Plant Physiol. (1977) 59, 86-90

Quantum Yields for CO_2 Uptake in C_3 and C_4 Plants

DEPENDENCE ON TEMPERATURE, CO_2, AND O_2 CONCENTRATION[1]

Received for publication July 20, 1976 and in revised form September 10, 1976

JAMES EHLERINGER AND OLLE BJÖRKMAN
Department of Plant Biology, Carnegie Institution of Washington, Stanford, California 94305
Department of Biological Sciences, Stanford University, Stanford, California 94305

ABSTRACT

The quantum yields of C_3 and C_4 plants from a number of genera and families as well as from ecologically diverse habitats were measured in normal air of 21% O_2 and in 2% O_2. At 30 C, the quantum yields of C_3 plants averaged 0.0524 ± 0.0014 mol CO_2/absorbed einstein and 0.0733 ± 0.0008 mol CO_2/absorbed einstein under 21 and 2% O_2. At 30 C, the quantum yields of C_4 plants averaged 0.0534 ± 0.0009 mol CO_2/absorbed einstein and 0.0538 ± 0.0011 mol CO_2/absorbed einstein under 21 and 2% O_2. At 21% O_2, the quantum yield of a C_3 plant is shown to be strongly dependent on both the intercellular CO_2 concentration and leaf temperature. The quantum yield of a C_4 plant, which is independent of the intercellular CO_2 concentration, is shown to be independent of leaf temperature over the ranges measured. The changes in the quantum yields of C_3 plants are due to changes in the O_2 inhibition. The evolutionary significance of the CO_2 dependence of the quantum yield in C_3 plants and the ecological significance of the temperature effects on the quantum yields of C_3 and C_4 plants are discussed.

Since the discovery of the C_4 pathway (16), it has become well established that this pathway enables 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 the CO_2 concentration in the intercellular spaces (4, 5, 8). The advantages of C_4 photosynthesis over C_3 photosynthesis have been shown to be maximal under conditions of high light intensities, high temperatures, and limited water supply (5, 8, 10). These climatic conditions are prevalent in many of the deserts, grasslands, and other subtropical regions of the world. It is thus not surprising to find that C_4 plants commonly occur in these habitats.

In the cooler and more temperate climates, C_4 plants occur only infrequently and can be considered relatively rare (25). In view of the relative abundance of C_4 plants in some habitats and their paucity in others, it is interesting to ascertain what physiological factors associated with the C_4 pathway might make it unfavorable in those environments where it is uncommon.

Hatch (15) discussed the possibility that the higher intrinsic energy requirement of C_4 photosynthesis (2 additional ATP/CO_2 fixed) in comparison with the conventional C_3 pathway might result in lower efficiency of light utilization at low light intensities by C_4 plants. A lower quantum efficiency for CO_2 fixation would, of course, be an important disadvantage in shaded habitats. It could also have a marked effect under moderate light intensities since the rate of primary production of many plant canopies is light-limited (26).

Björkman *et al.* (7) have measured the quantum yields for CO_2 uptake in a C_3 and a C_4 *Atriplex* species and observed no differences between them in normal air. However, Bull (13) measured the light dependence of photosynthesis of several C_3 and C_4 crop species and found that the C_4 plants had markedly higher rates both at high and low intensities than the C_3 species. This would indicate that the C_4 species possessed a higher quantum efficiency of CO_2 uptake. McKree (21) measured the spectral quantum yield between 350 and 750 nm for several C_3 and C_4 crop species, and found no significant differences between them.

To elucidate this question and to ascertain what effects CO_2 and temperature might have on the quantum yield, precise measurements of the quantum yield for CO_2 uptake at rate-limiting light intensities of photosynthetically active radiation (400–700 nm) were made on intact, attached leaves of a number of C_3 and C_4 plants. These included C_3 species from three families: Chenopodiaceae (*Atriplex glabriuscula, A. heterosperma, A. hortensis, A. triangularis*), Polygonaceae (*Plantago lanceolata*) and Compositeae (*Encelia californica, E. farinosa*). The C_4 plants measured were of two types, those utilizing NADP malic enzyme for decarboxylation of C_4 acids in the bundle sheath cells, and those utilizing NAD malic enzyme for this step (17). *Tidestromia oblongifolia* (Amaranthaceae) utilizes NADP malic enzyme, whereas the other C_4 plants, *Atriplex argentea, A. rosea, A. sabulosa,* and *A. seranana,* utilize the NAD malic enzyme. The native habitats of the plants in this study were ecologically quite diverse and included coastal strand, coastal sage, grassland, and desert habitats.

