

Canopy quantum yield in a mesocosm study

Yiqi Luo^{a,*}, Dafeng Hui^a, Weixin Cheng^b, James S. Coleman^c,
Dale W. Johnson^c, Daniel A. Sims^d

^a Department of Botany and Microbiology, University of Oklahoma, Norman, OK 3019, USA

^b Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

^c Biological Sciences Center, Desert Research Institute, Reno, NV 89512, USA

^d Department of Biology and Microbiology, California State University, Los Angeles, CA 90032, USA

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Abstract

Due to past limitations in experimental technology, canopy function has generally been inferred from leaf properties through scaling and/or indirect measurements. The development of a facility (EcoCELLs) at the Desert Research Institute has now made it possible to directly measure canopy gas exchange. In this experiment, sunflowers (*Helianthus annuus*) were planted in the EcoCELLs and grown under ambient ($399 \mu\text{mol mol}^{-1}$) and elevated ($746 \mu\text{mol mol}^{-1}$) CO_2 concentrations. We continuously measured carbon flux during canopy development from which canopy quantum yield (ϕ_C) was estimated. The results indicated that the total daily carbon flux was similar between elevated and ambient CO_2 treatments in the early stage of canopy development. After the canopy closed, carbon flux under elevated CO_2 averaged 53% higher than that under ambient CO_2 . Assimilation/incident irradiance (A/I) curves of leaves at different canopy positions were used to estimate leaf quantum yields (ϕ_L), and A/I curves of canopies at late development stages were used to estimate ϕ_C . Elevated CO_2 enhanced ϕ_L by 24%. There was little difference in ϕ_L at different canopy positions, averaging 0.0542 at ambient CO_2 and 0.0671 at elevated CO_2 . Canopy quantum yield (ϕ_C) was higher by 32% at elevated than ambient CO_2 . It increased with canopy development and was strongly correlated with leaf area index (LAI) by $\phi_C = 0.0094 \text{ LAI}/(0.0829 + 0.1137 \text{ LAI})$ at ambient CO_2 and $\phi_C = 0.01382 \text{ LAI}/(0.1129 + 0.1224 \text{ LAI})$ at elevated CO_2 . In addition, the curvilinear relationship between radiation and canopy carbon fluxes suggests that canopy radiation use efficiency (CRUE) varied with radiation availability. The variability in ϕ_C and CRUE with canopy development and light levels warrants further research on the notion drawn from earlier work that CRUE in non-stressed conditions is relatively constant. ©2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Plant canopy plays a critical role in determining ecosystem primary productivity and also in regulating biosphere-atmosphere exchanges in energy, water, at-

mospheric CO_2 , and various pollutants. Photosynthesis, which determines the rate of CO_2 exchange, has been extensively studied at biochemical and leaf levels during the past few decades. As a consequence, we have developed a firm understanding of the biochemistry and ecophysiology of leaf photosynthesis (Farquhar et al., 1980; Harley et al., 1992). Our knowledge of canopy photosynthesis, however, is limited due to technological constraints in experimentation.

* Corresponding author. +1-405-325-1651

fax: +1-405-325-7619.

E-mail address: yluo@ou.edu (Y. Luo).

Direct measurement of canopy photosynthesis is very difficult although some indirect methods have been employed. Micrometeorological techniques, such as the eddy correlation method, have become very useful tools in measuring net ecosystem CO₂ exchange (Baldocchi, 1993). Together with other experimental data (e.g. CO₂ flux from the soil surface and plant respiration), the net ecosystem CO₂ fluxes can be partitioned to quantify canopy photosynthetic activity. Remotely sensed data of vegetation indices have been used to estimate absorbed photosynthetically active radiation (PAR), providing time-integrated estimates of photosynthesis across landscapes (Waring et al., 1995). Such estimation requires prior knowledge of the apparent quantum efficiency of canopies and the extent to which environmental factors constrain stomatal conductance.

Modeling studies of canopy photosynthesis usually consider heterogeneity in direct versus diffuse radiation, temperature profile, and nitrogen distribution within the canopy (Raupach and Finnigan, 1988; Reich et al., 1990; Whitehead and Hinckley, 1991; Norman, 1993; Amthor, 1994; McNaughton, 1994; Waring et al., 1995). It has been shown that simulation of sun and shade leaves is crucial in estimating canopy carbon fluxes. Modeling studies that consider nitrogen distribution can also substantially improve estimation of canopy assimilation (Hirose et al., 1997). Among all these variables, light environment probably is the driving variable in determining other biological and environmental variation within the canopy. Modeling studies of canopy photosynthesis, based on the light response of photosynthesis by individual leaves and the attenuation of PAR in the canopy, show that the apparent quantum yield (ϕ) is of greater importance to productivity than the maximum rate of photosynthesis (Lawlor, 1995; de Pury and Farquhar, 1997). A similar conclusion that increases in quantum yield could account for major changes in canopy photosynthesis was reached earlier by Charles-Edwards (1982) and Baker and McKiernan (1988).

