Oecologia (Berl.) 31, 255–267 (1978)

Oecologia

Implications of Quantum Yield Differences on the Distributions of C_3 and C_4 Grasses*

James R. Ehleringer**

Department of Plant Biology Carnegie Institution of Washington, and
Department of Biological Sciences, Stanford University, Stanford, CA 94305, USA

Summary. The implications of a reduced quantum yield (initial slope of the photosynthetic light response curve) in C_4 plants and temperature dependence of quantum yield in C_3 plants on total canopy primary production were investigated using computer simulations. Since reduced quantum yield represents the only known disadvantage of the C_4 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 C_4 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 C_4 grasses identical to the abundance patterns of C_4 grasses observed in the field. It is thus concluded that while the C_4 photosynthetic mechanism may be highly advantageous in specific environments, it may be disadvantageous in others.

Introduction

Since the initial discovery of the C_4 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 C_4 pathway serves as a mechanism to concentrate CO_2 within the chloroplast environment where the carboxylation of ribulose bisphosphate (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, C_4 plants often have high rates of photosynthesis under ambient atmospheric conditions. Black (1971) contended that C_4 species in general have photosynthetic rates exceeding those of C_3 species, and that C_4 species are

---

* C.I.W.-D.P.B. Publication No. 598

** *Present address:* Department of Biology, University of Utah, Salt Lake City, UT 84112, USA

0029-8549/78/0031/0255/$02.60

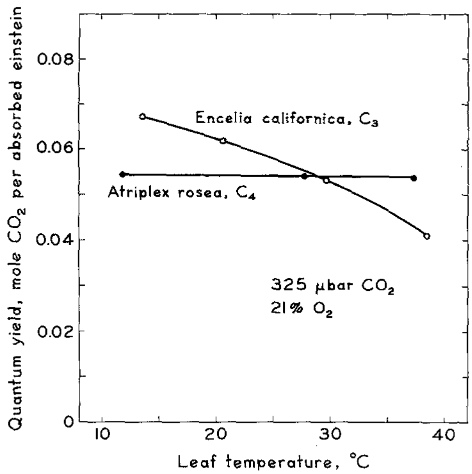

Fig. 1. Quantum yield for CO_2 uptake in C_3 species *Encelia california*, and C_4 species *Atriplex rosea*, as a function of leaf temperature. Quantum yield was measured in normal air of 325 μbar CO_2 and 21% O_2. This figure is based on data from Ehleringer and Björkman (1977)

in effect superior to C_3 species. However, C_3 species do exist which possess maximum photosynthetic rates on a leaf area basis equal to or exceeding the highest known C_4 species rates (Ehleringer et al., 1976; Mooney et al., 1976).

The advantages of C_4 photosynthesis over C_3 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 CO_2 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 C_4 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 C_4 species suggests that C_4 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 C_4 species to invade all habitats or are there possible limitations or disadvantages directly attributed to the C_4 pathway? It has been suggested that certain steps of the C_4 pathway cannot operate efficiently at cool temperatures (10–20° C). However, this is not an intrinsic property of the C_4 pathway, as Björkman et al. (1975) have shown that the photosynthetic machinery of *Atriplex sabulosa*, a C_4 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 C_4 pathway. Quantum yields (initial slope of the photosynthetic light response curve) of C_3 and C_4 plants were shown to differ (Fig. 1). Quantum yields of C_4 plants, which lack an oxygen inhibition of photosynthesis under normal atmospheric conditions, are 0.053 mole CO_2 per absorbed einstein and remain constant with temperature. However, quantum yields of C_3 plants, which exhibit an oxygen inhibition of photosynthesis, decline as temperatures increase, falling from 0.069 mol CO_2 per absorbed einstein at 14°C to 0.042 mol CO_2 per absorbed einstein at 38°C. At low leaf temperatures, quantum yields of C_3 are greater than those of C_4 plants, reflecting the lower intrinsic cost of this pathway. The reduction of the quantum yield of C_3 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 C_4 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 C_3 and C_4 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 C_3 grass canopy and a C_4 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 C_3 versus C_4 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)

