general differences in the chloroplast capacity to generate reducing energy within mesophyll cells (which is then translocated into the bundle sheath cells), one would expect a slightly higher light-use efficiency in all C_4 NADP-me leaves relative to C_4 NAD-me leaves. Yet other factors may be contributing to the enhanced quantum yields of C_4 NADP-me dicots over

those of C₄ NAD-me dicots. For instance, Herbst (1971) described an unusual cell arrangement in *Euphorbia*, one of the relatively few NADP-me dicots, that effectively decreased the PCA-to-PCR ratio. In between the multi-branched veins of many *Euphorbia* leaves are short, isolated veinlets, consisting only of tracheids and associated bundle sheath cells. Because they are detached from the leaf vein network, the isolated tracheids and bundle sheath cells are not associated with water or nutrient transport. Yet the bundle sheath cells in these isolated veinlets contain PCR cells and are likely increasing the light-use efficiency by the same means as the reduced interveinal distances in C₄ NADP-me monocots. A functionally equivalent pattern may occur in some *Salsola* and *Suaeda*, where PCR activities occur in a ring that surrounds the entire leaf instead of being limited only to the vascular bundle tissues (Carolin et al. 1975; Shomer-Ilan et al. 1975; P'yankov et al. 1997).

C₄ species should be favored in reduced atmospheric CO₂

Ehleringer et al. (1991) proposed that declining atmospheric CO₂ concentrations could be a major selective force for the expansion of C₄ ecosystems at the end of the Miocene. The palaeogeological and paleoecological evidence of the near simultaneous global expansion of C₄ ecosystems at the end of the Miocene (Cerling et al. 1993, 1997a, b; Quade and Cerling 1995) implies a common selective force, such as would be expected with a reduction in atmospheric CO₂ conditions. The development of the Himalayas and the Tibetan Plateau, which exposed massive amounts of unweathered silicate rock in a climatic zone where carbonate formation would then be high, may have been a mechanism for a global reduction in CO₂ (Raymo and Ruddiman 1992).

We modeled quantum yield for CO₂ uptake in C₃ plants as a function of both temperature and CO₂ concentration (Fig. 1), using the basic equations and parameters to describe leaf-level photosynthesis (Farquhar and von Caemmerer 1982; Jordan and Ogren 1984). The range of CO₂ concentrations was chosen to span that range thought to have occurred within the last several million years, from a low of 180 ppmV during the glacial maximum to a high of about 500 ppmV at the end of the Miocene (Jouzel et al. 1987; Berner 1991; Cerling 1991). The model predicts a family of quantum yield curves, each exhibiting a continual decrease in the quantum yield with increasing temperature and each indicating that the quantum yield at any specified temperature should increase with CO₂ concentration (Fig. 1 left diagram). The validity of this model was tested by a comparison of the predicted and observed quantum yields for C₃ plants under current CO₂ conditions (Fig. 1 middle diagram). The extremely close association between predicted and observed quantum yield values lends credence to this modeling effort. We also com-

pared CO₂ compensation points predicted by this model with extensive values summarized by Brooks and Farquhar (1985) and again observed a very close agreement between modeled and observed results (data not shown). In contrast to C₃ plants, the quantum yield for CO₂ uptake in C₄ plants does not change with temperature and CO₂ concentration over the biologically relevant range of temperatures (Fig. 1 right diagram).

By comparing the temperature and CO₂ dependence of the quantum yields of C₃ and C₄ plants, one can calculate the crossover temperature, which will be the daytime temperature at which the quantum yields of C₃ and C₄ plants are identical for a given atmospheric CO₂ concentration. When these crossover temperatures are compiled (intersection of lines in left and right diagrams of Fig. 1), it is clear that the transition between C₃ and C₄ superiority is a function of both atmospheric CO₂ and temperature (Fig. 2). Variation in the C₃/C₄ crossover temperature occurs because of the dependence of the C₃ quantum yield on both temperature and [CO₂]/[O₂] (Ehleringer and Björkman 1977; Ku and Edwards 1978). The inherent differences in quantum yields among C₄ monocots and C₄ dicots (but not among C₃ monocots and C₃ dicots) leads to fundamentally different combinations of CO₂ and temperature favoring C₄ monocots over C₃ plants or C₄ dicots over C₃ plants (Fig. 2).