Quantum yield is the initial slope of the photosynthetic light response curve and represents the maximum efficiency of light utilization in photosynthesis. It has been extensively studied at the leaf level (Emerson, 1958; Ehleringer and Björkman, 1977; Ehleringer and Pearcy, 1983; Kirschbaum and Farquhar, 1987; Long and Drake, 1991; Lai and Edwards, 1995; Kubiske and Pregitzer, 1996). Since the theoretical

minimum light requirement for fixation of 1 mol CO₂ is 8 mol photons, the maximum ϕ is 0.125 mol CO₂ per quanta. In real plants, the quantum requirements are between 8.4 and 13.7 mol photon mol⁻¹ CO₂ as demonstrated by Ehleringer and Björkman (1977), Ku and Edwards (1978), and Farquhar and von Caemmerer (1982). Experimental measurements have indicated that ϕ of CO₂ fixation under ambient CO₂ levels and moderate temperatures is similar in C₃ plants and C₄ plants. Other studies have confirmed that ϕ is fairly insensitive to growth environments and species but varies with measurement temperature as well as CO₂ and O₂ concentration. The insensitivity of ϕ to growth environment and interspecific variation within either C₃ or C₄ species has a very important implication for predicting relative C₃ and C₄ species distributions over global terrestrial ecosystems (Ehleringer, 1978; Ehleringer et al., 1997).

Canopy CO₂ fluxes have been studied in relation to solar radiation (see an extensive review by Ruimy et al., 1995). Measurements of canopy CO₂ fluxes are usually made by micrometeorological methods (e.g. eddy correlation) or using enclosure chambers. The measurements with the eddy correlation apparatus represent an integration of vegetation gas exchange over large, upwind areas. A so-called footprint issue (see Kaharabata et al., 1997), however, makes it difficult to relate the measurements to particular plants or groups of plants and thus, to probe ecological mechanisms underlying the eddy-correlation measurements. In addition, the eddy-correlation method may substantially overestimate net ecosystem carbon exchange because of its limitation in quantifying nighttime carbon release via ecosystem respiration (Lee, 1997). Measurements with enclosure chambers have generally been conducted with plants in pot studies or small areas of vegetation in natural ecosystems. Plants in pot studies rarely form a canopy with typical structure of light and nitrogen distributions. Enclosure chambers used in field studies are often designed for portability and not for long-term flux measurements.

This study was designed to examine canopy quantum yield (ϕ_C) by taking advantage of the unique growth facility (EcoCELLS, Griffin et al., 1996) developed at the Desert Research Institute. EcoCELLS have the capability of providing highly accurate, continuous measurements of whole ecosystem gas exchange. Such measurements have been useful for addressing

leaf-to-canopy scaling issues (Griffin et al., 1996), for balancing ecosystem carbon budget (Cheng et al., 1999), for understanding canopy photosynthetic acclimation (Sims et al., 1999), and for quantifying canopy radiation and water use efficiencies (Hui et al., 1999). In this study, we utilized data from continuous measurements (24 h per day) of canopy photosynthetic CO₂ fluxes during the experimental period of 58 days to examine how canopy development and elevated CO₂ interactively affect ecosystem carbon fluxes. By combining these results with leaf-level measurements, we also compare ϕ_C with leaf quantum yield (ϕ_L).

2. Material and methods

2.1. Experimental facility, plant material and experiment design

This project utilized a facility (EcoCELLs) developed at the Desert Research Institute, Reno, NV, USA (Griffin et al., 1996) to study leaf and canopy quantum yield and carbon flux during canopy development. An EcoCELL is a large environmentally controlled and naturally lit plant growth chamber ($7.3 \times 5.5 \times 2.4 \text{ m}^3$). There are three soil containers ($2.85 \times 1.3 \times 1.8 \text{ m}^3$) within each EcoCELL. The main features of the facility include: (1) the EcoCELLs have the same theory of operation as leaf-level gas exchange systems but work at a much larger scale with continuous flux measurements; (2) by providing ecosystem-level measurements under controlled environmental conditions, the EcoCELLs can provide data to independently evaluate canopy and ecosystem models under ambient and non-ambient CO₂ conditions. Our previous (Griffin et al., 1996) and present studies indicate that canopy CO₂ flux measurements can be made with a high degree of accuracy in the EcoCELLs. In this study, all soil containers were filled with a constructed soil profile including three layers from top down: 0–0.4 m with 1:1 mix of top soil from Kansas Tallgrass prairie and washed river sand; 0.4–0.8 m with washed river sand; 0.8–1.8 m with washed river bed pebbles. We have chosen the Kansas prairie soil because its isotopic signal is useful in quantifying rhizosphere carbon processes (Cheng et al., 1999).

Seeds of sunflowers (*Helianthus annuus*, Johnny's, Albin, ME, USA) were planted in rows with a space of 30 cm in two EcoCELLs at ambient CO₂ ($399 \pm 13 \mu\text{mol mol}^{-1}$, mean \pm standard deviation) and elevated CO₂ ($746 \pm 14 \mu\text{mol mol}^{-1}$), respectively. There were 108 plants in each EcoCELL. Sunflowers were used in this experiment because of (1) their typical CO₂ responsiveness, (2) large leaf areas allowing for leaf-level measurements, and (3) clear understory for soil surface measurements. Water supply was controlled by whole system weight data and plants were watered with a drip irrigation system to maintain soil water content in the range from 60 to 90% of field water holding capacity in both EcoCELLs. Temperatures were controlled at 28°C in the daytime and 13°C at night. Relative humidity was set at 30% during day and 60% at night. The experiment started on 7 July, 1997 and was terminated on 28 August, 1997. Most of the days during the experimental period were cloudless.