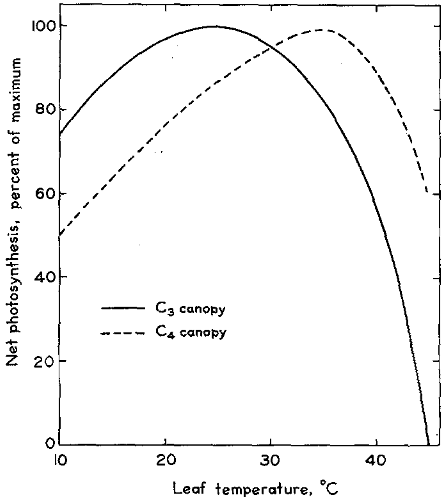

Fig. 2. Relationships between net photosynthesis and leaf temperature at high light intensities used in the primary production simulations

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)

$$Pn=\frac{IPmQ}{IQ+Pm}-R \tag{1}$$

where Pn is the net photosynthetic rate at a given temperature, Pm 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

$$Q=0.081-0.000053T-0.000019T^2 \tag{2}$$

and for the C_4 species,

$$Q=0.053 \tag{3}$$

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,

$$I_l = I_0 e^{(-KF)} \tag{4}$$

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

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

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 turbiditiy. These equations, taken from List (1968), were

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

$$I_0 = S \sin(\text{alt}) A^{(\sin[\text{alt}])} \tag{7}$$

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 CO_2 cm^{-2} s^{-1} at 25°C was chosen for the C_3 canopy. The maximum photosynthetic rate of the C_4 species was 20 percent higher than that of the C_3 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 CO_2 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 C_3 and C_4 canopies.

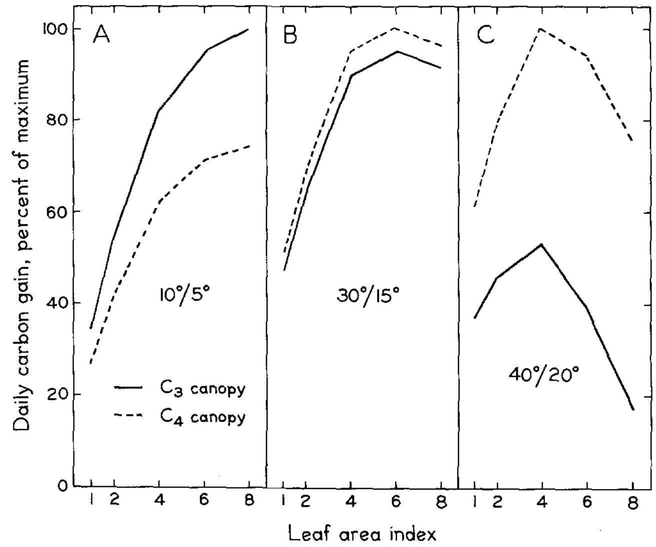

Fig. 3. Simulation of total daily carbon gain by C_3 canopies and C_4 canopies as a function of canopy leaf area indexes. The three plates represent different daily maximum/minimum air temperatures. The daily carbon gained by each canopy is plotted as a percent of the maximum rate of carbon gain for 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 C_3 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 C_3 and C_4 canopies had essentially identical rates of carbon gain at each of the different LAI. However, in the 40°/20° C environment, the C_4 canopy had the greatest productivity. At an LAI of 8 in the 40°/20° C regime, the daily carbon gain of the C_4 canopy was 59% greater than that of the C_3 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 C_3 and C_4 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 C_3 and C_4 grasses in North America by Teeri and Stowe (1976) showed that the percentage of C_4 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 C_3 and C_4 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