MATERIALS AND METHODS

Plants were grown from seed in 10-cm pots containing Perlite. These were placed in trays of nutrient solution (22). Nutrient solution levels were adjusted daily and the solution replaced weekly. The plants were grown in controlled environment cabinets with a 16-hr, 30 C day and a 8-hr, 20 C night regime. Light was provided by a bank of Sylvania VHO cool white fluorescent lamps. The quantum flux (400–700 nm) incident on the plants was 40 nanoeinsteins cm^{-2} sec^{-1}.

For gas exchange measurements on an incident light basis, a single attached leaf was inserted in a ventilated open system leaf chamber (total volume 150 ml) similar to that described by Björkman and Holmgren (6). Light was provided from a 2.5-kw short arc xenon lamp (Christie Electric Corp., Los Angeles) in conjunction with appropriate lenses, heat filters, and neutral density filters. Quantum flux incident on the leaves was continuously measured with silicon cells that had been specially calibrated against a quantum sensor (model LI 190-SR, Lambda Instruments, Lincoln, Neb.). Over 95% of the radiant energy was in the 400 to 700 nm waveband. Leaf temperature was measured with very fine copper-constantan thermocouples at-

[1] C.I.W.-D.P.B. Publication No. 577.

tached to the lower surface and was adjusted by means of water jackets. Gas from a cylinder containing 2 or 21% O_2 in N_2 (CO_2 free air) was continuously and precisely mixed with 1% CO_2 in N_2 by a high capacity gas mixing pump (model G-27/3-F, Wöstoff OHG, Bochum, Germany). The resulting gas stream was humidified by passing through a vessel, maintained at 5 C above the desired dew point temperature, and containing a large area of Miracloth and wetted by capillary uptake of water which was slightly acidified with H_2SO_4. The gas stream was then passed through a dual coil water-jacketed condenser whose temperature was kept at the desired dew point. A small portion of this humidified gas stream was passed at a constant rate (250 ml min^{-1}) through a humidity sensor (hygrometer HM-111, Weathermeasure Corp., Sacramento, Calif.) and then through the reference cell of a differential CO_2 analyzer (model 865, Beckman Instruments, Fullerton, Calif.). Another portion (300–800 ml min^{-1}) was passed via an electronic flowmeter (model DP45, Validyne Corp., Northridge, Calif.) to the leaf chamber. A portion (250 ml min^{-1}) of the gas returning from the chamber was passed through another humidity sensor, the sample cell of the differential CO_2 analyzer, and then through an O_2 analyzer (model 209, Westinghouse Electric Corp., Pittsburgh, Pa.). All sensor inputs were connected to a real time computer based data acquisition system (model S-9, Non-Linear Systems, Del Mar, Calif.) briefly described earlier (9). The system averaged 10 to 50 scans of each data point and was programmed to make appropriate linearizations, corrections, and conversions and to compute immediately rates of CO_2 and water vapor exchange, stomatal conductance to gaseous diffusion, and intercellular CO_2 pressure. It also provided a record of the incident quantum flux, leaf temperature, and of the O_2, CO_2, and water vapor partial pressures in the leaf chamber. Several parameters were continuously displayed on analogue recorders, providing a back-up record and permitting qualitative assessment of the experimental manipulations.

Light-absorptance values for individual leaves used in the gas exchange experiments were determined with an Ulbricht integrating sphere. The light source for the sphere was a xenon lamp with the same spectral distribution as used in the photosynthetic measurements. Quantum absorption to photosynthetically active radiation was measured with a quantum sensor (Lambda Instruments) attached from the outside to the inside wall of the integrating sphere. Further details about the Ulbricht integrating sphere and setup have been described by Rabideau *et al.* (24). Quantum absorptances varied between 76 and 88% depending on the species, but less than 3% within a species.

In these experiments, leaves were first exposed to light an an intensity of 30 nanoeinstins cm^{-2} sec^{-1} (400–700 nm). After a constant photosynthetic rate was achieved, the light was lowered in eight steps to total darkness, at each step achieving a constant photosynthetic rate before advancing to the next lower light intensity. Leaf temperature was held constant during each experiment. The CO_2 partial pressure was that of normal air (310–330 μbar), except for the series of experiments in which CO_2 concentration was varied. Since photosynthesis in C_3 plants is inhibited by O_2 at atmospheric concentrations even at rate-limiting intensities (2), quantum yields were determined in both 21 and 2% O_2.

