

# Variation in Quantum Yield for CO<sub>2</sub> Uptake among C<sub>3</sub> and C<sub>4</sub> Plants<sup>1</sup>

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## ABSTRACT

The quantum yield for CO<sub>2</sub> uptake was measured on a number of C<sub>3</sub> and C<sub>4</sub> monocot and dicot species. Under normal atmospheric conditions (330 microliters per liter CO<sub>2</sub>, 21% O<sub>2</sub>) and a leaf temperature of 30°C, the average quantum yields (moles CO<sub>2</sub> per einstein) were as follows: 0.052 for C<sub>3</sub> dicots, 0.053 for C<sub>3</sub> grasses, 0.053 for NAD-malic enzyme type C<sub>4</sub> dicots, 0.060 for NAD-malic enzyme type C<sub>4</sub> grasses, 0.064 for phosphoenolpyruvate carboxykinase type C<sub>4</sub> grasses, 0.061 for NADP-malic enzyme C<sub>4</sub> dicots, and 0.065 for NADP-malic enzyme type C<sub>4</sub> grasses. The quantum yield under normal atmospheric conditions was temperature dependent in C<sub>3</sub> species, but apparently not in C<sub>4</sub> species. Light and temperature conditions during growth appeared not to influence quantum yield. The significance of variation in the quantum yields of C<sub>4</sub> plants was discussed in terms of CO<sub>2</sub> leakage from the bundle sheath cells and suberization of apoplastic regions of the bundle sheath cells.

The quantum yield for CO<sub>2</sub> uptake in higher plants under normal atmospheric conditions is far below the maximum possible quantum yield reported for algae by Emerson and Lewis (8). Apparent differences in quantum yields between C<sub>3</sub> dicots and C<sub>4</sub> grasses were first noted by Ludlow and Wilson (17). More recently, Ehleringer and Björkman (7) surveyed the quantum yields for CO<sub>2</sub> uptake by C<sub>3</sub> and C<sub>4</sub> dicots. Their results showed that under normal atmospheric conditions and at a leaf temperature of 30°C, the quantum yield for CO<sub>2</sub> uptake averaged 0.052 and 0.053 mol CO<sub>2</sub> E<sup>-1</sup> for C<sub>3</sub> and C<sub>4</sub> dicot species, respectively. Robichaux and Pearcy (22) reported similar quantum yields for the C<sub>3</sub> plant *Claoxylon sandwicense*, but a much higher quantum yield of 0.062 mol CO<sub>2</sub> E<sup>-1</sup> for the C<sub>4</sub> dicot *Euphorbia forbesii*. At the same time, Ku and Edwards (15) reported that under similar environmental conditions, the quantum yield of the C<sub>3</sub> grass *Triticum aestivum* was 0.054 mol CO<sub>2</sub> E<sup>-1</sup>, while that of the C<sub>4</sub> grass *Zea mays* was 0.059 mol CO<sub>2</sub> E<sup>-1</sup>. These data indicate that, although there appears to be little variation in the quantum yield of C<sub>3</sub> plants, substantial variation may occur in C<sub>4</sub> plants.

Variations in the quantum yields might be anticipated for two reasons: a) the three subpathway types may differ in intrinsic energy requirements or other factors that influence light energy conversion; and b) differential rates of CO<sub>2</sub> leakage from bundle sheath cells may occur, which would then tend to reduce quantum yield.

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To resolve this question of the variation in quantum yields among C<sub>4</sub> plants and the relationships to the quantum yields of C<sub>3</sub> plants, precise measurements of the quantum yield for CO<sub>2</sub> uptake were made at rate limiting light intensities under normal atmospheric conditions (330 μl l<sup>-1</sup> CO<sub>2</sub>, 21% O<sub>2</sub>). The species investigated represented a mixture of C<sub>3</sub>, C<sub>4</sub>, and C<sub>3</sub>-C<sub>4</sub> intermediate photosynthetic pathways, monocot as well as dicot species, and all three C<sub>4</sub> subpathway types.

## MATERIALS AND METHODS

For quantum yield measurements, plant material was grown both by seed or by cuttings. Plants were grown under several growth conditions in growth chambers with fluorescent lighting or in greenhouses that had natural illumination (summer months), shading, or supplemental HID-lamp lighting (winter months). Plants were watered daily and fertilized with Hoagland solution through the watering system.