Considering a reasonable range of growing-season temperatures, the quantum yield model predicts that both monocot and dicot C₄ species should be rare under globally high CO₂ concentrations, but expanding as atmospheric CO₂ levels decrease (Fig. 3). The C₃/C₄ crossover temperature for current CO₂ concentrations (approximately 350 ppmV) is at about a daytime growing-season temperature of 21°C for C₄ grasses

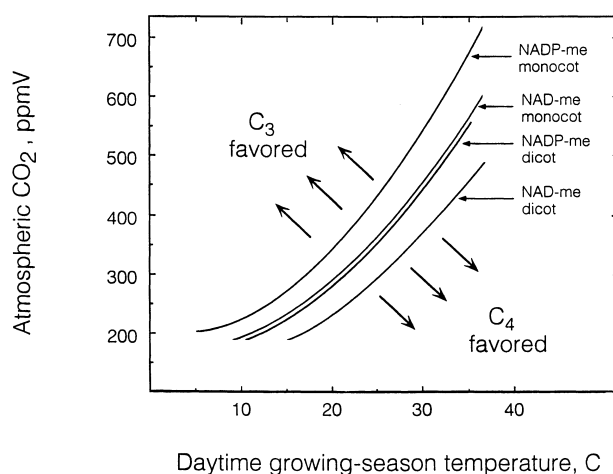


Fig. 2 Modeled crossover temperatures of the quantum yield for CO₂ uptake for monocots and dicots as a function of atmospheric CO₂ concentrations. The boundary conditions for both monocots and dicots are NADP-me C₄ plants (upper boundaries) and NAD-me C₄ plants (lower boundaries). The crossover temperature is defined as the temperature (for a particular atmospheric CO₂ concentration) at which the quantum yields for CO₂ uptake are equivalent for both the C₃ and the C₄ plant. Data are based on average values from Table 4

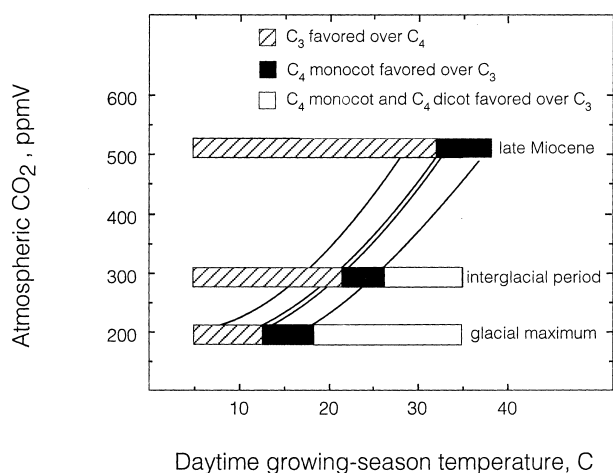


Fig. 3 Predicted superiority of different photosynthetic pathways. Modeled crossover temperatures of the quantum yield for CO_2 uptake for monocotyledonous and dicotyledonous plants as a function of three atmospheric CO_2 concentrations: estimated late Miocene values (upper bar), modern values during interglacial periods (middle bar), and values during maximum glacial periods (lower bar). The boundary conditions for both monocotyledonous and dicotyledonous plants are NADP-me C_4 plants (upper boundaries) and NAD-me C_4 plants (lower boundaries). The crossover temperature is defined from simulation values in Fig. 2

(NADP-me subtype) dominance over C_3 grasses (Fig. 2); the crossover temperature for NAD-me C_4 grasses is somewhat higher at 25°C . This range of crossover temperatures for C_4 grasslands is well corroborated by field observations worldwide (Table 2; see also Tieszen et al. 1997). Interestingly, the expected C_3/C_4 crossover temperature for the pre-industrial CO_2 concentration level of about 280 ppmV is at a daytime growing season temperature of ca. 17°C , implying that C_4 grasses may have been more prevalent historically than they are today. In support of this, the recent geological record provides evidence for changing proportions of C_3 and C_4 biomass during periods of both higher and lower CO_2 levels compared to the present.