In the series of experiments in which atmospheric CO_2 partial pressures were varied, the results are expressed as a function of the intercellular CO_2 concentrations. This expression allows for the removal of CO_2 gradients associated with low stomatal conductances. The intercellular CO_2 concentration is calculated as

$$CO_{2\ int} = CO_{2\ amb} - P/C$$

where $CO_{2\ int}$ and $CO_{2\ amb}$ are the intercellular and ambient CO_2 partial pressures, respectively, P is the net photosynthetic rate, and C is the leaf conductance to CO_2.

RESULTS

Quantum Yields of C_3 and C_4 Plants. The typical responses of C_3 and C_4 plants to changes in the quantum flux absorbed by the leaves in the light-limiting range and at 30 C are shown in Figure 1. In the C_3 species, *A. glabriuscula*, the quantum yield (slope of curve) is 0.051 mol CO_2/absorbed einstein in normal air (325 μbar CO_2 and 21% O_2). A decrease in the O_2 concentration to 2% results in an increase in the quantum yield to 0.073 mol CO_2/absorbed einstein. In the C_4 species, *A. argentea*, the absorbed quantum yield is 0.052 mol CO_2/absorbed einstein in normal air and no enhancement is observed when the O_2 concentration is reduced.

The measured values of the absorbed quantum yields within the C_3 species and also within the C_4 species in normal air and at 30 C are similar (Table I). This internal consistency within each photosynthetic type is expected since no biochemical pathway differences that would alter the requirement for $NADPH_2$ and ATP per CO_2 fixed are thought to occur within the C_3 or the C_4 pathway.

The values of the quantum yields averaged 0.0524 mol CO_2/absorbed einstein for the C_3 species. However, under low O_2 (2%), the mean quantum yield rises to 0.0733 mol CO_2/absorbed einstein. This 39% enhancement in the photosynthetic rate under low O_2 is typical of the enhancement rates observed in other studies (2, 7).

In normal air, the quantum yield of the C_4 species averaged 0.0534 mol CO_2/absorbed einstein, very close to that of the C_3 species. When measured under low O_2 conditions, there was no

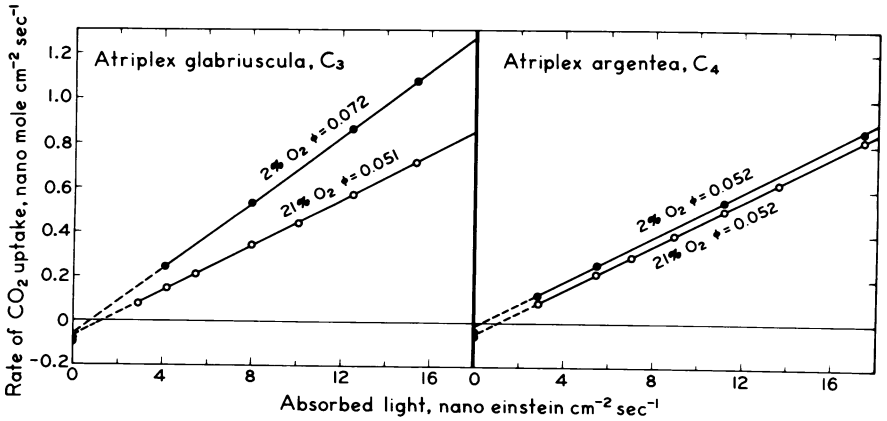

FIG. 1. Rate of CO_2 uptake in *A. glabriuscula* (C_3) and *A. argentea* (C_4) *versus* absorbed quantum flux in 21 and 2% O_2. Leaf temperature was 30 C and CO_2 pressure was 325 μbar.

Table 1. *Quantum Yields for CO_2 Uptake (Mol CO_2/Absorbed Einstein) of Different C_3 and C_4 Species Measured at a Leaf Temperature of 30° C and an Atmospheric CO_2 Pressure of 325 μbar*

	O_2 concentration	
C_3 species	2%	21%
Atriplex glabriuscula	0.072	0.051
Atriplex heterosperma	0.073	0.053
Atriplex hortensis	0.073	0.055
Atriplex triangularis	0.073	0.051
Encelia californica	0.074	0.052
Encelia farinosa	0.074	0.052
Plantago lanceolata	0.074	0.052
mean and standard deviation	0.0733 ± 0.0008	0.0524 ± 0.0014
C_4 species		
Atriplex argentea	0.052	0.052
Atriplex rosea	0.054	0.052
Atriplex sabulosa	0.054	0.054
Atriplex semenana	0.055	0.054
Tidestromia oblongifolia	0.054	0.054
mean and standard deviation	0.0538 ± 0.0011	0.0534 ± 0.0009

significant change in the quantum yield, indicating a lack of O_2 inhibition in these plants. There appear to be no differences in the quantum yields of C_4 species utilizing NADP and those utilizing NAD malic enzyme decarboxylating systems.