Gas exchange measurements were collected independently on two gas exchange systems at the University of California, Davis and at the University of Utah. At UC Davis, photosynthetic rates on an incident light basis were determined in an open gas exchange apparatus described previously by Pearcy (21). Single attached leaves were enclosed in a circular, nickel-plated brass chamber with a glass window water-jacketed lid, and after equilibrium, the steady state responses to different light levels were determined. Light was supplied from a 2.5-kw xenon-arc lamp and within the cuvette was measured with a photon sensor (model LI-190SR, Lambda Instruments). CO<sub>2</sub> and water vapor exchange were measured simultaneously with an IR gas analyzer (model VIA 500R, Horiba Instruments) and a RH sensor (model HM III, Weathermeasure Corp.), respectively.

For gas exchange measurements at the University of Utah, an open system similar to the one at UC Davis was used. This system has been described previously by Ehleringer (6). Attached leaves were inserted into a ventilated nickel plated cuvette, which was water jacketed for temperature control. Photon flux incident on the leaves was measured with silicon cells that had been calibrated against a photon sensor (model LI-190SR, Lambda Instruments). Light was supplied by a 1000-w sodium vapor HID lamp. CO<sub>2</sub> and water vapor exchange were measured simultaneously with an IR gas analyzer (model 865, Beckman Instruments) and a RH sensor (model HM III, Weathermeasure Corp.).

For both gas exchange systems, light gradients within the chamber between the leaf and the light sensor were taken into account and the incident photon flux on the leaf was corrected accordingly. Leaf absorbance values for the individual leaves used in the gas exchange measurements over the 400 to 700 nm range were measured in an Ulbricht integrating sphere as described by Ehleringer (5).

Only a few of the quantum yield values reported in this study were measured simultaneously in both laboratories. However, to

Table I. Absorbed Quantum Yields for CO<sub>2</sub> Uptake by Dicots under Normal Atmospheric Conditions (330 μl l<sup>-1</sup> CO<sub>2</sub>, 21% O<sub>2</sub>) and a Leaf Temperature of 30°C

Data are means ± 1 SE, except when no SE appears the sample size is 1. Species followed by an asterisk are from Ehleringer and Björkman (7) and are presented only as means.

C <sub>3</sub> Species	Quantum Yields mol CO <sub>2</sub> E <sup>-1</sup>	C <sub>4</sub> Species	Quantum Yields mol CO <sub>2</sub> E <sup>-1</sup>	Subpathway Type
<i>Abronia villosa</i>	0.053	<i>Amaranthus palmeri</i>	0.053	NAD-ME
<i>Antidesma platyphyllum</i>	0.047	<i>Amaranthus retroflexus</i>	0.051 ± 0.003	NAD-ME
<i>Atriplex glabriuscula</i> *	0.051	<i>Amaranthus tricolor</i>	0.053	NAD-ME
<i>Atriplex heterosperma</i> *	0.053	<i>Atriplex argentea</i> *	0.052	NAD-ME
<i>Atriplex hortensis</i> *	0.055	<i>Atriplex lentiformis</i>	0.050 ± 0.003	NAD-ME
<i>Atriplex triangularis</i> *	0.051	<i>Atriplex rosea</i> *	0.054	NAD-ME
<i>Claoxylon sandwicense</i>	0.050 ± 0.003	<i>Atriplex sabulosa</i> *	0.054	NAD-ME
<i>Encelia californica</i>	0.052 ± 0.001	<i>Atriplex serenana</i> *	0.055	NAD-ME
<i>Encelia farinosa</i> *	0.052	<i>Euphorbia celastroides</i>	0.061 ± 0.002	NADP-ME
<i>Encelia frutescens</i>	0.052	<i>Euphorbia clusiaefolia</i>	0.059 ± 0.001	NADP-ME
<i>Larrea divaricata</i>	0.055	<i>Euphorbia forbesii</i>	0.058 ± 0.005	NADP-ME
<i>Lupinus arizonicus</i>	0.053	<i>Euphorbia hillebrandii</i>	0.065 ± 0.004	NADP-ME
<i>Malvastrum rotundifolium</i>	0.053	<i>Euphorbia multififormis</i>	0.060 ± 0.001	NADP-ME
<i>Plantago insularis</i> *	0.052	<i>Euphorbia remyi</i>	0.061 ± 0.002	NADP-ME
		<i>Gomphrena globosa</i>	0.057 ± 0.001	NAD-NADP-ME
		<i>Tidestromia oblongifolia</i> *	0.054	NAD-ME

check for consistency within the data set, a number of grass species were measured independently in both laboratories. The differences in quantum yield estimates were less than 5% for these paired comparisons. Determination of photosynthetic subpathway type was according to previously published observations (1, 2, 10, 12, 13, 19).

