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Implications of Quantum Yield Differences on the Distributions of C₃ and C₄ Grasses*

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Summary. The implications of a reduced quantum yield (initial slope of the photosynthetic light response curve) in C₄ plants and temperature dependence of quantum yield in C₃ plants on total canopy primary production were investigated using computer simulations. Since reduced quantum yield represents the only known disadvantage of the C₄ photosynthetic pathway, simulations were conducted with grass canopies (high LAI and hence photosynthesis in most leaves will be light-limited) to see if quantum yield is a significant factor in limiting the primary production and thus distributions of C₄ grasses. Simulations were performed for three biogeographical or environmental conditions: the Great Plains region of North America, the Sonoran Desert of North America, and shade habitats. For all three cases, the simulations predicted either spatial or temporal gradients in the abundances of C₄ grasses identical to the abundance patterns of C₄ grasses observed in the field. It is thus concluded that while the C₄ photosynthetic mechanism may be highly advantageous in specific environments, it may be disadvantageous in others.

Introduction

Since the initial discovery of the C₄ photosynthetic pathway (Kortshack et al., 1965; Hatch and Slack, 1966), many studies have been aimed at understanding the biochemistry and significance of this pathway. It is now widely accepted that the C₄ pathway serves as a mechanism to concentrate CO₂ within the chloroplast environment where the carboxylation of ribulose biphosphate (RuBP) by RuBP carboxylase-oxygenase occurs (Hatch, 1971; Björkman, 1973). This concentrating mechanism also suppresses the deleterious effects of oxygen on photosynthesis (Black, 1973; Björkman, 1973; Chollet and Ogren, 1975). Consequently, C₄ plants often have high rates of photosynthesis under ambient atmospheric conditions. Black (1971) contended that C₄ species in general have photosynthetic rates exceeding those of C₃ species, and that C₄ species are

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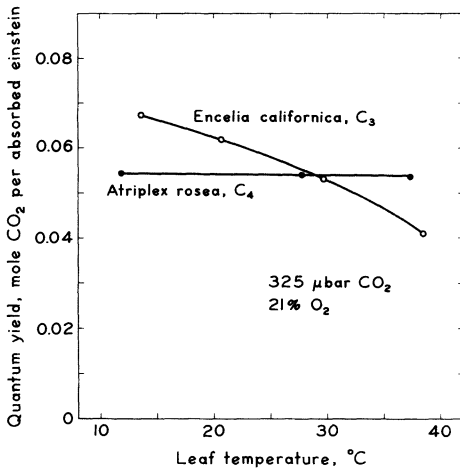


Fig. 1. Quantum yield for CO₂ uptake in C₃ species *Encelia californica*, and C₄ species *Atriplex rosea*, as a function of leaf temperature. Quantum yield was measured in normal air of 325 μbar CO₂ and 21% O₂. This figure is based on data from Ehleringer and Björkman (1977)

in effect superior to C₃ species. However, C₃ species do exist which possess maximum photosynthetic rates on a leaf area basis equal to or exceeding the highest known C₄ species rates (Ehleringer et al., 1976; Mooney et al., 1976).

The advantages of C₄ photosynthesis over C₃ photosynthesis are greatest under conditions of high light intensities, high leaf temperatures, and reduced stomatal conductances. Under these conditions, photosynthesis is usually limited by the intercellular CO₂ concentration (Black, 1973; Björkman, 1973; Björkman et al., 1975). Such conditions are common in many deserts and other subtropical regions of the world. Consequently, it is not surprising to find that C₄ plants commonly occur in these habitats (Negbi, 1968; Gupta and Saxena, 1971; Teeri and Stowe, 1976), but are relatively rare in cool or temperate climates (Mooney et al., 1974; Teeri and Stowe, 1976).