At a leaf temperature of 30 C, the quantum yields of the C_3 species were consistently about 39% higher than those of the C_4 species under low O_2 conditions. This higher energy requirement by C_4 species is consistent with the notion that C_4 photosynthesis requires more ATP per CO_2 fixed than does C_3 photosynthesis. These extra ATP molecules are needed for the regeneration of the CO_2 acceptor phosphoenolpyruvate from pyruvate.

CO_2 Dependence of the Quantum Yield. Since at atmospheric O_2 concentrations the rate of net photosynthesis in C_3 plants but not C_4 plants (2) is dependent on the atmospheric CO_2 concentrations, the quantum yield of a C_3 plant was determined as a function of the intercellular CO_2 concentration. Figure 2 illustrates the dependence of the quantum yield in *E. californica* (C_3) as the intercellular CO_2 pressure is increased. As with previous experiments, leaf temperature was held constant at 30 C and the quantum yield was determined in both 21 and 2% O_2. Over the range of intercellular CO_2 concentrations normally encountered by leaves (8–14 μM, equivalent to a partial pressure of 200–350 μbar) the quantum yield in 21% O_2 is markedly dependent on CO_2 concentration, ranging from 0.042 to 0.059 mol CO_2/absorbed einstein over this span. Even at intercellular CO_2 pressures as high as 1500 μbar, the quantum yield is still measurably inhibited by 21% O_2. At low CO_2 intercellular pressures (less than 200 μbar), the dependence of quantum yield is quite high, and the quantum yield extrapolates to zero at the CO_2 compensation point. In contrast, when O_2 concentration is lowered to 2%, no changes in the quantum yield were observed between 300 and 1500 μbar CO_2 intercellular pressure.

Oxygen inhibition of the quantum yield decreases in an asymptotic fashion as the intercellular CO_2 pressure is increased (Fig. 2). Oxygen inhibition of CO_2 uptake in *E. californica* at 88 μbar CO_2 is 72%, but by an intercellular CO_2 pressure of 1510 μbar has fallen to 6%. The kinetics of the decrease of O_2 inhibition of the quantum yield as CO_2 pressure is increased follow Michaelis-Menten competition kinetics. From these data on O_2 inhibition, 50% inhibition of the quantum yield in 21% O_2 occurs at approximately 200 μbar CO_2. Under normal atmospheric conditions (325 μbar CO_2) and a leaf temperature of 30 C, inhibition by 21% O_2 of the quantum yield was approximately 35%.

Temperature Dependence of the Quantum Yield. The temperature dependence of the quantum yield for CO_2 uptake in the C_3 species, *E. californica*, was compared with the C_4 species, *A. rosea*, in normal air of 325 μbar CO_2 and 21% O_2 (Fig. 3). The quantum yield actually measured for *E. californica* is denoted by curve A in Figure 3. It is possible that changes in the quantum yield at different temperatures may arise because the solubilities and therefore the concentrations of CO_2 and O_2 in solution vary with temperature. To account for this, curve B of *E. californica* represents the quantum yield adjusted for changes in the liquid phase solubilities of CO_2 and O_2 relative to the reference temperature of 30 C. The solubility adjustments were made utilizing the CO_2 dependence of the quantum yield from Figure 2 and values of the solubilities of CO_2 and O_2 at different temperatures.

These data show clearly that the observed quantum yield of *E. californica*, the C_3 plant, is superior to that of *A. rosea*, the C_4 plant, at leaf temperatures below 30 C. Yet above 30 C, the quantum yield of the C_4 plant is superior to that of the C_3 plant.