Ice cores provide a detailed record of CO_2 concentration changes in the last 100,000+ years, and peat bogs and lake sediments preserve a quantitative record of the proportions of C_3 versus C_4 biomass in the catchment areas. The ice core record from many cores shows that glacial-maximum CO_2 concentrations were between about 180 and 200 ppmV from about 50 ka to about 18 ka BP, when they began to increase to the post-glacial level, reaching about 280 ppmV by around 12 ka BP (Neftel et al. 1988; Leuenberger et al. 1992). At the same time, global temperatures were significantly lower during the glacial periods. Temperature estimates based on gas solubilities suggest an approximately 5°C temperature differential in equatorial regions (Stute et al. 1995) and between about $8^\circ\text{--}15^\circ\text{C}$ in the polar regions based on stable isotope temperatures or geothermal inversion temperatures, respectively (Jouzel et al. 1987; Cuffey et al. 1995). From both Figs. 1 and 2 it is clear that the vector of $\Delta T/\Delta[\text{CO}_2]$ between glacial and inter-

glacial conditions is important in determining whether C_4 ecosystems expanded or contracted during the glacial/interglacial transition.

Our modeling efforts predict an expansion of C_4 -dominated ecosystems globally during glacial periods, because of the substantially reduced quantum yields in C_3 plants under low atmospheric CO_2 conditions (Fig. 3). There is supporting evidence from pedogenic carbonate and sediment data in the literature, which can be interpreted as indicating that C_4 ecosystems were more widespread during the glacial maxima than they are today. Pedogenic carbonates are formed from CO_2 derived from soil respiration and are therefore a long-term indicator of the vegetation within an ecosystem. In the arid regions of New Mexico in the southwestern United States, Cole and Monger (1994) reported soil carbonate evidence of C_4 -dominated ecosystems during the last glacial maximum, followed by a rapid decline in C_4 abundance during deglaciation. Today that region is dominated by a C_3 semi-arid ecosystem. Although there may be alternative explanations why the C_4 taxa disappeared from these ecosystems, the carbonate pattern is consistent with quantum yield model results suggesting that atmospheric CO_2 was an important factor. Liu et al. (1996) conducted a related study of pedogenic carbonates in southern Arizona and reported observations very similar to those of Cole and Monger (1994). This raises the possibility that extensive portions of southwestern North America, which are currently dominated by C_3 ecosystems, may have had a much more significant C_4 component during the last glacial maxima. Further linkages between ecology and geology should be directed at trying to resolve this issue, since it not only has impacts on the nature of primary productivity and plant distribution, but also on the mammalian grazing systems that would have occupied these habitats.

Numerous sites in central Africa also provide similar evidence for a more extensive distribution of C_4 ecosystems in glacial periods than occurs today or existed even in recent interglacial periods (Fig. 4). The $\delta^{13}\text{C}$ values of organic matter in the Buyongwe Valley core (Burundi; Hillaire-Marcel et al. 1989), Lake Bosumtwi (Ghana; Talbot et al. 1984; Talbot and Johannessen 1992; Street-Perrott 1994), Lake Barombi Mbo (Cameroon; Giresse et al. 1994), a Kashiru Peat Bog (Burundi; Aucour et al. 1993), Sacred Lake (Kenya; Huang et al. 1995), and southern Lake Tanganyika (Hillaire-Marcel et al. 1989) were all higher during the last glacial period (15 to 25 ka BP) than in the Holocene (0 to 10 ka BP), indicating C_4 -dominated ecosystems during the glacial maxima on each of these sites. Lakes Bosumtwi and Barombi Mbo are both low elevation sites (< 500 m), the Buyongwe Valley is an intermediate-elevation site (1,370 m), while the Kashiru peat bog is a high-elevation site ($> 2,000$ m). All localities show increased grass pollen during periods of high $\delta^{13}\text{C}$ values, suggesting an expansion of C_4 grasslands during the glacial maxima with a retreat to C_3 -dominated ecosystems during deglaciation. Jolly and Haxeltine (1997) also showed