The restricted abundance of C₄ species suggests that C₄ photosynthesis may not be superior in all environments and may even be disadvantageous in others. The question then arises, has there simply not been enough evolutionary time for C₄ species to invade all habitats or are there possible limitations or disadvantages directly attributed to the C₄ pathway? It has been suggested that certain steps of the C₄ pathway cannot operate efficiently at cool temperatures (10–20°C). However, this is not an intrinsic property of the C₄ pathway, as Björkman et al. (1975) have shown that the photosynthetic machinery of *Atriplex sabulosa*, a C₄ species of the North Atlantic coasts, can operate efficiently even when grown under native environmental conditions of 16°C days and 10°C nights. Recent studies by Ehleringer and Björkman (1977) indicate a possible disadvantage of the C₄ pathway. Quantum yields (initial slope of the photosynthetic light response curve) of C₃ and C₄ plants were shown to differ (Fig. 1). Quantum yields of C₄ plants, which lack an oxygen inhibition of photosynthesis under normal atmospheric conditions, are 0.053 mole CO₂ per absorbed einstein and remain constant with temperature. However, quantum yields of C₃ plants, which exhibit an oxygen inhibition of photosynthesis, decline as temperatures increase, falling from 0.069 mol CO₂ per absorbed einstein

at 14°C to 0.042 mol CO₂ per absorbed einstein at 38°C. At low leaf temperatures, quantum yields of C₃ are greater than those of C₄ plants, reflecting the lower intrinsic cost of this pathway. The reduction of the quantum yield of C₃ plants was directly attributed to an increase in oxygen inhibition with temperature.

For individual leaves, the quantum yield influences the rate of net photosynthesis primarily at low and moderate light levels. However, for an entire plant canopy, the rate of primary production is often light-limited at all light levels, even for full noon sunlight conditions (Zelitch, 1972; Biscoe et al., 1975). Consequently, quantum yield exerts a sizeable influence on the rate of canopy primary production at all times during the day. As the difference in quantum yields represents the only known disadvantage of the C₄ pathway, an analysis of the effect of these quantum yield differences on the rates of primary production of entire plant canopies under different environmental conditions was undertaken.

This study uses the canopy structure and physiological parameters characteristic of grass species. There are three reasons why I used grass species: (1) both C₃ and C₄ photosynthetic pathways are common within this family; (2) grasses occur over very wide geographical regions, including tropical, desert, temperate, and tundra habitats; and (3) since grasses form canopies with high leaf area indexes (LAI), primary production is more likely to be influenced by quantum yield than it would be in dicotyledonous canopies with generally lower LAI.

For this analysis, a model was constructed which calculated the hourly and daily rates of primary production (as net carbon dioxide fixed) for two adjacent canopies: a C₃ grass canopy and a C₄ grass canopy. To evaluate solely the influence of the quantum yield on primary production, the two canopies were physically and physiologically identical except for (1) differences in the effects of temperature on quantum yield and (2) temperature dependence of light-saturated photosynthesis.

In this study it was assumed that for two canopies identical in all respects excepting intrinsic differences in quantum yield and temperature dependence of light-saturated photosynthesis, the canopy with the highest daily net-carbon gain would be more successful and would outcompete and replace the less productive one, since the more productive canopy would have a greater amount of carbon available both for growth and reproduction. Consequently, in biogeographic interpretations of the simulations of comparative productivity of C₃ versus C₄ grass canopies, the canopy with the highest productivity rate should represent the dominant photosynthetic pathway in that particular environment.