2.2. Carbon flux measurements

Leaf-level light response curves were recorded with an open flow infrared gas analysis system (Li-6400, Li-cor, Lincoln, NE, USA) at the end of the experiment. Three plants were randomly selected from the edge to the middle of the canopy in each EcoCELL. Five or six leaves (leaf number 6, 9, 12, 15, 18 and 21 counting from the oldest leaves) of each plant were used to measure photosynthetic response to incident light intensity. Light response curves were measured by varying the light intensity using a LED light source (Li-6400-02, Li-Cor, Lincoln, NE, USA) and recording the steady-state photosynthetic rates at eight intensities: 10, 50, 100, 200, 500, 1500, and 2000 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$. In total, 35 light response curves were obtained in two EcoCELLs.

The flux of carbon through the EcoCELLs was continuously monitored and recorded in real time (every 15 min) during the experiment. Carbon flux calculations were made as open system differential measurements as described by Field et al. (1991) and expressed on a unit surface area basis. In this experiment, we did not physically confine canopy within the base surface of the three soil containers in each EcoCELLs. (The base soil surface is 2.85×3.90 , equaling 11.12 m^2 .)

Rather, we considered canopy edge effect and adjusted carbon fluxes to the ground surface area that varied as canopy was developing.

Light levels in each of the EcoCELLs were monitored with a quantum sensor (9901–013, Li-Cor, Lincoln, NE, USA) mounted parallel to the surface of the pots, well above the plant canopy. Because the canopy in the EcoCELLs has a cubic shape and did not form an infinite canopy surface area like in the natural field, quantum fluxes in the EcoCELLs were adjusted by considering direct solar radiation on the edges using an equation $C = 1 + ((W \cdot \cos(\theta) + L \cdot \cos(90 - \theta)) / (W \cdot L)) (H / \tan(\beta))$ where C is the correction factor, W the width of canopy, L the length of canopy, H the height of canopy, θ is the solar beam angle from true north measured in the horizontal plane (i.e. azimuth angle), and β is the zenith angle. The term $W \cdot L$ represents the area of the canopy top surface. The term $(W \cdot \cos(\theta) + L \cdot \cos(90 - \theta)) (H / \tan(\beta))$ is projected side surface area that received light. Calculation of θ and β follows formula given by Campbell and Norman (1998).

2.3. Estimation of leaf and canopy quantum yields

Assimilation/irradiance (A/I) curves from 35 leaf measurements were used to derive leaf quantum yield (ϕ_L). Canopy gross photosynthetic CO₂ fluxes and incident irradiance in the morning from sunrise to noon (31 July–27 August, 1997) were used to derive canopy quantum yield (ϕ_C). In order to compare results of this study with others (Ruimy et al., 1995), we selected the rectangular hyperbolic equation as the primary model to fit both leaf and canopy A/I curves by

$$P_n = \frac{\phi P_g^* I}{P_g^* + \phi I}$$

where P_n is net photosynthesis, P_g^* the maximal value of gross photosynthesis, ϕ either leaf (ϕ_L) or canopy (ϕ_C) quantum yield, I the irradiance, and R is the dark respiration. Leaf dark respiration was estimated by P_g at $I = 0$ for leaf-level measurements. Ecosystem dark respiration was plant and soil respiration during the daytime that was estimated from nighttime respiration of entire ecosystem corrected with Q_{10} equaling 2 for the temperature difference between night and day

(13 °C and 28 °C, respectively). Leaf and canopy gross photosynthesis was calculated from measurements of leaf and canopy carbon fluxes, respectively, plus respiration.

To evaluate the robustness of the estimated ϕ_C by the rectangular hyperbolic model, we also used two other methods to compute ϕ_C . One is the non-rectangular hyperbolic model:

$$\theta P_g^2 - (\phi'_C I + P_g^*) P_g + \phi'_C I P_g^* = 0$$

where ϕ'_C is the canopy quantum yield estimated by the non-rectangular hyperbolic model and θ is the curvature of the non-rectangular function. When $\theta = 0$, the above equation reduces to the rectangular hyperbola. The other is a linear equation assuming $P_g = 0$ when $I = 0$:

$$P_g = \phi''_C I$$

where ϕ''_C is the canopy quantum yield estimated by the linear model from the A/I data with $I \leq 250 \mu\text{mol m}^{-2} \text{s}^{-1}$.

2.4. Measurements of leaf area index (LAI)

The total number of leaves per plant from a random subset of plants in each EcoCELL was counted. Actual leaf areas were calculated from measurements of leaf length and width using an allometric relationship developed for a similar set of leaves. The means of four measurements in each EcoCELL were used as observed LAI values.