Fig. 4 Chronological profiles of $\delta^{13}\text{C}$ of organic matter in Lake Bosumtwi (Ghana; Talbot and Johannessen 1992), Lake Barombi Mbo (Cameroon; Giresse et al. 1994), Kashiru peat bog (Burundi; Aucour et al. 1994), and Sacred Lake (Kenya; Huang et al. 1995) since the last glacial maximum and up to the present. These records from central Africa show that C_4 ecosystems were more abundant near the end of the last glacial period than they are today

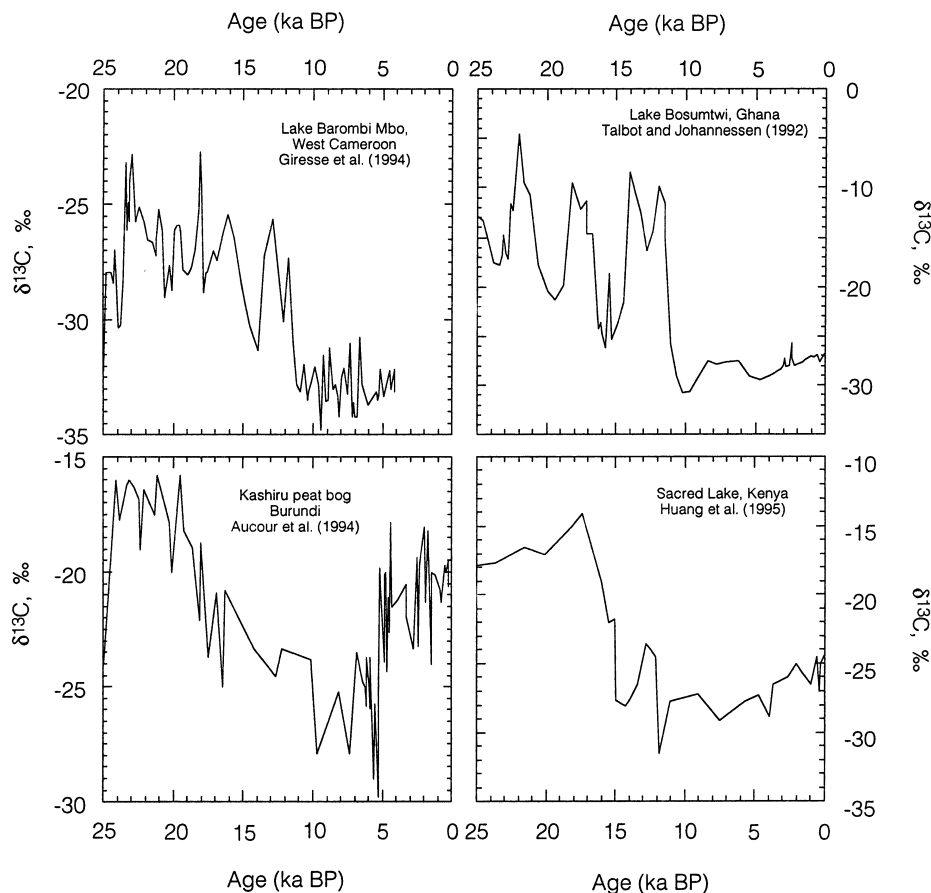
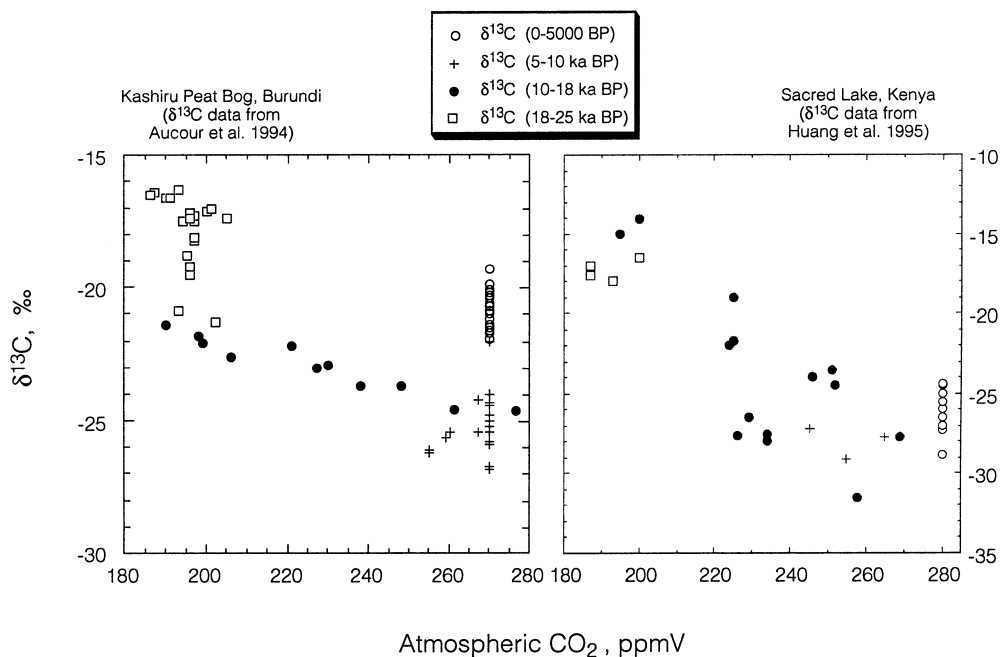