## RESULTS

**Quantum Yields of C<sub>3</sub> and C<sub>4</sub> Plants.** The absorbed quantum yields for CO<sub>2</sub> uptake were measured on 44 different species under normal atmospheric conditions (330 μl l<sup>-1</sup> CO<sub>2</sub>, 21% O<sub>2</sub>) and at a leaf temperature of 30°C. For presentation, the data are separated as to grass *versus* dicot, C<sub>3</sub> *versus* C<sub>4</sub> photosynthetic type, and within the C<sub>4</sub> pathway according to subpathway type. For comparative purposes within the dicots, the absorbed quantum yield data of Ehleringer and Björkman (7) are also presented.

The quantum yield of dicot species showed considerable variation depending on photosynthetic pathway (Table I). For a phylogenetically diverse group of C<sub>3</sub> species, the quantum yield averaged 0.052 ± 0.001 mol CO<sub>2</sub> E<sup>-1</sup> (mean ± SE) at 30°C. The only significant departure from this mean value among all 14 species measured was *Antidesma platyphyllum*, which had a quantum yield of 0.047 mol CO<sub>2</sub> E<sup>-1</sup>. This plant grows on the Hawaiian rainforest floor. Leaves of this species have significant quantities of anthocyanin, which would contribute to light absorption, but not photosynthesis (Percy, personal observation).

Within the C<sub>4</sub> dicot species, quantum yield at a leaf temperature of 30°C varied with species between 0.050 and 0.065 mol CO<sub>2</sub> E<sup>-1</sup> (Table I). When species were arranged according to subpathway type, the NAD-malic enzyme type C<sub>4</sub> species had an average quantum yield of 0.053 ± 0.001 mol CO<sub>2</sub> E<sup>-1</sup>, whereas the NADP-malic enzyme type species had an average quantum yield of 0.061 ± 0.001 mol CO<sub>2</sub> E<sup>-1</sup>. There was no overlap in the ranges of quantum yields between the two photosynthetic pathway types. *Gomphrena globosa* is a mixed NAD-malic enzyme and NADP-malic enzyme C<sub>4</sub> dicot (10). Not too surprising, quantum yield in this species averaged 0.057 mol CO<sub>2</sub> E<sup>-1</sup>, an intermediate value.

The quantum yields of C<sub>3</sub> monocot species (all grasses) were similar to those of C<sub>3</sub> dicot species (Table II). The average quantum yield for C<sub>3</sub> grasses was 0.053 ± 0.001 mol CO<sub>2</sub> E<sup>-1</sup> at 30°C. There was no significant departure from the mean value

by any of the nine species. Within the C<sub>3</sub> grass species measured were four *Panicum* species in the *Laxa* group, which has C<sub>3</sub>, C<sub>4</sub>, and C<sub>3</sub>-C<sub>4</sub> intermediate species (1, 14, 19). Both *P. decipiens* and *P. milioides* show characteristics intermediate between C<sub>3</sub> and C<sub>4</sub> pathways, but the quantum yield values were not different from either the other C<sub>3</sub> *Panicum* or the other C<sub>3</sub> grasses measured.

As with the C<sub>4</sub> dicots, there was a large systematic variation in the quantum yield of C<sub>4</sub> grass species at 30°C, ranging from 0.060 to 0.069 mol CO<sub>2</sub> E<sup>-1</sup> (Table II). The variation in quantum yield of these grasses was correlated with photosynthetic subpathway. The NAD-malic enzyme type C<sub>4</sub> species had an average quantum yield of 0.060 ± 0.001 mol CO<sub>2</sub> E<sup>-1</sup>, whereas NADP-malic enzyme type C<sub>4</sub> species averaged 0.064 ± 0.001 mol CO<sub>2</sub> E<sup>-1</sup>, and PCK<sup>2</sup> type C<sub>4</sub> species 0.065 ± 0.001 mol CO<sub>2</sub> E<sup>-1</sup>. The range of quantum yield values was quite low in the NAD-malic enzyme type species and quite high in the NADP-malic enzyme species. The potential significance and causes of this variation will be discussed later.