2.5. Pseudo-replication and statistical analysis

Due to the limitation of experiment facility and operation costs, it was impractical to set replicates of treatments at the ecosystem scale. In this study, we used two EcoCELLs to quantify ϕ_L and ϕ_C at ambient and elevated CO₂. There was no replication of the CO₂ treatments. By definition, all the measurements made within each of the CO₂ treatments are pseudo-replicated (Hurlbert, 1984). Even if we have less statistical power to detect differences between CO₂ treatments, quantification of ϕ_L and ϕ_C is valid for at least two reasons. First, measurements of canopy gas exchange have a very high accuracy. Before we conducted this experiment, we quantified the accuracy

of system-level measurements and found that more than 95% of 96 data points over a 24 h period varied within $\pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in both the EcoCELLS. This variation is extremely small compared to the magnitude of canopy CO_2 exchange, which ranged from $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the early stage of canopy development to $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ toward the end of the experiment. It is a common practice in biophysical studies that measurements are made with no or less replication if the instruments have high accuracy. For example, canopy flux measurements made by Wofsy et al. (1993), in Harvard Forests with an eddy-correlation apparatus were not replicated. Second, the primary objective of this study was to quantify ϕ_L and ϕ_C while comparison between the CO_2 treatments was secondary.

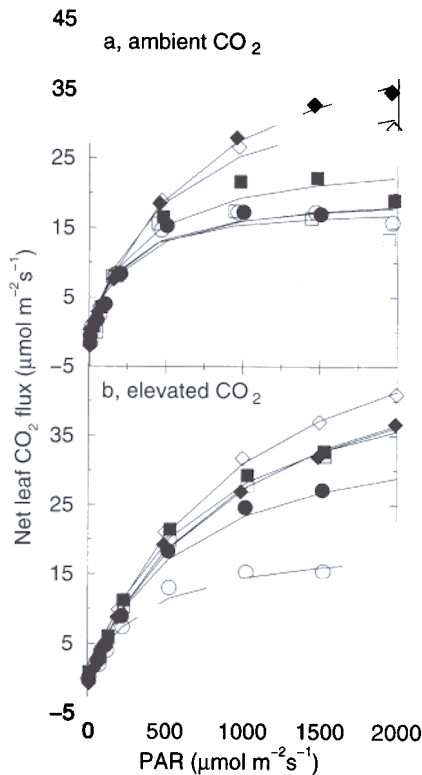


Fig. 1. Representative response curves of leaf assimilation with irradiance at different plant positions at ambient CO_2 (a) and elevated CO_2 (b). Symbols represent measured photosynthesis of Leaf 1 (the bottom leaf, O), Leaf 2 (●), Leaf 3 (□), Leaf 4 (■), Leaf 5 (◇), and Leaf 6 (the top leaf, ◆). Lines represent fitted A/I curves.

Quantum yield estimation was carried out with SAS NLIN procedure. Difference in quantum yield among canopy positions was tested using ANOVA procedure (SAS Institute, Cary, North Carolina USA).

3. Results

3.1. Leaf-level A/I curves and quantum yields

Leaf photosynthesis increased with light for three plants in different positions at both ambient and elevated CO_2 (Fig. 1). Younger leaves at the top of the canopy had higher photosynthetic rates than older ones in the bottom of canopy. The observed maximum leaf CO_2 flux changed from approximately 13 to $36 \mu\text{mol m}^{-2} \text{s}^{-1}$ at ambient CO_2 and from 15 to $42 \mu\text{mol m}^{-2} \text{s}^{-1}$ at elevated CO_2 . Elevated CO_2 slightly increased the leaf photosynthesis. All A/I curves were well fitted by the hyperbolic function. The determinant coefficients (R^2) were above 0.85 for all of the 35 data sets. Estimated leaf quantum

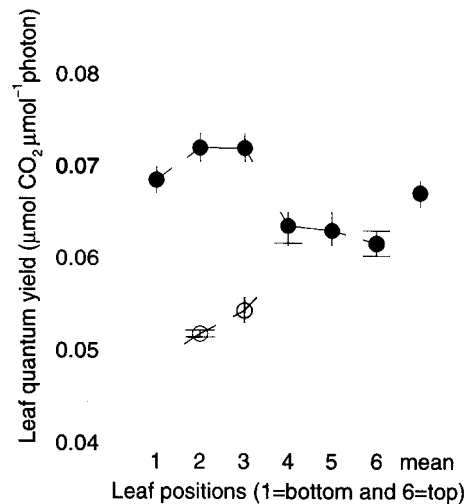


Fig. 2. Leaf quantum yield (ϕ_L , mean \pm standard error) at six canopy positions from the bottom (Leaf 1) to the top (Leaf 6) of the canopy at ambient CO_2 (O) and elevated CO_2 (●). The averaged ϕ_L (mean \pm standard error) from all the six positions within the canopy at ambient and elevated CO_2 is plotted on the right side of figure for reference. The difference in ϕ_L is not statistically significant between canopy positions at either ambient or elevated CO_2 . The difference in ϕ_L is statistically significant between the two CO_2 treatments.