Fig. 5 A plot of the ^{13}C of organic matter in Kashiru peat bog (Burundi; Aucour et al. 1994) (LEFT PLATE) and Sacred Lake (Kenya; Huang et al. 1995) (RIGHT PLATE) as a function of atmospheric CO_2 concentrations derived from the Byrd ice core (Antarctica; Neftel et al. 1988). Chronology of the Byrd ice core is from Sowers and Bender (1995), and ^{14}C chronologies of the organic samples are corrected to absolute years using the ^{14}C to U-Th calibration (Bard et al. 1990, 1993; Edwards et al. 1993). These records from central Africa show that C_4 ecosystems were more abundant near the end of the last glacial period than they are today, and that declining CO_2 levels in the atmosphere were accompanied by a contraction of C_4 biomass in the tropics



that the upper elevation C_3 shrub limits shifted during the full glacial period in central Africa. It will be very interesting to see if these trends are sustained when more localities are examined in tropical and subtropical regions throughout the world.

When data from Fig. 4 are plotted with reconstructed atmospheric CO_2 data from the Byrd ice cores, there is a clear indication that C_4 biomass decreased as atmospheric CO_2 increased at the end of the last glacial maximum. In Fig. 5, we present two examples, Kashiru

Peat Bog (Burundi) and Sacred Lake (Kenya), of this pattern. This relationship is remarkably consistent with the C₃/C₄ crossover pattern predicted in Fig. 2. With end member δ¹³C values of -27‰ for C₃ and -15‰ for C₄, the C₃/C₄ transition at these sites is predicted to have occurred at about 210–220 ppmV.

Recent global modeling studies of biome distributions during the last glacial maximum do not provide a clear picture of the extent of C₄-dominated ecosystems, although there is a trend for more extensive grasslands and savannas than observed now (Adams et al. 1990; van Campo et al. 1993; Crowley 1995). Crowley (1990, 1995) suggested that changes in the marine carbon isotope ratio record could be interpreted as suggesting that C₄ plants were more extensive during the full glacial period than they are today, although this point has been challenged by Prentice and Sarnthein (1993).

Atmospheric CO₂ levels greater than about 500 ppmV favor C₃ photosynthesis under most global conditions (Fig. 2). While the palaeo record of atmospheric CO₂ levels is poorly known, geological evidence is compatible with much higher CO₂ levels in the Mesozoic (ca. 220–65 Ma BP). Modeling of the global carbon budget indicates high CO₂ levels for most of the Mesozoic (Berner 1991, 1994), and the palaeosol CO₂ barometer also indicates CO₂ levels > 1,000 ppmV for the Mesozoic (Cerling 1991; Ehleringer and Cerling 1995). If these levels are correct, then CO₂ concentration levels declined in the Tertiary and crossed a threshold where C₄ plants would have a competitive advantage. Studies of fossil soils (Quade et al. 1989; Quade and Cerling 1995) and fossil tooth enamel (Cerling et al. 1993, 1997a, b) indicate that abundant C₄ biomass suddenly appeared in North America, South America, southern Asia, and Africa between 8 and 6 million years ago, perhaps in response to atmospheric CO₂ levels declining through the window where C₄ plants were now more efficient than C₃ plants.