The Model

The model used to calculate primary production consisted mainly of four sets of equations: (1) a set of equations to describe the effect of light intensity and temperature on the rate of net photosynthesis of individual leaves, (2)

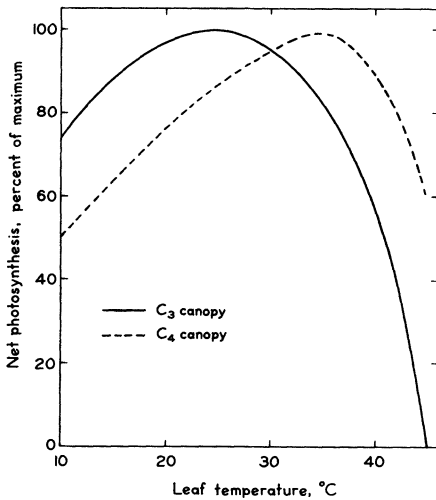


Fig. 2. Relationships between net photosynthesis and leaf temperature at high light intensities used in the primary production simulations

a set of equations to describe light attenuation within a canopy and light absorption by a layer of leaves within that canopy, (3) an equation to describe the daily course of air temperature, and (4) a set of equations to describe the daily path (altitude and azimuth) of the sun for different latitudes and declinations. Net photosynthesis was calculated as gross fixation minus dark respiration. The equation describing net photosynthesis as a function of light intensity was essentially a hyperbolic function, which has been utilized in several previous photosynthetic models (e.g., Chartier et al., 1970; Allen et al., 1974)

$$P_n = \frac{I P_m Q}{I Q + P_m} - R \quad (1)$$

where P_n is the net photosynthetic rate at a given temperature, P_m is the maximum photosynthetic rate at saturating light intensities, I is the light intensity absorbed by the leaf, Q is the quantum yield, and R is the dark respiration rate. Data on the dependence of the quantum yield on temperature were derived from Ehleringer and Björkman (1977).

For the C_3 species, the derived regression was

$$Q = 0.081 - 0.000053T - 0.000019T^2 \quad (2)$$

and for the C_4 species,

$$Q = 0.053 \quad (3)$$

where T is the leaf temperature.

The temperature dependence of light-saturated photosynthesis used in the simulations was different between the C_3 and C_4 species (Fig. 2). Temperature optima for photosynthesis were 25° and 35°C for the C_3 and C_4 species, respectively. These curves were to represent typical temperature dependence curves for C_3 and C_4 grass species. Maximum rates of photosynthesis versus temperature were calculated from polynomial regressions describing these curves.

Light attenuation within the canopy was described using the light-extinction equations developed and used by Monsi and Saeki (1953), Anderson (1966), Miller (1972), and others. Basically,

$$I_L = I_0 e^{(-KF)} \quad (4)$$

where I_L is light intensity at level L within the canopy, I_0 is the light intensity above the canopy, K is the extinction coefficient, and F is the cumulative leaf area index of the canopy above level L .

The daily course of air temperature was described using a sine curve, with the amplitude of daily temperature fluctuation depending on the daily minimum and daily maximum temperatures. In this equation, the peak or daily maximum occurred at 1200. The equation was

$$T = (T_{\max} + T_{\min})/2 + [(T_{\max} - T_{\min})/2] \sin(H - 90) \quad (5)$$

where T is the air temperature, T_{\max} and T_{\min} are the daily maximum and minimum air temperatures, respectively, and H is the hour angle of the day. Unless otherwise stated, T_{\min} was taken to be one half of T_{\max} . In the simulations, leaf temperature was set equal to air temperature.

The change in solar radiation intensity and the path of the sun during the course of a day were defined by a series of equations relating the solar constant, latitude, declination, and atmospheric turbidity. These equations, taken from List (1968), were

$$\sin(\text{alt}) = \sin(\text{lat})\sin(\text{dec}) + \cos(\text{lat})\cos(\text{dec})\cos(H) \quad (6)$$

$$I_0 = S \sin(\text{alt}) A^{(\sin(\text{alt}))} \quad (7)$$

where alt is the solar altitude, dec is the solar declination, lat is the latitude, S is the solar constant, and A is the atmospheric transmission coefficient.

Vegetation canopy characteristics were selected to be representative of a typical grass canopy in North America. The total canopy leaf area index was 4. The canopy was divided from top to bottom into 10 levels, having the following leaf area indexes per level: 0.1, 0.2, 0.4, 0.6, 0.8, 0.8, 0.5, 0.3, 0.2, and 0.1. The leaf angle of leaves at each level was 45°. This angle is representative of the average leaf angle for many grass canopies.