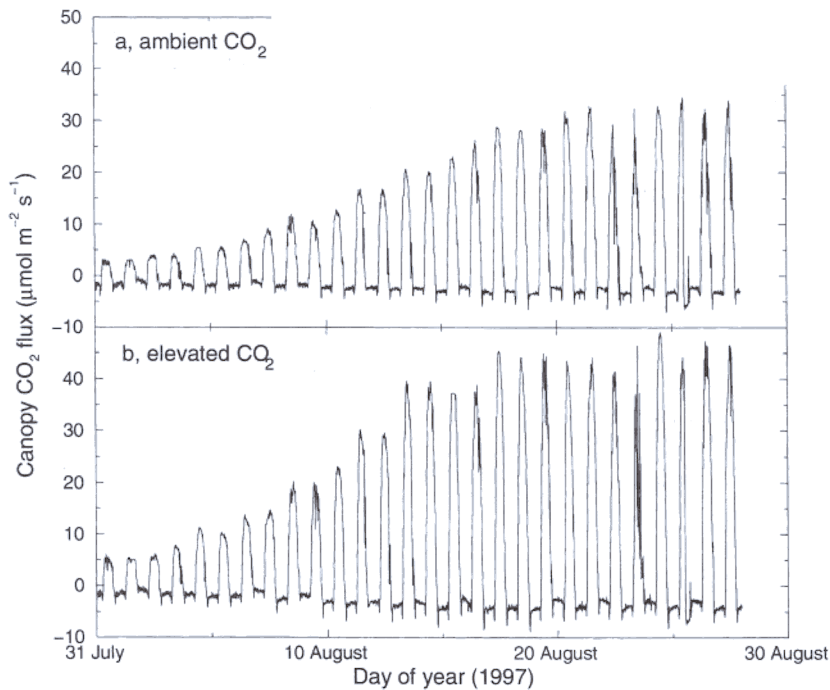


Fig. 3. Measured CO₂ fluxes from 31 July to 27 August, 1997 at ambient CO₂ (a) and elevated CO₂ (b). Partially cloudy conditions prevailed on 9, 19, 16 and 24 August, 1997. Two EcoCELLs were completely covered with black sheets from 1200 to 1600, 26 August to measure daytime respiration.

yields (ϕ_L) varied little with light levels at different plant positions (Fig. 2) ranging from 0.0487 to 0.0596 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon with an average of 0.0542 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon at ambient CO₂. At elevated CO₂, the values of ϕ_L changed from 0.0616 to 0.0720 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon with an average of 0.0671 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon. The ϕ_L values of middle leaves (Leaf 4 at ambient CO₂ and Leaf 3 at elevated CO₂) were slightly higher than those of lower and upper leaves. Analysis of variance (ANOVA), however, did not show significant difference in ϕ_L between different leaf positions at either ambient ($p=0.21$) or elevated CO₂ ($p=0.88$). Elevated CO₂ resulted in an average of 24% higher ϕ_L than ambient CO₂. The difference in ϕ_L between the two CO₂ treatments was significant ($p=0.009$) (Fig. 2).

3.2. Canopy carbon fluxes

Net canopy carbon fluxes increased during the experimental period, from approximately 5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on 31 July 1997 (25 days after planting) to 35 and

48 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at ambient and elevated CO₂, respectively, in the late growing stage when the canopy was closed (Fig. 3). The fluxes increased exponentially up to 17 August, 1997 and then slowly increased at both CO₂ treatments. At the early stage of canopy development, no substantial difference was observed between the two CO₂ treatments. From 4 August, 1997 on, the canopy developed rapidly; and CO₂ flux at elevated CO₂ averaged 53% higher than that at ambient CO₂. Although this study lacks the statistical power to assert that the difference between the CO₂ treatments at any given point of time was due to the treatment effect, the high accuracy of the continuous measurements with a time series of 29 days offered by the EcoCELL instruments strongly suggests the possibility that the CO₂ treatments stimulated large differences in canopy carbon fluxes.

Within a single day, net canopy CO₂ flux was negative at night and positive during the day with the short-duration respiratory spikes of carbon release at both dawn and dusk as illustrated in the four representative diurnal courses (Fig. 4). The spikes likely