Why are C₄ dicots at a disadvantage compared to C₄ monocots?

While the palaeogeological literature does not allow one to specify whether it was C₄ monocots, C₄ dicots, or both that expanded globally at the end of the Miocene, the available evidence suggests that the C₄ expansion occurred in grasslands and savannas. These ecosystems are currently dominated by C₄ monocots and there is no evidence to indicate that C₄ dicots were ever significant components of these ecosystems. The modeling results in Fig. 3 strongly suggest that C₄ monocots would have been more efficient and thus more likely selected over C₄ dicots as atmospheric CO₂ decreased. One can speculate on the extent to which each C₄ group would have been favored by natural selection as global CO₂ decreased through analyses of three major time periods: the end of the Miocene, recent glacial periods, and recent interglacial periods. Global CO₂ concentrations are known

to have averaged 180–200 ppmV during glacial periods and 270–290 ppmV during interglacial periods (Jouzel et al. 1987). The atmospheric CO₂ concentration at the end of the Miocene has not yet been quantified, but 500 ppmV is not unreasonable (Berner 1991; Cerling 1991).

Examining plant responses at these three atmospheric CO₂ concentrations, C₄ photosynthesis is expected to have been selected first in the warmest ecosystems as atmospheric CO₂ decreased through time (Fig. 3). At the end of the Miocene, we speculate that C₄ photosynthesis would have been favored in only the warmest of terrestrial ecosystems with adequate soil moisture. Given the reduced photorespiration rates that would be expected to have occurred in C₃ plants, only NADP-me monocots would have had a selective advantage over C₃ plants in these warm ecosystems. It is likely that summer precipitation (monsoons) would have played a key role in allowing NADP-me monocots to prosper under these high temperature conditions. As global CO₂ concentrations decreased to current and ultimately to interglacial concentrations, C₄ photosynthesis is predicted to have expanded into even cooler ecosystems than predicted for the late Miocene (Fig. 3). Most of this expansion is predicted to have been C₄ NADP-me and C₄ NAD-me monocots. The C₄ dicots are predicted to have had an advantage only in the warmest or saline ecosystems and then only under low CO₂ conditions. Even then, C₄ dicots would be at a competitive disadvantage to C₄ monocots unless a factor such as disturbance played a significant role. However, we propose that it is not until the modern glacial periods (last 3 million years) that the global CO₂ concentrations would become low enough for C₄ dicots to have expanded beyond the warmest ecosystems (Fig. 3).

Given that quantum yields of C₄ dicots tend to be lower than those of C₄ monocots, there are limited canopy-level situations in which C₄ dicots have a competitive advantage over C₄ monocots. The quantum yield model predicts that competitive situations with equivalent canopy stature should favor the C₄ monocots over the C₄ dicots. However, given the woody nature of most dicots, secondary growth and a perennial habit would provide dicots with a mechanism to overshadow a shorter monocot. Upon closer examination though, most C₄ dicots, with the exception of some *Chenopodiaceae* and *Euphorbiaceae tuxa*, are annuals or nonwoody perennials and so there are few realistic opportunities to realize a C₄ dicot competitive advantage.

Success of the C₄ monocots may also have been influenced by their growth habit with a basal meristem, since monocots have a significant meristematic advantage over dicots in their response to grazing pressure. Evolution of grasslands preceded the appearance of the first known C₄ taxa, implying that C₄ taxa originating within the monocots would have had a significant grazing-tolerance advantage over dicots. This may have been enough to provide an early advantage for C₄ monocots over C₄ dicots. Disturbance or habitats with a short growing season, however, may provide a selective

opportunity for C_4 dicots, especially in habitats with warm temperatures (Fig. 3). Here the Stowe and Teeri (1978) data suggest that the percent C_4 dicots within the flora reach their highest values. Mulroy and Rundel (1977) pointed out that C_4 photosynthesis was only significant among the warm-season desert ephemerals, many of which were dicots. This is also consistent with observations by Elmore and Paul (1983) that C_4 dicots comprised a significant fraction of weedy species. Under such conditions, the competitive advantages of C_4 monocots over C_4 dicots may be sufficiently reduced and C_4 dicots would still have a competitive advantage over C_3 species. All of this is untested speculation at present, although it does suggest a sequence of events that could lead to present-day distributions.