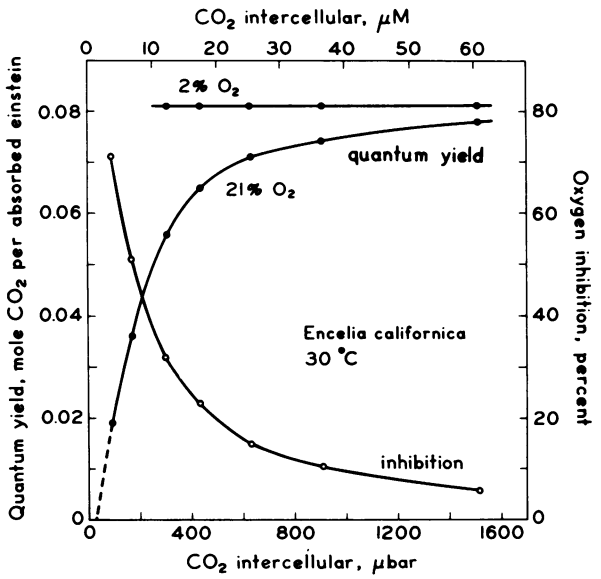

FIG. 2. Quantum yield for CO_2 uptake in *E. californica* (C_3) determined as a function of intercellular CO_2 pressure in 21 and 2% O_2 (●) and O_2 inhibition of quantum yield in 21% O_2 as a function of intercellular CO_2 pressure (○). Leaf temperature was 30 C.

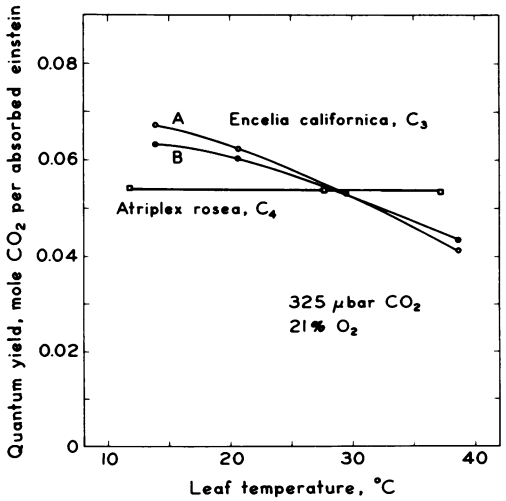

FIG. 3. Quantum yield for CO_2 uptake in *E. californica* (C_3) *and A. rosea* (C_4) as a function of leaf temperature. Curve A of *E. californica* represents the measured quantum yields and curve B represents the quantum yields adjusted for changes in liquid phase solubilities of CO_2 and O_2. The CO_2 pressure was held constant at 325 μbar and O_2 concentration was 21%.

The quantum yield of *E. californica* is strongly dependent on leaf temperature, ranging from 0.069 mol CO_2/absorbed einstein at 14 C to 0.042 mol CO_2/absorbed einstein at 38 C. However, the quantum yield of *A. rosea* is independent of leaf temperature over the range of 12 to 39 C, remaining constant at a value of 0.053 mol CO_2/absorbed einstein. This change in the quantum yield of *E. californica* is not due to changes in the liquid phase solubilities of CO_2 and O_2 over the temperature span in which they were measured, since adjustments for changes in solubility of these gases fail to account for the changes in the observed quantum yield. The quantum yield of *E. californica* in 2% O_2 remained constant between 14 and 38 C.

The change in the quantum yield of *E. californica* with leaf temperature reflects changes in the O_2 inhibition of the quantum yield (Fig. 4). The O_2 inhibition is again calculated from the reduction of the quantum yield in 21% O_2 relative to the quantum yield at that temperature in 2% O_2. Oxygen inhibition of the quantum yield increases in a logarithmic fashion over the range of 10 to 40 C. At 14 C, O_2 inhibition is only 14%, but is 47% at 38 C.

An Arrhenius plot of the change in the quantum yield between 21 and 2% O_2 in *E. californica* reveals an apparent energy of activation equivalent to -8.1 Kcal mol^{-1} (Fig. 5), which is quite similar to the "activation energy" of the CO_2 compensation point of C_3 plants (7). The compensation point is not a rate, and can therefore not have an activation energy. However, an Arrhenius plot of the CO_2 compensation in 21% O_2 does yield a linear relationship, with a slope equivalent to -7.6 Kcal mol^{-1} (7). This activation energy was determined under conditions in which net photosynthesis was linear with light intensity and should not be confused with the temperature dependence of photosynthesis under light-saturating conditions.

DISCUSSION

The values of the quantum yield presented in this study suggest that there are no differences among species within the C_3 type and among species within the C_4 type. Moreover, there are no significant differences between C_3 and C_4 species at 25 to 30 C in normal air (325 μbar CO_2 and 21% O_2). These results are consistent with the earlier observations of quantum yields of *A. patula* (C_3) and *A. rosea* (C_4) by Björkman *et al.* (7). In that study, quantum yield of the C_4 species was found to be equivalent to that of the C_3 species in normal air. Our results, however, are in conflict with those of Bull (13), whose results suggest that the quantum yields of C_4 plants were higher than those of the C_3 plants studied. In fact, Bull's measurements indicated that the quantum yields of C_3 and C_4 species were equivalent only under low O_2 conditions. His measurements were made at a leaf temperature of 26 C. Measurements from this study as well as those of Björkman (3, 7) show that the quantum yield and, consequently, the photosynthetic rate at low light intensities of C_3 species are greatly enhanced under conditions of low atmospheric O_2. Under these low O_2 conditions, the quantum yields of C_3 plants are significantly greater than those of all C_4 species.