When compared across photosynthetic pathway types, two interesting trends emerged (Fig. 1). First, the average quantum yields as well as the ranges of values were quite similar in C<sub>3</sub> dicots, C<sub>3</sub> grasses, and NAD-malic enzyme type C<sub>4</sub> dicots. Second, within the C<sub>4</sub> subpathway types, the data indicated that quantum yield values were always higher in grasses than in dicots (e.g. 0.060 *versus* 0.053 for NAD-malic enzyme types and 0.065 *versus* 0.061 for NADP-malic enzyme types). There appears to be some intrinsic difference in the photosynthetic efficiency of the C<sub>4</sub> pathway between grass and dicot species.

**Temperature Dependence of the Quantum Yield.** Our previous measurements of the quantum yield in C<sub>3</sub> and C<sub>4</sub> dicot species (7, 22) demonstrated that the quantum yields of C<sub>3</sub> species were temperature dependent, whereas those of C<sub>4</sub> species were not. To complete the data set, we measured the temperature dependence of the quantum yield in several C<sub>3</sub> and C<sub>4</sub> grass species.

In the C<sub>3</sub> grass species measured (*Agropyron desertorum*, *Avena sativa*, and *Hordeum vulgare*), the quantum yield decreased with increasing leaf temperature over the range of leaf temperatures that the plants are normally physiologically active (Fig. 2). The responses were similar in all three species, with quantum yields

<sup>2</sup> Abbreviation: PCK, phosphoenolpyruvate carboxykinase.

Table II. Absorbed Quantum Yields for CO<sub>2</sub> Uptake by Monocots under Normal Atmospheric Conditions (330 μl l<sup>-1</sup> CO<sub>2</sub>, 21% O<sub>2</sub>) and a Leaf Temperature of 30°C

Data are means ± 1 SE.

C <sub>3</sub> Species	Quantum Yield <i>mol CO<sub>2</sub> E<sup>-1</sup></i>	C <sub>4</sub> Species	Quantum Yield <i>mol CO<sub>2</sub> E<sup>-1</sup></i>	Subpathway Type
<i>Agropyron spicatum</i>	0.054 ± 0.001	<i>Andropogon gerardi</i>	0.065 ± 0.003	NADP-ME
<i>Avena sativa</i>	0.053 ± 0.001	<i>Bouteloua hirsuta</i>	0.067 ± 0.001	PCK
<i>Hordeum vulgare</i>	0.052 ± 0.002	<i>Chloris gayana</i>	0.067 ± 0.003	PCK
<i>Lycurus pheoides</i>	0.052 ± 0.001	<i>Chloris virgata</i>	0.062 ± 0.001	PCK
<i>Panicum decipiens</i>	0.056 ± 0.000	<i>Cynodon dactylon</i>	0.061 ± 0.002	NAD-ME
<i>Panicum hylaeicum</i>	0.052 ± 0.001	<i>Hemarthria altissima</i>	0.066 ± 0.001	NADP-ME
<i>Panicum laxum</i>	0.053 ± 0.002	<i>Melinis minutiflora</i>	0.060 ± 0.003	PCK
<i>Panicum milioides</i>	0.054 ± 0.003	<i>Panicum maximum</i>	0.064 ± 0.004	PCK
<i>Oryzopsis hymenoides</i>	0.052 ± 0.000	<i>Panicum virgatum</i>	0.060 ± 0.004	NAD-ME
		<i>Paspalum dilatatum</i>	0.069 ± 0.002	NADP-ME
		<i>Paspalum vaginatum</i>	0.066 ± 0.002	NADP-ME
		<i>Pennisetum purpureum</i>	0.066 ± 0.004	NADP-ME
		<i>Sorghum bicolor</i>	0.061 ± 0.002	NADP-ME
		<i>Sorghum vulgare</i>	0.068 ± 0.003	NADP-ME
		<i>Sporobolus cyrptandrus</i>	0.060 ± 0.001	NAD-ME
		<i>Zea mays</i>	0.062 ± 0.001	NADP-ME

