# Quantum Yields for $CO_2$ Uptake in $C_3$ and $C_4$ Plants

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

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## 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-

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 $\mu$bar), 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 $\mu$bar $CO_2$ 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
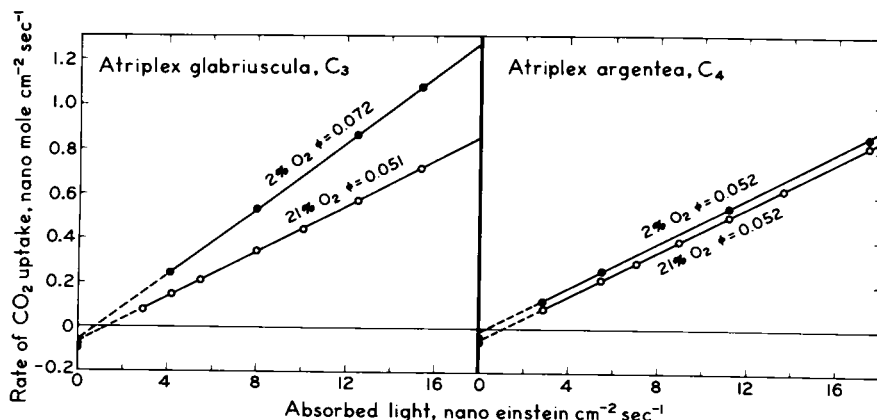


FIG. 1. Rate of $CO_2$ uptake in A. glabriuscula ($C_3$) and A. argentea ($C_4$) versus absorbed quantum flux in 21 and 2% $O_2$. Leaf temperature was 30 C and $CO_2$ pressure was 325 $\mu$bar.

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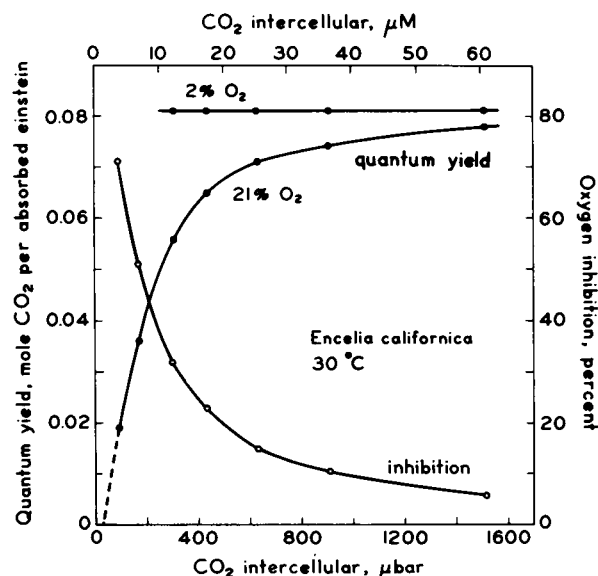
FIG. 2. Quantum yield for $CO_2$ uptake in *E. californica* ($C_3$) determined as a function of intercellular $CO_2$ pressure in 21 and 2% $O_2$ (●) and $O_2$ inhibition of quantum yield in 21% $O_2$ as a function of intercellular $CO_2$ pressure (○). Leaf temperature was 30 C.
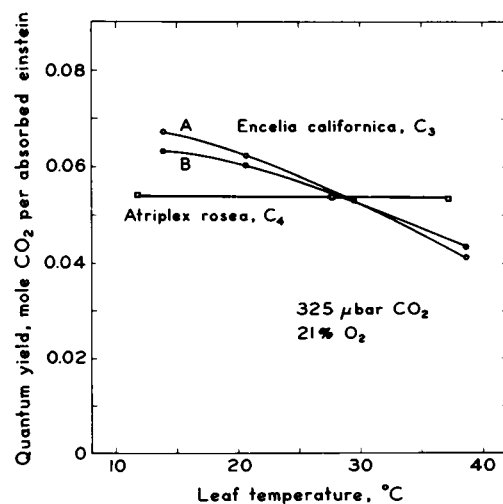


FIG. 3. Quantum yield for $CO_2$ uptake in *E. californica* ($C_3$) and *A. rosea* ($C_4$) as a function of leaf temperature. Curve A of *E. californica* represents the measured quantum yields and curve B represents the quantum yields adjusted for changes in liquid phase solubilities of $CO_2$ and $O_2$. 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 $\mu$bar $CO_2$ 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, conse-
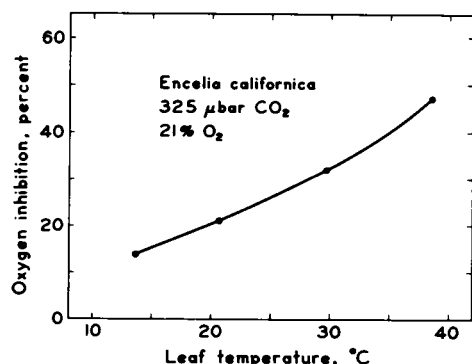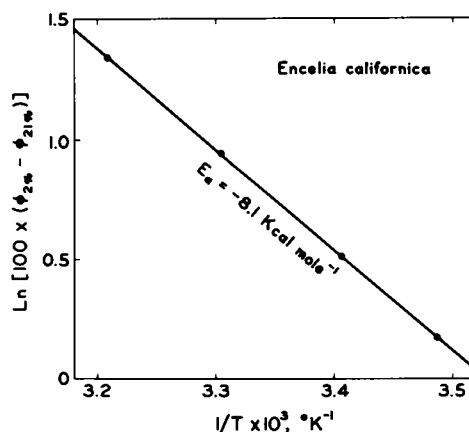


FIG. 5. Arrhenius plot of the difference in quantum yield as determined in 2 and 21% $O_2$ and at 325 $\mu$bar $CO_2$ for *E. californica* (C$_3$).

quently, 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.

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 $\mu$bar $CO_2$ 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-



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 $\mu$bars.

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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 $\mu$bar (61 $\mu$M). 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 $\mu$M 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.

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