The physiological input parameters were representative values for North American grass species. A maximum photosynthetic rate (P_m) of 4 nmol CO₂ cm⁻² s⁻¹ at 25°C was chosen for the C₃ canopy. The maximum photosynthetic rate of the C₄ species was 20 percent higher than that of the C₃ species, reflecting a conservative estimate of the increase in photosynthesis due to a lack of oxygen inhibition of photosynthesis in these species. A value for dark respiration at 30°C of 0.3 nmol CO₂ cm⁻² s⁻¹ was chosen for both canopies. The dark respiration rate was allowed to vary with temperature. The Q_{10} for this change was assumed to be 2.

Simulation Results

Two types of simulations were conducted to estimate the impact of the quantum yield on daily rates of net primary production of identical C₃ and C₄ canopies.

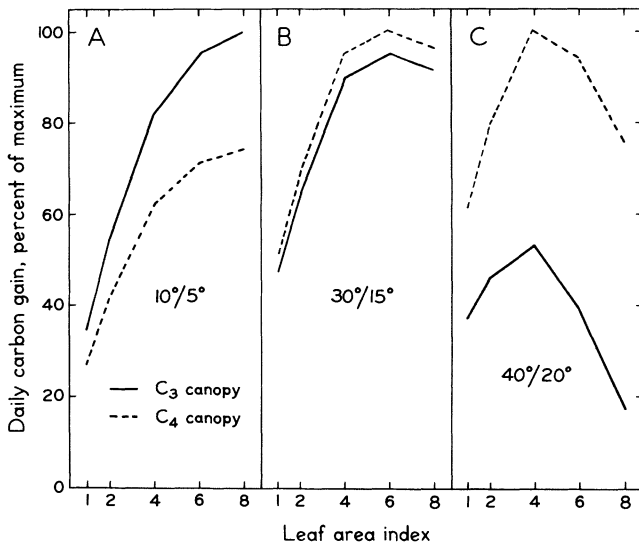


Fig. 3. Simulation of total daily carbon gain by C_3 canopies and C_4 canopies as a function of canopy leaf area indexes. The three plates represent different daily maximum/minimum air temperatures. The daily carbon gained by each canopy is plotted as a percent of the maximum rate of carbon gain for each set of maximum/minimum air temperatures

One set of simulations considered the effects of canopy size (LAI) on primary production, while the other considered the effects of three different biogeographical or environmental regimes on primary production in a canopy of constant size (LAI=4). The first biogeographical regime was a latitudinal transect in the Great Plains region of North America from a latitude of 25°N to 60°N. This transect is characterized by having predominantly grass species with a single growing season annually. The second simulated environment, the Sonoran Desert region in southwestern North America, has two distinct growing seasons during the year. The region around Tucson, Arizona, was used for these simulations. The third environment was a shaded environment, a habitat which can occur almost anywhere geographically. Thus, in these simulations, I compared the productivity of C_3 and C_4 canopies in shaded habitats under different thermal regimes.

Influence of Canopy Size

The effect of the interaction between canopy size, temperature, and quantum yield on the productivity of C_3 and C_4 canopies was determined using simulations with canopies having total leaf area indexes of 1, 2, 4, 6, and 8. The distribution of this leaf area within the canopy was according to the same proportions as described above.