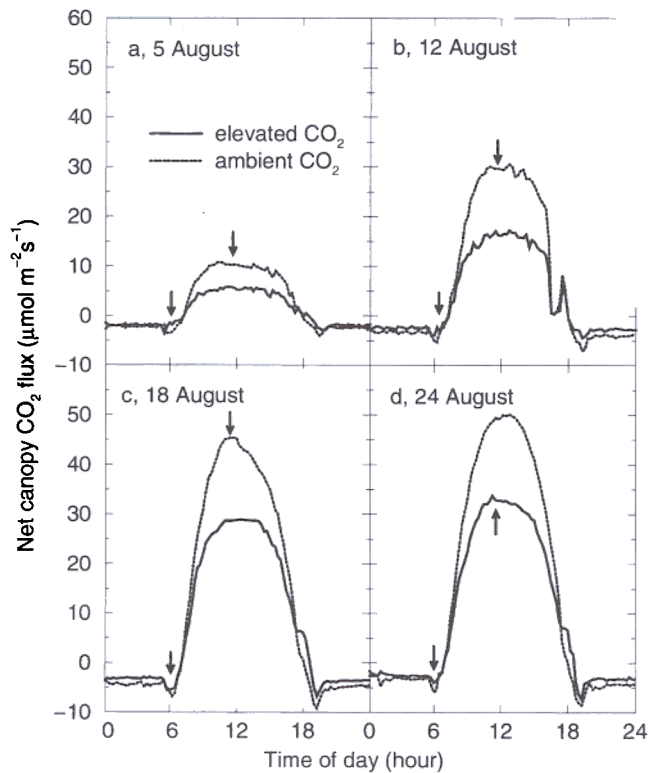


Fig. 4. Diurnal canopy CO₂ fluxes measured at ambient CO₂ (solid lines) and elevated CO₂ (dotted lines) on (a) 5 August; (b) 12 August; (c) 18 August and (d) 24 August, 1997. High respiratory carbon release either in the early morning or late afternoon resulted from step changes between night (13°C) and day (28°C) temperature. The sudden decrease in net CO₂ fluxes after 1600 on 12 August was due to clouds. The morning data between the two arrows were used to construct canopy assimilation/incident irradiance (A/I) curves in Figs. 5 and 6.

resulted from ecosystem degassing associated with sudden switches in EcoCELL temperature, but the mechanism is not clear yet. During daytime, CO₂ flux increased in the morning, reached the maximum at noon, and declined in the afternoon. The diurnal course purely resulted from the diurnal change in radiation because temperature and humidity in the EcoCELLs were controlled at constant levels. The daily maximum of net canopy CO₂ fluxes changed from approximately 6 µmol m⁻² s⁻¹ on 5 August to 33 µmol m⁻² s⁻¹ on 24 August at ambient CO₂ and from 11 to 50 µmol m⁻² s⁻¹ at elevated CO₂ during the same period (Fig. 4).

3.3. Canopy-level A/I curves and quantum yields

We used canopy photosynthetic rates and incident photosynthetically active radiation (PAR) from sunrise

to noon to obtain assimilation responses to irradiation (i.e. A/I) curves at both ambient and elevated CO₂. The A/I curves derived from the four representative diurnal courses of CO₂ exchange (Fig. 4) are shown for 5, 12, 18, and 24 August, 1997 in Figs. 5 and 6. Canopy photosynthesis increased quickly at low PAR and slowly at high PAR for all the eight cases (Figs. 5 and 6). Most of the canopy A/I curves were well fitted by the rectangular hyperbolic equation for estimating ϕ_C and maximum photosynthetic capacity (P_g^*). Data on 24 August, 1997, however, apparently deviated from equation 1 at both ambient and elevated CO₂ (Figs. 5 and 6 (d)) in spite of the fact that values of determinant coefficients (R^2) were generally higher than 0.90 (Table 1). Estimated ϕ_C increased with canopy development, from 0.024 µmol CO₂ µmol⁻¹ photon on 31 July, 1997 to 0.072 µmol CO₂ µmol⁻¹ photon by the end of the experiment at ambient CO₂ (Table 1).

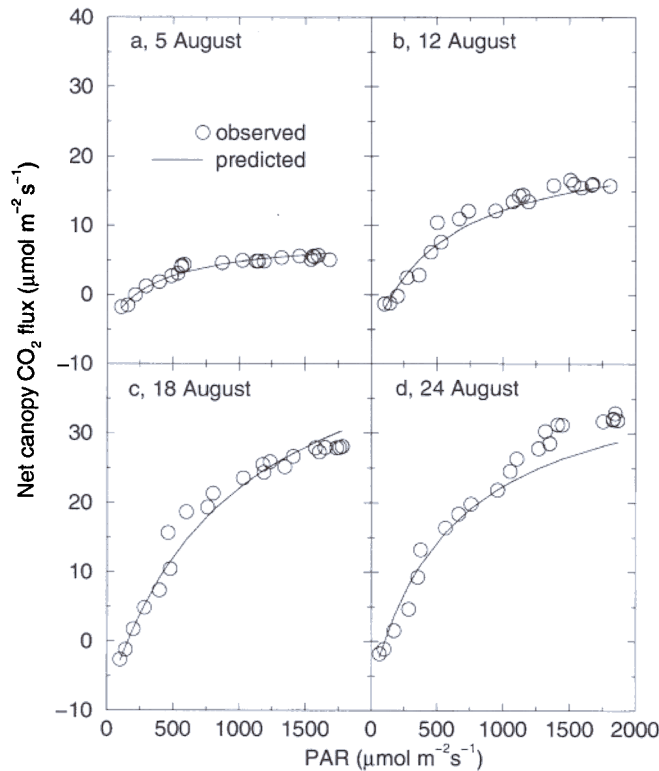


Fig. 5. Net canopy photosynthetic response to photosynthetically active radiation (PAR) on (a) 5 August; (b) 12 August; (c) 18 August and (d) 24 August, 1997 in ambient CO_2 . Open circles represent observed CO_2 fluxes, and the lines are the fitted AI curves using the rectangular hyperbolic equation.