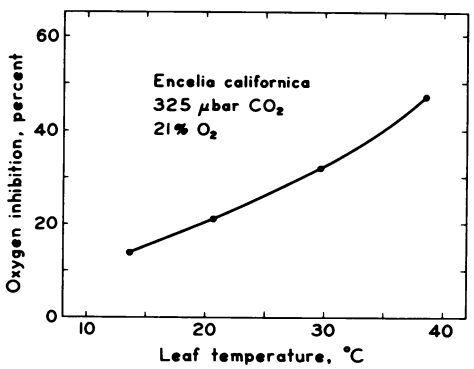

FIG. 4. Oxygen inhibition of *E. californica* in 21% O_2 as a function of leaf temperature. The CO_2 pressure was held constant at 325 μbars.

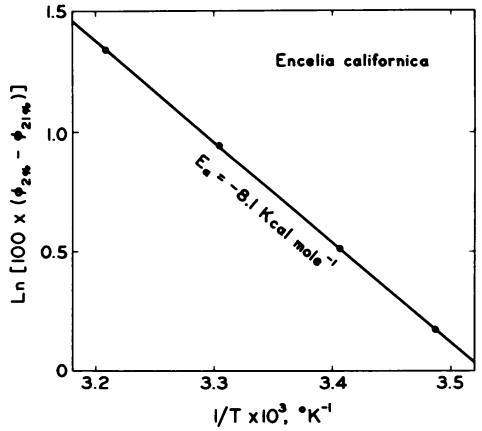

FIG. 5. Arrhenius plot of the difference in quantum yield as determined in 2 and 21% O_2 and at 325 μbar CO_2 for *E. californica* (C_3).

The C_4 photosynthetic pathway requires at least two additional ATP more than the C_3 pathway to complete each cycle (15). For this reason, Hatch (15) speculated that the quantum requirement of C_4 plants may be higher than that of C_3 plants. Evans (14), however, pointed out the data of Björkman (7) concerning this point. He speculated that it was possible that the lack of photorespiration by C_4 plants offset the increased ATP requirement, so that in effect, the quantum requirements of C_3 and C_4 plants in normal air would not be different from each other. The results from this study show that the quantum requirements of C_3 and C_4 plants in normal air are equivalent only when leaf temperatures are approximately 30 C.

The absence of a CO_2 dependence of the quantum yield under low O_2 in the C_3 plant suggests that the carboxylase activity of RuDP carboxylase-oxygenase *in vivo* is saturated by 300 μbar CO_2 at rate-limiting light intensities. Our results are discussed in relation to the widely held view that O_2 inhibition of net CO_2 uptake is primarily caused by the oxygenase activity of RuDP carboxylase-oxygenase (11, 12). Although our results are consistent with this view, we wish to point out that they are not necessarily inconsistent with certain other proposed mechanisms of O_2 inhibition. Plants possessing the C_4 pathway do not show oxygenase activity *in vivo* under atmospheric O_2 concentrations, and therefore, their quantum yields *should* not show and *do* not show a dependence on CO_2 concentration (3, 23).

Similarly, the absence of a temperature dependence of the quantum yield under low O_2 conditions in the C_3 plant and under normal atmospheric conditions for the C_4 plant would suggest that under low light intensities, the carboxylase activity of RuDP carboxylase-oxygenase is temperature-independent between 13 and 39 C. Under 21% O_2 conditions, however, the quantum yield of the C_3 plant showed a marked dependence on leaf temperature. This dependence in the quantum yield in the C_3 species cannot be accounted for by changes in the liquid phase solubilities of CO_2 and O_2 over the temperature span, since adjustments for changes in the solubilities of these gases fails to significantly alter the observed quantum yields. A similar increase in the quantum yield with decreasing temperature can be found in the data of McKree (21) for *Avena sativa*, a C_3 plant.

Jolliffe and Tregunna (18, 19) have shown that there is an increase in O_2 inhibition with temperature at higher light intensities in wheat. Our quantum yield data for the C_3 plant *E. californica* also show an increase in O_2 inhibition with temperature. The similarity of the temperature dependence of the O_2 inhibition of the quantum yield has been noted. The CO_2 com-

pensation point has been suggested to be a measure of the balance between the carboxylase and oxygenase activities of RuDP carboxylase-oxygenase (1, 20); therefore, it is possible that the temperature and O_2 effects upon the quantum yield reported here are also reflective of the balance between the carboxylase and oxygenase activities of RuDP carboxylase-oxygenase.