$$\text{max temperature} = 51.95 - 0.507 \text{ latitude} \tag{8}$$

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

$$\text{min temperature} = 40.56 - 0.576 \text{ latitude} \tag{9}$$

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

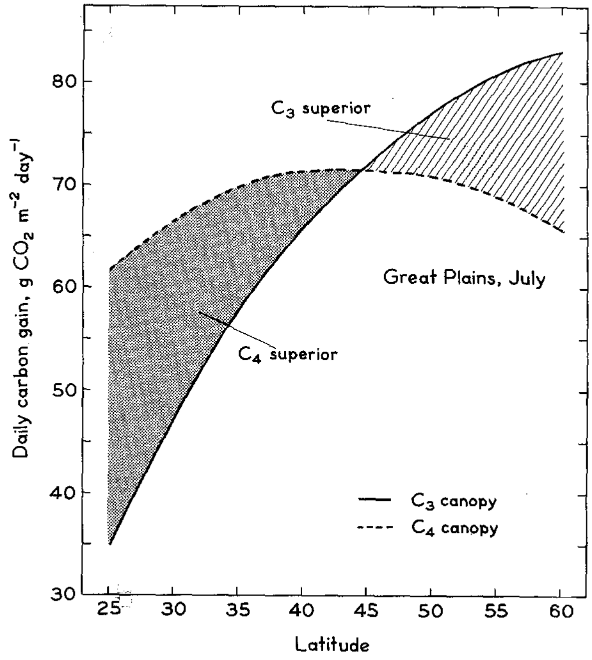

Fig. 4. Simulation of the total daily carbon gain for identical C_3 and C_4 grass canopies (LAI = 4) at different latitudes within the Great Plains of North America during the month of July

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 C_3 and C_4 canopy at a LAI of 4 at those latitudes were calculated.

The calculated rates of net daily carbon gain for July indicated that the C_4 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 CO_2 m^{-2} day^{-1} at 25°N. Thus the C_4 canopy gained carbon at a rate 73% higher than the C_3 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 C_3 canopy become progressively more productive than the C_4 canopy. By 60°N, the difference in daily productivity was calculated to be 17.3 g CO_2 m^{-2} day^{-1}. This difference is equivalent to a 26% greater rate of carbon gain by the C_3 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).

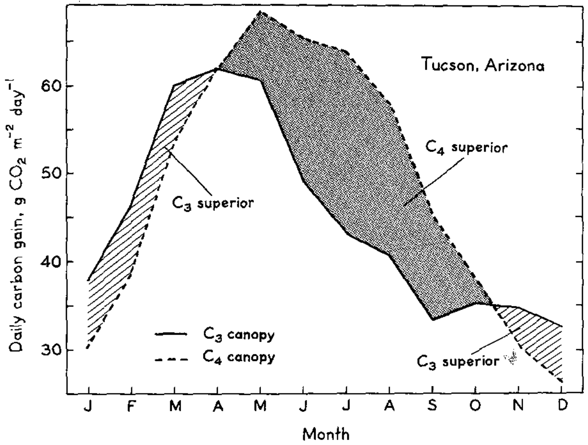

Fig. 5. Simulation of total daily carbon gain for identical C_3 and C_4 grass canopies (LAI = 4) at monthly intervals for Tucson, Arizona, within the Sonoran Desert

In a manner similar to the Great Plains simulations, total net carbon gain of a C_3 and a C_4 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 C_3 and a C_4 grass canopy was calculated at monthly intervals (Fig. 5). The results of this simulation show the C_3 canopy to be more productive than the C_4 canopy from mid-October through April. From May through early October, the C_4 canopy has a greater rate of daily carbon gain than the C_3 canopy. The periods during which the C_3 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 C_3 canopy is predicted to exceed that of the C_4 canopy by 12 to 25%. Conversely, the period during which the C_4 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 C_4 canopy exceeds that of the C_3 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