During the same period, the change in ϕ_C was from 0.030 to 0.094 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon at elevated CO_2 . Values of ϕ_C were higher, on average of 28 points, by 31.5% at elevated CO_2 than that at ambient CO_2 . The maximum photosynthetic capacity (P_g^*) also increased with canopy development, ranging from 10.6 to 73.2 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ at ambient CO_2 and 12.4 to 107.5 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ at elevated CO_2 (Table 1). Estimated daytime plant and soil respiration increased from 3.5 to 9.5 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ at ambient CO_2 and from 3.2 to 11.8 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ at elevated CO_2 during the canopy development. The estimates using Q_{10} equaling 2 and night-time ecosystem respiration were highly consistent with weekly daytime measurements of soil surface respiration plus estimated plant respiration (data not shown). Sensitivity analysis indicated that the values of ϕ_C and P_g^* are fairly sensitive to the estimates of daytime plant and soil respiration. In addition, we derived ϕ_C

using data either from the afternoon or full day. Results were similar to those derived from the morning data with slightly higher variability (data not shown).

3.4. Leaf area index and canopy quantum yield

Observed leaf area index (LAI) increased from 0.59 on 5 August to 4.48 on 28 August 1997 at ambient CO_2 (Table 2). LAI was 0.66 on 5 August and 4.98 on 28 August, 1997 at elevated CO_2 . There was very little difference in the total number of leaves between the two CO_2 treatments (data not shown). This slight increase in canopy leaf area at elevated CO_2 was due to the increased expansion of individual leaves in the center of canopy.

We used a linear interpolation method to estimate daily values of LAI, which we then used to correlate ϕ_C at both ambient and elevated CO_2 treatments (Fig. 7). Canopy quantum yield (ϕ_C) increases with

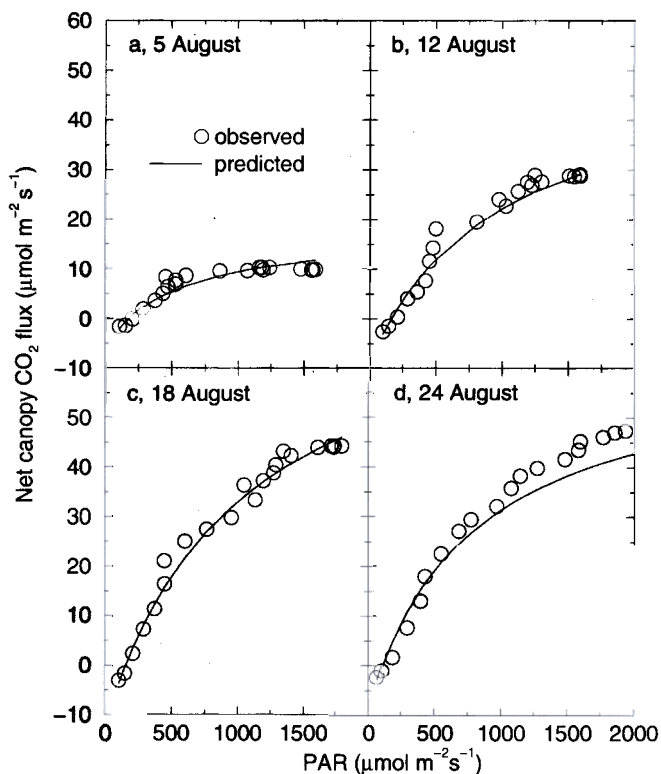


Fig. 6. Net canopy photosynthetic response to photosynthetically active radiation (PAR) on (a) 5 August; (b) 12 August; (c) 18 August; and (d) 24 August, 1997 in elevated CO₂. Symbols are the same as in Fig. 5.

LAI and reached the values of leaf-level quantum yield (ϕ_L) at both ambient ($\phi_L = 0.0542 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$) and elevated ($\phi_L = 0.0671 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$) CO₂ treatments when LAI was approximately 1.5. When LAI approached 2.5–3.0, ϕ_C gradually stabilized at $0.073 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$ at ambient CO₂ and $0.090 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$ at elevated CO₂. Using a hyperbolic equation, $\phi_C = a \cdot \phi_C^* \cdot \text{LAI} / (\phi_C^* + a \cdot \text{LAI})$ where a is a coefficient indicating the initial slope of the hyperbolic function and ϕ_C^* is the maximal value of ϕ_C , we obtain $a = 0.1137 \pm 0.0111$ (standard error) and $\phi_C^* = 0.0829 \pm 0.0030$ at ambient CO₂. At elevated CO₂ $a = 0.1224 \pm 0.0099$ and $\phi_C^* = 0.1129 \pm 0.0036$. Statistical analysis indicated a significant difference in the ϕ_C^* values between the two CO₂ treatment ($p < 0.01$) but no significant difference in the a values between the CO₂ treatments ($p > 0.10$).