If it is the oxygenase activity of RuDP carboxylase-oxygenase which is responsible for changes in the quantum yields of C_3 plants as both CO_2 concentration and/or temperature vary, then the CO_2 concentration at the Calvin cycle carboxylation sites of C_4 plants (which do not exhibit O_2 inhibition of net CO_2 uptake at 21% O_2) must be high enough to overcome this competitive inhibition. In the C_3 plant under 21% O_2, O_2 inhibition is not quite completely removed at an intercellular CO_2 concentration of 1500 μbar (61 μM). Presumably, this concentration is slightly lower at the site of carboxylation within the chloroplast, but since net photosynthesis was determined close to the light compensation point, the CO_2 gradient between the intercellular air spaces and the carboxylation sites must be small. By inference, the CO_2 concentration at the Calvin cycle carboxylation sites of C_4 plants under normal atmospheric conditions must be at least 61 μM since no O_2 inhibition was observed.

The steep dependence of the quantum yield in C_3 plants such as *E. californica* on CO_2 concentration under normal atmospheric O_2 concentration and the independence of the quantum yield on CO_2 in C_4 plants (3, 23) such as *A. rosea* point out two of the selective pressures favoring the evolution of the C_4 pathway. The ability of the C_4 pathway to concentrate CO_2 at the Calvin cycle carboxylation sites effectively makes light-limited photosynthesis of C_4 plants independent of intercellular pressure over a very wide range. However, in a primitive atmosphere of high CO_2 concentration, low O_2 concentration, or both, selective pressures would strongly favor the C_3 pathway because of its lower intrinsic quantum requirement for CO_2 fixation. Under present atmospheric conditions, the O_2 inhibition of the quantum yield in C_3 plants almost precisely offsets the additional ATP requirement of the C_4 pathway at 25 to 30 C, resulting in nearly identical quantum yields.

The distribution of C_3 and C_4 species in nature correlates generally with daylight temperature, *i.e.* C_4 species are more common in hot climates than in cool or cold climates. Since the rate of photosynthesis and primary production in many plant canopies is strongly light-limited (26), the observed difference in quantum yield between C_3 and C_4 species as a function of leaf temperature may be an important factor in determining their distributions. Under conditions of sufficient soil moisture, a C_3 plant will have greater potential for C gain at low temperatures. Conversely, a C_4 plant will have greater potential for C gain at high temperatures with a crossover point at approximately 25 to 30 C. This would imply that C_4 photosynthesis would be at a disadvantage in cool *low* light habitats such as the floor of cool temperate forests and the arctic tundra. On the other hand, the C_4 pathway would be selectively more advantageous in shaded habitats of high temperature and in dense stands in high light, high temperature habitats such as tropical grasslands. C_4 photosynthesis would, of course, be particularly advantageous in hot sunbaked desert habitats where little mutual shading of the leaves occurs within the plant stands. However, under these conditions, the advantage of C_4 photosynthesis is largely due to the increased capacity for photosynthesis at high light intensities. Nevertheless, the higher quantum yield at high temperatures would also be expected to confer a significant advantage. It is apparent that both the increased capacity for photosynthesis at high light intensities and the higher quantum yield at high temperatures are the 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 RuDP carboxylase-oxygenase.

Acknowledgments – We thank J. A. Berry, M. Badger, and A. Kaplan for their comments on this manuscript and E. Ehleringer for her encouragement.