Simulations were conducted for maximum day temperatures of 10°, 30°, and 40°C (Fig. 3). Three significant results appeared: (1) Quantum yield appeared to have a strong influence on the rate of primary production at all

leaf area indexes simulated. (2) The effect of differences in quantum yield on primary production was progressively magnified as leaf area index increased. (3) The photosynthetic pathway yielding the greatest productivity changed according to environmental regime. The highest rate of carbon gain in the C₃ canopy was in the 10°/5°C environment, where the difference in net daily productivity reached 26% at an LAI of 8. Under environmental conditions of 30°/15°C, the C₃ and C₄ canopies had essentially identical rates of carbon gain at each of the different LAI. However, in the 40°/20°C environment, the C₄ canopy had the greatest productivity. At an LAI of 8 in the 40°/20°C regime, the daily carbon gain of the C₄ canopy was 59% greater than that of the C₃ canopy. For both canopy types, the LAI yielding the greatest daily carbon gain declined as the environment warmed. For environmental regimes of 10°/5°, 30°/15°, and 40°/20°C, the LAI with the highest rates of carbon gain were 8, 6, and 4, respectively.

Great Plains

The daily carbon gain of C₃ and C₄ canopies in the Great Plains area was simulated using environmental data for the month of July. This month was chosen because it is the warmest month of the growing season and the period of peak growth for plants in this region. A previous study of distributions of C₃ and C₄ grasses in North America by Teeri and Stowe (1976) showed that the percentage of C₄ species in a flora was most closely correlated with the July minimum air temperature. To assess the effects of fluctuations in air temperatures on the productivity of C₃ and C₄ canopies, weather records for mean maximum and mean minimum air temperatures during July were collected for Great Plains sites in the United States and Canada. Data were gathered from two sources: U.S. Dept. of Commerce (1965) and Kendrew and Currie (1955). Mean maximum and mean minimum air temperatures for 66 sites were regressed against latitude. The latitudes of these sites ranged from 29°N as the southern extreme to 55°N for the northern extreme.

The regressions of mean maximum air temperature versus latitude and mean minimum air temperature versus latitude were both highly significant. The correlation coefficient for the regression of mean maximum air temperature versus latitude was $r=0.95$ and significant ($P<0.01$). The regression yielded the equation

$$\text{max temperature} = 51.95 - 0.507 \text{ latitude} \quad (8)$$

Similarly, the correlation coefficient for the regression of mean minimum air temperature versus latitude was $r=0.94$ and significant ($P<0.01$). The least square fit to these data was

$$\text{min temperature} = 40.56 - 0.576 \text{ latitude} \quad (9)$$

Maximum and minimum air temperatures for latitudes 25° to 60°N were calculated from Equations (8) and (9). These air temperatures, calculated at

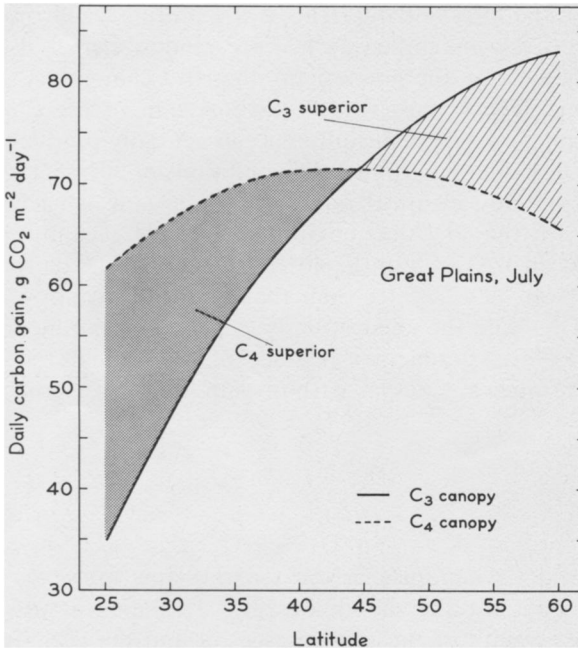


Fig. 4. Simulation of the total daily carbon gain for identical C₃ and C₄ grass canopies (LAI = 4) at different latitudes within the Great Plains of North America during the month of July