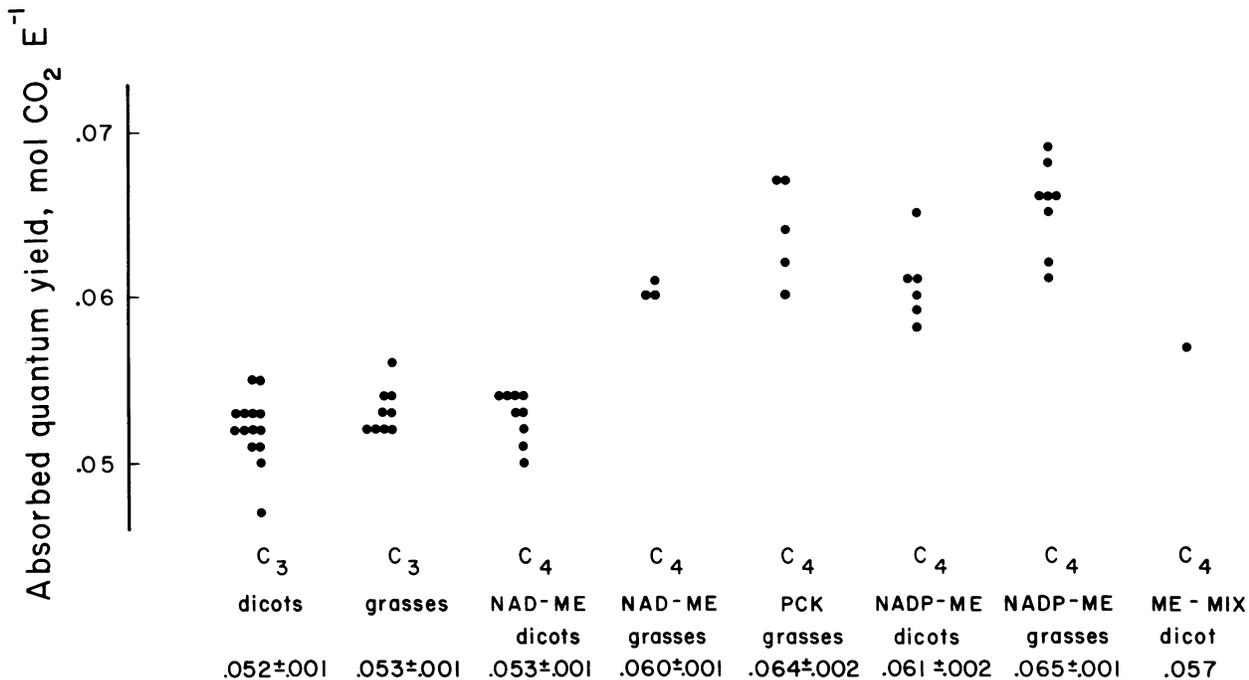


FIG. 1. Absorbed quantum yields for CO<sub>2</sub> uptake for C<sub>3</sub> and C<sub>4</sub> species at a leaf temperature of 30°C and 330 μl l<sup>-1</sup> CO<sub>2</sub>, 21% O<sub>2</sub>. Data are organized by pathway subtypes. Each datum is the average for one of the species presented in Tables I and II. Means and SE for each pathway subtype are also presented.

decreasing from 0.073 mol CO<sub>2</sub> E<sup>-1</sup> at 16°C. The rate of decrease in quantum yield was approximately 0.0013 mol CO<sub>2</sub> E<sup>-1</sup> °C<sup>-1</sup>.

In the C<sub>4</sub> grass species, no significant decrease in the quantum yield was observed over a 20 to 40°C leaf temperature range (Fig. 2). Measurements were collected on both NAD-malic enzyme (*Cynodon dactylon*) and NADP-malic enzyme type C<sub>4</sub> species (*Paspalum vaginatum* and *Zea mays*). At the highest leaf temperatures in the two NADP-malic enzyme type species, there were slight but consistent decreases in the quantum yield, although they were not significant enough to affect a change in the slope of the relationship.

**Effect of O<sub>2</sub> Concentration on Quantum Yield.** The effect of changing O<sub>2</sub> concentration from 21% to 2% was measured in

*Agropyron desertorum*, a C<sub>3</sub> grass species at an ambient CO<sub>2</sub> concentration of 330 μl l<sup>-1</sup> and a leaf temperature of 30°C. The quantum yield for CO<sub>2</sub> uptake was enhanced by an average 49 ± 1.8% (mean ± SE) by switching to a low O<sub>2</sub> atmosphere. This enhancement was similar to that which has been reported for other C<sub>3</sub> grass and dicot species (7, 15).