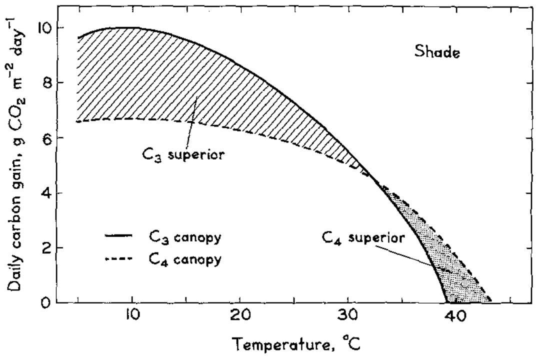

Fig. 6. Simulation of total daily carbon gain for identical C_3 and C_4 grass canopies (LAI = 1) in a shade habitat (10% of full sun) as a function of daily maximum temperature

differences in productivity of the C_3 and C_4 canopies. For the shaded habitat simulations, a realisitic 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 5–10° C environments. In habitats warmer than 32°/16° 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 C_4 grasses along the latitudinal transect from 25° to 60°N. The simulations predict that C_4 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 C_4 species should be less abundant than C_3 species and should continue to decline in importance as latitude increases, while C_3 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 C_4 abundance. An integration of the primary production estimates for all months of the growing season may suggest that the crossover point in C_4 abundance occurs at a latitude of less than 45°N.

Information on the abundances of C_3 and C_4 grasses in habitats along this Great Plains transect is not available, but data on the percentages of C_4 species in the flora along this transect have been presented by Teeri and Stowe (1976). The values of the abundance of C_4 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 C_4 species in the grass flora were 50 and 52%, respectively. They also reported that the percentage of C_4 grasses in the flora increased along a north-to-south transect. The percentage of C_4 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 C_4 grasses was always less than 50% and continually declined with increasing latitude. This observation agrees with the simulation prediction that above 45°N, C_3 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 C_3 type and summer grasses of the C_4 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 C_4 photosynthetic pathway. Conversely, the two species of winter Sonoran Desert grass possess the C_3 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 C_3 species, while of the summer ephemerals 57% are C_4 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 C_4 grass species are unlikely to be found in low light environments that have either cool of moderate temperatures. Rather, it is predicted that C_4 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 C_4 grasses. A search of the available grass literature reveals that there is a general lack of C_4 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 C_4 photosynthetic pathway and occur in the understory tropical forests of Hawaii (Pearcy and Troughton, 1976).

It is now well documented that the C_4 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 CO_2 concentration in the intercellular spaces (Black, 1973; Björkman, 1973; Chollet and Ogren, 1975; Björkman et al., 1975). For single leaves, the advantages of C_4 photosynthesis over C_3 photosynthesis are maximal under conditions of high light intensities, high temperatures, and limited water supply. However, at the canopy level the C_4 pathway can be markedly disadvantageous. As this study shows, the lower quantum yield in C_4 species at low and moderate temperatures is probably an important factor in limiting the distribution of C_4 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 C_4 dicots is likely to be smaller than this study has predicted for grasses.

It is apparent that both increased capcity to photosynthesize at high light intensities and higher quantum yield at high temperatures are results of the same mechanism, namely, the ability of the C_4 pathway to increase the concentration of CO_2 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 C_4 pathway can be a significant liability in other habitats.

Acknowledgments. I am grateful to O. Björkman and H.A. Mooney for their valuable discussions and comments on this manuscript. I thank also A. Kaplan and N. Chiariello for their comments and E. Ehleringer for her constant encouragement. This study has been supported by NSF grant BMS 75-03933 and a Carnegie Institution of Washington Predoctoral Fellowship.

References

Allen, L.H., Jr., Stewart, D.W., Lemon, E.R.: Photosynthesis in plant canopies—effect of light response curves and radiation source geometry. Photosynthetica **8**, 184–207 (1974)

Anderson, M.D.: Stand structure and light penetration. II. A theoretical analysis. J. Appl. Ecol. **3**, 41–54 (1966)

Biscoe, P.V., Scott, R.K., Monteith, J.L.: Barley and its environment. III. Carbon budget of the stand. J. Appl. Ecol. **12**, 269–293 (1975)

Björkman, O.: Comparative studies on photosynthesis in higher plants. In: Photophysiology, Vol. 8 (A. Giese, ed.), pp. 1–63. New York: Academic Press 1973