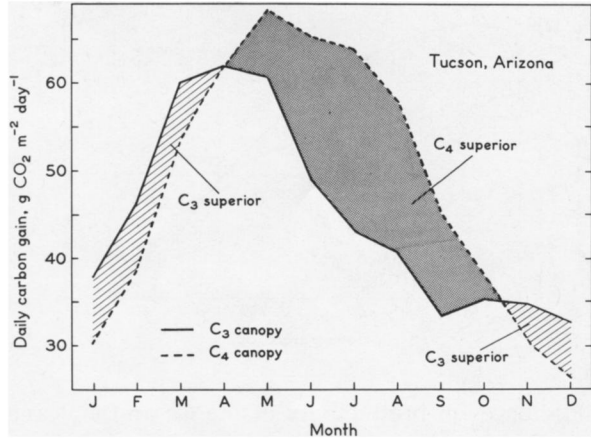
5° latitude intervals, were used to generate daily courses of air temperature using Equation 5. From these environmental data, the daily carbon gain by a C₃ and C₄ canopy at a LAI of 4 at those latitudes were calculated.

The calculated rates of net daily carbon gain for July indicated that the C₄ canopy had a higher rate of primary production at latitudes below 45°N (Fig. 4). The greatest difference in calculated productivity was 25.7 g CO₂ m⁻² day⁻¹ at 25°N. Thus the C₄ canopy gained carbon at a rate 73% higher than the C₃ canopy. The difference in daily carbon gain of the two canopies decreased going north from 25°N. At 45°N the calculated rates of daily carbon gain were nearly identical. However, moving north above a latitude of 45°N, the C₃ canopy become progressively more productive than the C₄ canopy. By 60°N, the difference in daily productivity was calculated to be 17.3 g CO₂ m⁻² day⁻¹. This difference is equivalent to a 26% greater rate of carbon gain by the C₃ canopy.

Sonoran Desert

Much of the Sonoran Desert is characterized by a bimodal rainfall pattern (Shreve and Wiggins, 1964). One such site within the Sonoran Desert with a bimodal rainfall pattern is Tucson, Arizona, where approximately half the rain falls in the winter months (November through March) and half in the summer months (July through September). Two distinct and different flora grow in these two rainy periods (Shreve and Wiggins, 1964).

Fig. 5. Simulation of total daily carbon gain for identical C₃ and C₄ grass canopies (LAI=4) at monthly intervals for Tucson, Arizona, within the Sonoran Desert



In a manner similar to the Great Plains simulations, total net carbon gain of a C₃ and a C₄ canopy was calculated for the Tucson site. However, rather than calculating carbon gain along a latitudinal gradient at a particular time of the year, the Tucson simulations were for a particular site in different months of the year. The mean maximum and mean minimum air temperatures at Tucson, Arizona varied greatly from 18.9° and 2.6°C in January to 38.4° and 22.9°C in July. Environmental data were from Sellers and Hill (1974) and were the basis for calculating the daily fluctuations in air temperature.

Total net carbon gain for a C₃ and a C₄ grass canopy was calculated at monthly intervals (Fig. 5). The results of this simulation show the C₃ canopy to be more productive than the C₄ canopy from mid-October through April. From May through early October, the C₄ canopy has a greater rate of daily carbon gain than the C₃ canopy. The periods during which the C₃ canopy is the most reproductive type are those months in which the winter rains occur. In fact during the four rainiest winter months, December through March, the daily carbon gain of the C₃ canopy is predicted to exceed that of the C₄ canopy by 12 to 25%. Conversely, the period during which the C₄ canopy is predicted to be the most productive canopy type corresponds identically with the summer rain period. In the wettest summer months, July through September, daily productivity in the C₄ canopy exceeds that of the C₃ canopy by 37 to 49%. It should be noted that these daily differences, when compounded over the period of 1 month or over an entire growing season, yield much larger differences in plant biomass.