**Effect of Growth Conditions on Quantum Yield.** It is conceivable that the growth conditions under which a plant developed may influence the quantum yield for CO<sub>2</sub> uptake. The two environmental parameters most likely to influence any developmental change in quantum yield would be the temperature and irradiance during growth. Certainly, temperatures or irradiance levels outside the ranges normally experienced by a plant

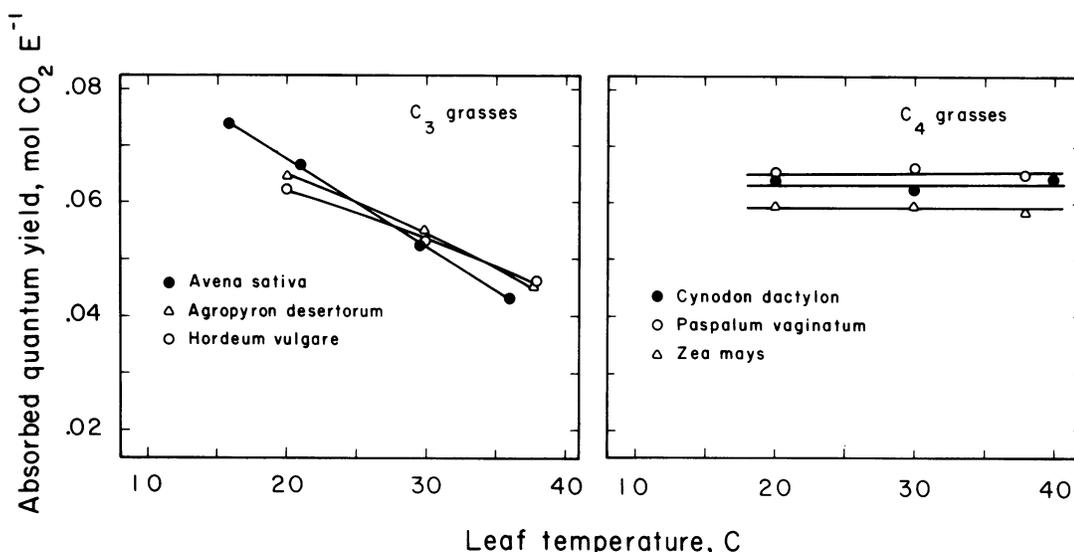


FIG. 2. The leaf temperature dependence of the absorbed quantum yield for  $\text{CO}_2$  uptake in  $\text{C}_3$  and  $\text{C}_4$  grasses. Measurements were made under normal atmospheric conditions ( $330 \mu\text{l l}^{-1} \text{CO}_2$ , 21%  $\text{O}_2$ ).

Table III. Absorbed Quantum Yields for  $\text{CO}_2$  Uptake for Plants Grown under Contrasting Irradiance Regimes

Measurements were made under normal atmospheric conditions ( $330 \mu\text{l l}^{-1} \text{CO}_2$ , 21%  $\text{O}_2$ ) and a leaf temperature of  $30^\circ\text{C}$ . Data are means  $\pm$  1 SE.

	High Light	Low Light
	$\text{mol CO}_2 \text{ E}^{-1}$	$\text{mol CO}_2 \text{ E}^{-1}$
<i>Amaranthus retroflexus</i> <sup>a</sup>	$0.051 \pm 0.003$	$0.049 \pm 0.004$
<i>Euphorbia forbesii</i> <sup>b</sup>	$0.058 \pm 0.005$	$0.061 \pm 0.002$
<i>Gomphrena globosa</i> <sup>b</sup>	$0.057 \pm 0.001$	$0.057 \pm 0.002$
<i>Zea mays</i> <sup>a</sup>	$0.062 \pm 0.001$	$0.060 \pm 0.003$

<sup>a</sup> Growth chamber grown plants; the high light and low light plants received photon fluxes of  $550 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $80 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively.

<sup>b</sup> Greenhouse grown plants; the low light plants were grown under 90% shade cloth.

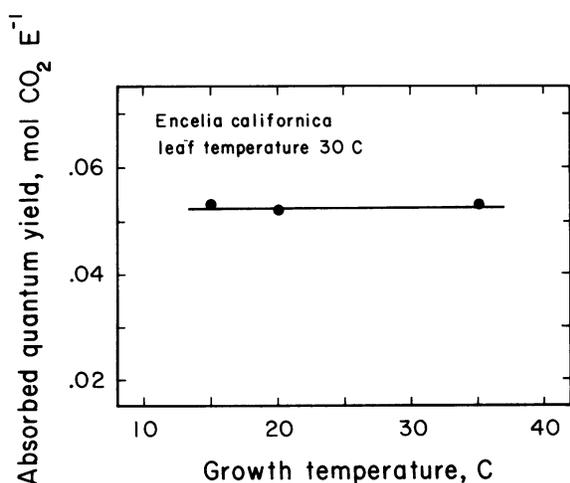


FIG. 3. The effect of daytime growth temperature on the absorbed quantum yield for  $\text{CO}_2$  uptake in *Encelia californica*, a  $\text{C}_3$  species. Measurements were collected at a leaf temperature of  $30^\circ\text{C}$  and under normal atmospheric conditions ( $330 \mu\text{l l}^{-1} \text{CO}_2$ , 21%  $\text{O}_2$ ).