Björkman, O., Mooney, H.A., Ehleringer, J.R.: Photosynthetic responses of plants from habitats with contrasting thermal environments. Carnegie Inst. Wash. Year Book **74**, 743–748 (1975)

Black, C.C.: Ecological implications of dividing plants into groups with distinct photosynthetic production capacities. Adv. Ecol. Res. **7**, 87–114 (1971)

Black, C.C., Jr.: Photosynthetic carbon fixation in relation to net CO_2 uptake. Annu. Rev. Plant Physiol. **24**, 253–286 (1973)

Chartier, P., Chartier, M., Catsky, J.: Resistances for carbon dioxide diffusion and for carboxylation as factors in bean leaf photosynthesis. Photosynthetica **4**, 48–57 (1970)

Chollet, R., Ogren, W.L.: Regulation of photorespiration in C_3 and C_4 species. Bot. Rev. **41**, 137–179 (1975)

Ehleringer, J.R., Björkman, O.: Quantum yields for CO_2 uptake in C_3 and C_4 plants: dependence on temperature, CO_2, and O_2 concentration. Plant Physiol. **59**, 86–90 (1977)

Ehleringer, J., Björkman, O., Mooney, H.A.: Leaf pubescence: effects on absorptance and photosynthesis in a desert shrub. Science **192**, 376–377 (1976)

Gupta, R.K., Saxena, S.K.: Ecological studies on the protected and overgrazed rangelands in the arid zone of west Rajasthan. J. Indian Bot. Soc. **50**, 289–300 (1971)

Hatch, M.D.: Mechanism and function of the C_4 pathway of photosynthesis. In: Photosynthesis and photorespiration (M.D. Hatch et al., eds.), pp. 139–152. New York: Wiley-Interscience 1971

Hatch, M.D., Slack, C.R.: Photosynthesis by sugar-cane leaves. Biochem. J. **101**, 103–111 (1966)

Kendrew, W.G., Currie, B.W.: The climate of central Canada. Ottawa: Edmond Cloutier 1955

Kortschak, H.P., Hartt, C.E., Burr, G.O.: Carbon dioxide fixation in sugar cane leaves. Plant Physiol. **40**, 209–213 (1965)

List, R.J.: Smithsonian meterological tables, 6th revised ed. Washington: Smithsonian Institution Press 1968

Miller, P.C.: Bioclimate, leaf temperature, and primary production in red mangrove canopies in south Florida. Ecology **53**, 22–45 (1972)

Monsi, M., Saeki, T.: Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jap. J. Bot. **14**, 22–52 (1953)

Mooney, H.A., Ehleringer, J., Berry, J.A.: High photosynthetic capacity of a winter annual in Death Valley. Science **194**, 322–324 (1976)

Mooney, H.A., Troughton, J.H., Berry, J.A.: Arid climates and photosynthetic systems. Carnegie Inst. Wash. Year Book **73**, 793–805 (1974)

Mulroy, T.W., Rundel, P.W.: Annual plants: adaptations to desert environments. Bioscience **27**, 109–114 (1977)

Negbi, M.: Status of summer annuals in Palestine. Israel J. Bot. **17**, 217–221 (1968)

Pearcy, R.W., Troughton, J.: C_4 photosynthesis in tree form *Euphorbia* species from Hawaiian rainforest sites. Plant Physiol. **55**, 1054–1056 (1975)

Sellers, W.D., Hill, R.H.: Arizona climate 1931–1972. Tucson, Arizona: University of Arizona Press 1974

Shreve, F., Wiggins, I.L.: Vegetation and flora of the Sonoran Desert, Vol. 1. Stanford, California: Stanford University Press 1964

Teeri, J.A., Stowe, L.G.: Climatic patterns and the distribution of C_4 grasses in North America. Oecologia (Berl.) **23**, 1–12 (1976)

U.S. Dept. of Commerce: Decennial Census of U.S. Climate. Climatic survey of the United States. Supplement for 1951–1960. Washington: U.S. Government Printing Office 1965

Zelitch, I.: Photosynthesis, photorespiration, and plant productivity. New York: Academic Press 1971

Received June 6, 1977