Shaded Habitat

The last physical environment considered was the shaded habitat. This environmental regime is defined as a habitat receiving only 10% of the sunlight that would otherwise be received at the top of the canopy. For the purposes of the simulation, the habitat was taken to be at a latitude of 0°N and the declination of the sun was 0°. Such conditions tend to minimize the predicted percentage

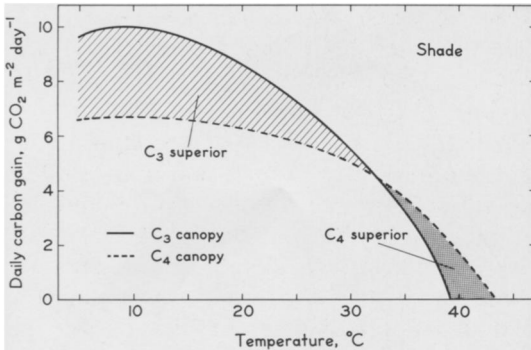


Fig. 6. Simulation of total daily carbon gain for identical C_3 and C_4 grass canopies ($LAI=1$) in a shade habitat (10% of full sun) as a function of daily maximum temperature

differences in productivity of the C_3 and C_4 canopies. For the shaded habitat simulations, a realistic canopy architecture for a plant in such habitats was used. The leaf area index used was 1.0 with a leaf angle of 0° .

The net daily rates of carbon gain in this shaded habitat as a function of the maximum air temperature are shown in Figure 6. At a daytime maximum air temperature of 32°C , productivity in both canopy types is equal. As temperatures decline below 32°C , the C_3 canopy becomes progressively more productive. The maximum differences in daily productivity are approximately 47% and occur in the cold $5\text{--}10^\circ\text{C}$ environments. In habitats warmer than $32^\circ/16^\circ\text{C}$, the daily carbon gain of the C_4 canopy is predicted to exceed that of the C_3 canopy. Daily productivities by the shade C_3 and C_4 canopies become zero at maximum day temperatures of 39° and 44°C , respectively.

Discussion

In this study, I attempted to assess the effects on daily primary production of known physiological differences between C_3 and C_4 grasses in North America. The assumptions throughout these simulations were that the only architectural or physiological differences between C_3 and C_4 grass canopies were differences in temperature dependence of the quantum yield and temperature dependence of light-saturated photosynthesis. Although probably an oversimplification, this approach is the only method currently available for directly assessing the effects of these factors alone on canopy primary productivity. Since (1) decreased quantum yield in C_4 plants is the only known intrinsic disadvantage of this pathway and since (2) both the quantum yield and temperature dependence of light-saturated photosynthesis have such a strong influence on canopy primary production, I consider the approach used justifiable. If the C_3 and C_4 plants used in the simulations are identical except for these two physiological differences, it follows that the plant having the greatest rate of carbon gain will be the most successful and replace the less productive type. Consequently, with some degree of certainty, the biogeographical simulations presented previously (Figs. 4, 5, and 6) allow us to predict whether or not C_4 grass species should be abundant in a specific habitat or during a specific period of the year.

The primary productivity data for the Great Plains simulation suggest a gradient in abundance of C₄ grasses along the latitudinal transect from 25° to 60°N. The simulations predict that C₄ grasses should be dominant at 25°N and that their abundance should decline as we go north from 25°N. Above a latitude of 45°N, the simulations predict that C₄ species should be less abundant than C₃ species and should continue to decline in importance as latitude increases, while C₃ grass species should become increasingly more abundant. This simulation was conducted for only the warmest month of the growing season (July) and is therefore biased toward predicted C₄ abundance. An integration of the primary production estimates for all months of the growing season may suggest that the crossover point in C₄ abundance occurs at a latitude of less than 45°N.