LITERATURE CITED

1. Badger, M. R. and T. J. Andrews. 1974. Effects of CO_2, O_2 and temperature on a high-affinity form of ribulose diphosphate carboxylase-oxygenase from spinach. Biochem. Biophys. Res. Commun. 60: 204–210.
2. Björkman, O. 1966. The effect of oxygen concentration on photosynthesis in higher plants. Physiol. Plant. 19: 618–633.
3. Björkman, O. 1971. Interaction between the effects of oxygen and CO_2 concentration on quantum yield and light-saturated rate of photosynthesis in leaves of *Atriplex patula* ssp. *spicata*. Carnegie Inst. Wash. Year Book 70: 520–526.
4. Björkman, O. 1973. Comparative studies on photosynthesis in higher plants. *In:* A. Giese, ed., Photophysiology, Vol. 8. Academic Press, New York. pp. 1–63.
5. Björkman, O. 1975. Environmental and biological control of photosynthesis: inaugural address. *In:* R. Marcelle, ed., Environmental and Biological Control of Photosynthesis. Dr. W. Junk, Publ., The Hague. pp. 1–16.
6. Björkman, O. and P. Holmgren. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiol. Plant. 16: 889–914.
7. Björkman, O., E. Gauhl, and M. A. Nobs. 1969. Comparative studies of *Atriplex* species with and without β-carboxylation photosynthesis and their first-generation hybrids. Carnegie Inst. Wash. Year Book 68: 620–633.
8. Björkman, O., H. A. Mooney, and J. Ehleringer. 1975. Photosynthetic responses of plants from habitats with contrasting thermal environments. Carnegie Inst. Wash. Year Book 74: 743–748.
9. Björkman, O., M. Nobs, J. Berry, H. Mooney, F. Nicholson, and B. Catanzaro. 1973. Physiological adaptation to diverse environments: approaches and facilities to study plant responses to contrasting thermal and water regimes. Carnegie Inst. Wash. Year Book 72: 393–403.
10. Black, C. C., Jr. 1973. Photosynthetic carbon fixation in relation to net CO_2 uptake. Annu. Rev. Plant Physiol. 24: 253–286.
11. Bowes, G. and W. L. Ogren. 1972. Oxygen inhibition and other properties of soybean ribulose 1,5-diphosphate carboxylase. J. Biol. Chem. 247: 2171–2176.
12. Bowes, G., W. L. Ogren, and R. H. Hageman. 1971. Phosphoglycolate production catalyzed by ribulose diphosphate carboxylase. Biochem. Biophys. Res. Commun. 45: 716–722.
13. Bull, T. A. 1969. Photosynthetic efficiencies and photorespiration in Calvin cycle and C_4-dicarboxylic acid plants. Crop Sci. 9: 726–729.
14. Evans, L. T. 1971. Evolutionary, adaptive, and environmental aspects of the photosynthetic pathway: assessment. *In:* M. D. Hatch, C. B. Osmond, and R. O. Slatyer, eds., Photosynthesis and Photorespiration. Wiley Interscience, New York. pp. 130–136.
15. Hatch, M. D. 1970. Chemical energy costs for CO_2 fixation by plants with differing photosynthetic pathways. *In:* Prediction and Measurement of Photosynthetic Productivity. Pudoc, Wageningen. pp. 215–220.
16. Hatch, M. D. and C. R. Slack. 1966. Photosynthesis by sugar-cane leaves. Biochem. J. 101: 103–111.
17. Hatch, M. D., T. Kagawa, and S. Craig. 1975. Subdivision of C_4-pathway species based on differing C_4 acid decarboxylating systems and ultrastructural differences. Austr. J. Plant Physiol. 2: 111–128.
18. Jolliffe, P. A. and E. B. Tregunna. 1968. Effect of temperature, CO_2 concentration, and light intensity on oxygen inhibition of photosynthesis in wheat leaves. Plant Physiol. 43: 902–906.
19. Jolliffe, P. A. and E. B. Tregunna. 1973. Environmental regulation of the oxygen effect on apparent photosynthesis in wheat. Can. J. Bot. 51: 841–853.
20. Laing, W. A., W. L. Ogren, and R. H. Hageman. 1974. Regulation of soybean net photosynthetic CO_2 fixation by the interaction of CO_2, O_2, and ribulose 1,5-diphosphate carboxylase. Plant Physiology 54: 678–685.
21. McKree, K. J. 1972. The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. Agric. Meteorol. 9: 191–216.
22. Medina, E. 1970. Relationships between nitrogen level, photosynthetic capacity, and carboxydismutase activity in *Atriplex patula* leaves. Carnegie Inst. Wash. Year Book 69: 655–662.
23. Osmond, C. B. and O. Björkman. 1972. Simultaneous measurements of oxygen effects on net photosynthesis and glycolate metabolism in C_3 and C_4 species of *Atriplex*. Carnegie Inst. Wash. Year Book 71: 141–148.
24. Rabideau, G. S., C. S. French, and A. S. Holt. 1946. The absorption and reflection spectra of leaves, chloroplast suspensions, and chloroplast fragments as measured in an Ulbricht sphere. Am. J. Bot. 33: 769–777.
25. Teeri, J. and L. G. Stowe. 1976. Climatic patterns and the distribution of C_4 grasses in ,orth America. Oecologia 23: 1–12.
26. Zelitch, I. 1971. Photosynthesis, Photorespiration, and Plant Productivity. Academic Press, New York. 347 pp.