species would be expected to cause damage and result in a decrease in quantum yield, and this has in fact been documented by a number of investigators. The interest here, however, was over the range of environmental parameters that a plant species might typically experience during its development.

There was no statistically significant trend for a change in the quantum yield for  $\text{CO}_2$  uptake either as a function of irradiance during growth (Table III) or temperature during development (Fig. 3).

## DISCUSSION

A number of recent studies have investigated the quantum yields for  $\text{CO}_2$  uptake in  $\text{C}_3$  and  $\text{C}_4$  species under normal atmospheric conditions. The absolute values reported in this study are consistent and similar to those reported previously by Ehleringer and Björkman (7) and Robichaux and Pearcy (22) for  $\text{C}_3$  and  $\text{C}_4$  dicot species and by Ku and Edwards (15) for  $\text{C}_3$  and  $\text{C}_4$  grass species. With respect to the quantum yield estimates of  $\text{C}_3$  and  $\text{C}_4$  grasses by Monson *et al.* (18), our estimates generally agree with their  $\text{C}_3$  values, but contrast with their  $\text{C}_4$  values.

Under normal atmospheric conditions and a leaf temperature of  $30^\circ\text{C}$ , there is a significant and systematic variation in the quantum yields of higher plants. In general, this is to be expected on the basis of energetic cost differences between the  $\text{C}_3$  and  $\text{C}_4$  photosynthetic pathways as well as to energetic cost differences within the  $\text{C}_4$  subpathways. We can estimate a probable upper limit for the quantum yield of  $\text{C}_4$  plants as follows. From the stoichiometry of electron transport and a proton requirement of 3 for ATP synthesis (11), a minimum of 9 quanta are needed for the  $\text{C}_3$  cycle. If, in  $\text{C}_4$  photosynthesis, the two extra ATP are derived from cyclic electron flow, then 6 more quanta are needed, giving a total of 15, or an upper limit quantum yield of  $0.067 \text{ mol CO}_2 \text{ E}^{-1}$ . It is apparent that the NADP-malic enzyme  $\text{C}_4$  are at or near this limit. Since  $\text{CO}_2$  leakage from the bundle sheath, as discussed below, and light absorption by nonphotosynthetically active pigments should lower the quantum yields, it is surprising that the measured efficiencies are so close to the calculated upper limit. Extrapolation of the measured quantum yield of *Agropyron desertorum* ( $\text{C}_3$ ) to a 0%  $\text{O}_2$  environment where losses due to  $\text{O}_2$  inhibition and photorespiration are absent, gives a quantum yield of  $0.081 \text{ mol CO}_2 \text{ E}^{-1}$ , which is substantially less than the calculated upper limit of  $0.111 \text{ mol CO}_2 \text{ E}^{-1}$ . Either ATP production may be more efficient than

assumed above or other factors contribute to the high quantum yields of the NADP-malic enzyme species. Bundle sheath cells of NADP-malic enzyme C<sub>4</sub> plants are capable of the transfer of <sup>14</sup>C label from C<sub>4</sub> acids to carbohydrates in 712 nm light, since only PSI activity is required; whereas, those of NAD-malic enzyme C<sub>4</sub> plants, which have both photosystems in the bundle sheath, are not (20). This could contribute to an enhanced action spectra for photosynthesis at wavelengths of 700 nm or greater, and consequently to an increase in the measured quantum yield of NADP-malic enzyme type C<sub>4</sub> plants.