The phylogenetic distribution of C_4 photosynthesis in dicots occurs among a very wide range of orders throughout the Angiospermae (Table 1), but ecologically C_4 photosynthesis in dicots occurs mostly in taxa that occupy ephemeral, disturbed, or saline habitats. Three lines of evidence suggest a relatively recent origin for C_4 photosynthesis in dicots: (a) this pathway is typically not widespread within any single family or genus, (b) there are a number of genera having C_3 - C_4 species where C_4 taxa do not yet exist, and (c) it only occurs among the more advanced Angiospermae. A relatively recent evolution/expansion is entirely consistent with model results indicating that C_4 dicots were not expected to have a strong selective advantage over C_3 species until atmospheric CO_2 concentrations reached levels as low as observed in recent glacial periods and then only in higher-temperature habitats. If the quantum yield model is correct, then C_4 dicots are not likely to have had a significant competitive advantage until atmospheric CO_2 concentrations reached glacial-maximum levels. With low atmospheric CO_2 during full glacial periods persisting for only 20,000–30,000 years, it is not surprising that C_4 dicots are not more common, because that length of time may not have been a sufficiently continuous period for the evolution of a stable C_3 - C_4 intermediate and ultimately the full expression of C_4 photosynthesis. Those dicots that are likely to have been the fastest to respond would be annuals and short-lived perennials, which could undergo many more generations of selection during full glacial, low atmospheric CO_2 conditions. In contrast, atmospheric CO_2 levels since the end of the Miocene have been continuously favorable for the evolution and expansion of C_4 monocots.

Herbivore evolution and C_4 photosynthesis expansion

The ecosystem-level aspects of changes in C_3/C_4 abundance have implications for both primary productivity and for the distributions of invertebrate and vertebrate animals that graze on these plants. Caswell et al. (1973) proposed that animal systems showed a tendency to avoid C_4 vegetation. Among the early evaluations of this hypothesis was Tieszen et al. (1979a), which quantified

the extent to which different vertebrate grazers in east Africa showed distinct preferences for either C_3 or C_4 vegetation components (using carbon isotope ratios). A key factor in the nutritional quality differences of C_3 and C_4 plants is that much of the protein in C_4 leaves is enclosed within the thicker cell walls of the bundle sheath cells, leading to a lower digestibility by some grazers (Wilson et al. 1983; Wilson and Hattersley 1983). Ehleringer and Monson (1993) reviewed the evidence indicating that while some invertebrate and vertebrate grazers do switch between C_3 and C_4 vegetation sources, there are clear patterns of grazers preferring plants with one pathway over the other. Recently, Cerling et al. (1997a, b) have proposed the possibility that changes in the abundance of C_3/C_4 plants within ecosystems could have significant impacts on both the evolution and composition of mammalian grazing systems. They note that the global expansion of C_4 biomass recorded in the diets of mammals from Asia, Africa, North America, and South America over the interval from about 8 Ma to 5 Ma BP was accompanied by the most significant mammalian faunal turnover on each of these continents during the Tertiary. These patterns strongly imply a common global factor for the ecological changes that played a role in mammalian extinction. Previously, changes in fauna and flora at the end of the Miocene have been attributed to changes in aridity; however, these changes are also compatible with expanded C_4 biomass due to the CO_2 starvation of C_3 plants and with animal abundance influenced by C_3/C_4 abundance. Similar arguments can be constructed for the expansion, migration, and/or extinction of mammalian groups during the glacial–interglacial cycles (such as the loss of large mammals in southwestern North America at the end of the last full glacial period). These ideas are testable and it will be very interesting to see what patterns emerge as the sediment, fossil, and carbonate data from different regions become available and are evaluated in this context.

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