Information on the abundances of C₃ and C₄ grasses in habitats along this Great Plains transect is not available, but data on the percentages of C₄ species in the flora along this transect have been presented by Teeri and Stowe (1976). The values of the abundance of C₄ grasses predicted by the simulations are remarkably similar to the percentages observed by Teeri and Stowe (1976), who showed that for the states of Missouri and Kansas (approx. latitude 40°N) the percentages of C₄ species in the grass flora were 50 and 52%, respectively. They also reported that the percentage of C₄ grasses in the flora increased along a north-to-south transect. The percentage of C₄ grass flora in Oklahoma was 61%. Further south, in Texas, the percentage climbed to 68%. Above a latitude of 45°N, Teeri and Stowe (1976) showed that the percentage of C₄ grasses was always less than 50% and continually declined with increasing latitude. This observation agrees with the simulation prediction that above 45°N, C₃ grasses should be the most abundant type and should also increase in abundance as latitude increases.

In the Sonoran Desert simulations, the predictions are that winter grasses should be of the C₃ type and summer grasses of the C₄ type. Since there are two distinct drought periods between rainy seasons, it is unlikely that there will typically be any significant overlap. Data on the photosynthetic pathways of grasses in the Sonoran Desert have been presented by Mulroy and Rundel (1977) and show that all 16 common summer Sonoran Desert grass species possess the C₄ photosynthetic pathway. Conversely, the two species of winter Sonoran Desert grass possess the C₃ photosynthetic pathway. Corroborating evidence is seen in the species lists of Shreve and Wiggins (1964) for Arizona Upland sites within the Sonoran Desert. Their data on winter and spring ephemerals (which includes herbs in addition to grasses) show that of the winter ephemerals 97% are C₃ species, while of the summer ephemerals 57% are C₄ species. Thus, for the Sonoran Desert simulations, there is a close agreement between predictions and observations of the photosynthetic type present in a particular season.

The results of the shade-habitat simulations suggest that C₄ grass species are unlikely to be found in low light environments that have either cool or moderate temperatures. Rather, it is predicted that C₄ grasses should be expected only in hot shady environments with daytime maximum temperatures exceeding 32°C. Globally, such hot, low light habitats are uncommon. Temperatures in

the understories of many forests such as coniferous, temperate deciduous, and tropical forests generally have temperatures at or below the 32°C level and, therefore, these forests would be predicted not to contain C₄ grasses. A search of the available grass literature reveals that there is a general lack of C₄ grass species in shaded habitats, again in agreement with the simulation predictions. However, it is interesting to note that there are several small tree species within the genus *Euphorbia* that possess the C₄ photosynthetic pathway and occur in the understory tropical forests of Hawaii (Percy and Troughton, 1976).

It is now well documented that the C₄ photosynthetic pathway allows the plant to photosynthesize at a higher rate under conditions where, in the absence of this pathway, the photosynthetic rate would be severely limited by CO₂ concentration in the intercellular spaces (Black, 1973; Björkman, 1973; Chollet and Ogren, 1975; Björkman et al., 1975). For single leaves, the advantages of C₄ photosynthesis over C₃ photosynthesis are maximal under conditions of high light intensities, high temperatures, and limited water supply. However, at the canopy level the C₄ pathway can be markedly disadvantageous. As this study shows, the lower quantum yield in C₄ species at low and moderate temperatures is probably an important factor in limiting the distribution of C₄ grasses. It is typically in the grass species that we find the best developed canopies and highest leaf area indexes. Under these conditions, the factors affecting light-limited photosynthesis, such as quantum yield, are likely to have the greatest importance. Dicot species are typically characterized by having lower leaf area indexes than grasses and many other monocots. Therefore, the effect of quantum yield in limiting the distributions of many C₄ dicots is likely to be smaller than this study has predicted for grasses.

It is apparent that both increased capacity to photosynthesize at high light intensities and higher quantum yield at high temperatures are results of the same mechanism, namely, the ability of the C₄ pathway to increase the concentration of CO₂ at the site of fixation by RuBP carboxylase-oxygenase. While this mechanism is undoubtedly a significant advantage for plants in some environments, the increased energy cost of the C₄ pathway can be a significant liability in other habitats.

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