Quantum yields of C<sub>4</sub> plants should be lower than the upper limit quantum yield because of CO<sub>2</sub> leakage from the bundle sheath cells (9). It is likely that a fraction of the CO<sub>2</sub> which has been decarboxylated from C<sub>4</sub> acids within the bundle sheath cells may diffuse out either through the symplast or the apoplast. Such CO<sub>2</sub> would then have to be refixed into C<sub>4</sub> acids, requiring additional ATP and therefore reducing quantum yield. CO<sub>2</sub> leakage through the bundle sheath cell walls may be small or even negligible if the cell walls are suberized. However, the presence of suberized lamella in bundle sheath cell walls is found only in the NADP-malic enzyme type and PCK-type C<sub>4</sub> grasses (4, 13). It does not occur in NAD-malic enzyme C<sub>4</sub> grasses and has not yet been reported in a C<sub>4</sub> dicot species. Additionally, the relative apoplastic surface area of bundle sheath cells in NAD-malic enzyme C<sub>4</sub> grasses is higher than in either NADP-malic enzyme type or PCK-type C<sub>4</sub> grasses (Hattersley, in press, cited in 13). From the paradermal sectioning data of Brown (3), one can infer that a similar trend should occur between NAD-malic enzyme type C<sub>4</sub> dicots and NADP-malic enzyme type C<sub>4</sub> dicots. On the basis of the above evidence, CO<sub>2</sub> leakage from bundle sheath cells should be lower in monocots than in dicots, and lower in NADP-malic enzyme type and PCK-type C<sub>4</sub> plants than in NAD-malic enzyme type C<sub>4</sub> plants. This trend is consistent with the observed differences in quantum yields between monocots and dicots and among C<sub>4</sub> subpathway types. The differences in quantum yields are also consistent with an independent estimate of CO<sub>2</sub> leakage rates, namely the carbon isotope discrimination values of C<sub>4</sub> grasses when grown in a common environment (12).

The two lowest quantum yield estimates among the NADP-malic enzyme type C<sub>4</sub> monocots were from the only crop species, *Sorghum bicolor* and *Zea mays*. The closely related wild species, *Sorghum vulgare*, had a much higher quantum yield. It is possible that in the course of developing modern cultivars of these crops that the thickness of the suberized lamella in the bundle sheath cells has been reduced and/or that there has been an increase in the relative apoplastic surface area of the bundle sheath cells, both of which could lead to a reduced quantum yield.

The decrease in quantum yield of C<sub>3</sub> species with increasing leaf temperature under ambient conditions can result in a transition or crossover point between C<sub>3</sub> and C<sub>4</sub> species. Ehleringer and Björkman (7) reported that this transition temperature was 28 to 29°C. Above that leaf temperature, *Atriplex rosea* (NAD-malic enzyme type C<sub>4</sub> dicot) had the higher quantum yield. Below that leaf temperature, *Encelia californica* (C<sub>3</sub> dicot) had the higher quantum yield. Robichaux and Pearcy (22) measured the temperature dependence of the quantum yield in *Claoxylon sandwicense* (C<sub>3</sub> dicot) and *Euphorbia forbesii* (NADP-malic enzyme type C<sub>4</sub> dicot) and observed a crossover temperature of 22 to 23°C, because of the higher quantum yield in *E. forbesii*. Our current study suggests that the quantum yield crossover temperature will depend very much on whether monocot or dicot species are being compared and on the C<sub>4</sub> subpathway type, and that will range between 16 and 28°C.

Ludlow (16) compared the photosynthetic efficiencies of trop-

ical grasses (C<sub>4</sub>) and legumes (C<sub>3</sub>) in response to changes in temperature. His data showed that the photosynthetic efficiency (essentially quantum yield except not corrected for leaf absorptance) of C<sub>4</sub> plants was always higher than that of C<sub>3</sub> plants. At first these data would appear to be in contrast with the data presented in this study. However, our interpretation is that they are not in disagreement. Ludlow's (16) measurements were made at an ambient CO<sub>2</sub> concentration of 300 μl l<sup>-1</sup>. At this CO<sub>2</sub> concentration, C<sub>4</sub> plants are CO<sub>2</sub> saturated, but the quantum yield of C<sub>3</sub> plants are still very much CO<sub>2</sub> dependent (7). At a CO<sub>2</sub> concentration of 300 μl l<sup>-1</sup>, the slope of the relationship between quantum yield and CO<sub>2</sub> concentration is 0.0003 mol CO<sub>2</sub> E<sup>-1</sup> μl<sup>-1</sup>. This translates into a 0.008 mol CO<sub>2</sub> E<sup>-1</sup> decrease in quantum yield in changing from a 330 to a 300 μl l<sup>-1</sup> CO<sub>2</sub> atmosphere. This CO<sub>2</sub>-dependent quantum yield reduction is sufficient to account for most of the differences in quantum yield between our data and those of Ludlow (16).

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