3.5. Comparison among three models

The non-rectangular hyperbolic model estimated canopy quantum yield (ϕ_C') that is equal to $1.0117 \phi_C - 0.0018$ with the determination coefficient $R^2 = 0.8879$ (Fig. 8 A), where ϕ_C is the canopy quantum yield estimated with the rectangular hyperbolic model. At ambient CO₂, $\phi_C' = 1.0355 \phi_C - 0.0088$ whereas $\phi_C' = 1.0107 \phi_C - 0.0095$ at elevated CO₂. No significant difference was found between the two CO₂ treatments. Comparison between the linear model and the rectangular hyperbolic model suggested $\phi_C'' = 0.8666 \phi_C - 0.0034$ with $R^2 = 0.9244$ (Fig. 8 B), where ϕ_C'' is the canopy quantum yield estimated with the linear model. It was found that $\phi_C'' = 0.8864 \phi_C - 0.0034$ at ambient CO₂ and $\phi_C'' = 0.8383 \phi_C - 0.0023$ at elevated CO₂. Overall, the linear model underestimated canopy quantum yield whereas the rectangular hyperbolic model

Table 1

Values of parameters ϕ_C (canopy quantum yield, $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon), P_g^* (maximum canopy gross photosynthesis, $\mu\text{mol mol}^{-2} \text{s}^{-1}$), and R (ecosystem respiration during the daytime, $\mu\text{mol mol}^{-2} \text{s}^{-1}$) of the rectangular hyperbolic equation and r^2 (determinant coefficient) derived by fitting the equation with individual data sets from 31 July to 27 August, 1997 at ambient and elevated CO_2

Date	Ambient CO_2				Elevated CO_2			
	ϕ_C	P_g^*	R	r^2	ϕ_C	P_g^*	R	r^2
31 July	0.0239		4.97	0.892			4.16	0.912
1 August	0.0230		4.40	0.947			3.58	0.946
2 August	0.0229		3.46	0.929			2.51	0.929
3 August	0.0261		4.82	0.970			4.36	0.965
4 August	0.0314		5.04	0.914			4.49	0.988
5 August	0.0376		5.08	0.970			5.72	0.945
6 August	0.0359		5.33	0.972			5.25	0.958
7 August	0.0302		3.96	0.916			3.15	0.879
8 August	0.0381		5.54	0.918			7.12	0.925
9 August	0.0470		4.96	0.964			5.60	0.960
10 August	0.0480		6.33	0.932			8.45	0.968
11 August	0.0534		6.73	0.928			9.33	0.987
12 August	0.0522		6.50	0.935			8.87	0.969
13 August	0.0510		7.18	0.990			10.53	0.976
14 August	0.0501		7.00	0.988			9.40	0.964
15 August	0.0616		8.18	0.983			12.10	0.971
16 August	0.0583		6.20	0.940			9.67	0.967
17 August	0.0607		9.02	0.930			12.04	0.970
18 August	0.0633		8.60	0.991			11.83	0.984
19 August	0.0752		9.47	0.985			12.43	0.981
20 August	0.0760		6.69	0.963			7.78	0.948
21 August	0.0690		8.53	0.977			11.67	0.976
22 August	0.0725		7.05	0.965			8.34	0.975
23 August	0.0708		9.30	0.882			11.14	0.885
24 August	0.0751		6.80	0.955			8.50	0.968
25 August	0.0727		8.74	0.977			11.18	0.973
26 August	0.0734		6.69	0.876			8.82	0.956
27 August	0.0716		9.12	0.946			11.81	0.927

resulted in similar estimates of quantum yield with the non-rectangular hyperbolic model. The underestimation by the linear model is consistent with the notion that ϕ_C is the highest as irradiance I approaches zero.

4. Discussion

This study indicates that canopy quantum yield (ϕ_C) ranged from 0.0229 to 0.0760 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon over LAI changes from 0.6 to 4.5 at ambient CO_2 and from 0.0234 to 0.0959 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon over LAI changes from 0.7 to 5.0 at elevated CO_2 . This range of ϕ_C is generally comparable to estimates provided by Ruimy et al. (1995), who found ϕ_C varying from 0.009 to 0.465 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon with an average of 0.044 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon for 122

data sets with 1362 data points. Out of the 122 data sets, 18 have ϕ_C values larger than 0.100 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon and 84 have ϕ_C values less than 0.054, the value of leaf-level quantum yield (ϕ_L) at ambient CO_2 found in this study. In addition, our results showed that ϕ_C increased by 31.5% at elevated CO_2 compared to that at ambient CO_2 . The CO_2 -induced increase in ϕ_C is similar to the stimulation reported by Monje and Bugbee (1998). Their study showed that CO_2 -induced increase in canopy quantum yield, which was calculated as daily average of gross photosynthesis divided by absorbed photosynthetic photon flux, ranges from 9 to 30%, depending on developmental stages of the canopy.

The curvilinear relationship between canopy carbon fluxes and incident light levels as illustrated in Figs. 5 and 6 indicates that canopy radiation use efficiency

Table 2

Measured leaf area index (LAI) at ambient and elevated CO₂ (mean ± standard error). *p* is the probability that LAI is significantly different between the two CO₂ treatments. 28 August, 1997 was the last harvesting day

Date	Ambient CO ₂	Elevated CO ₂	<i>p</i>
7 August			
15 August			
21 August			
28 August			

(CRUE) varies over the diurnal course within one day as well as over the course of canopy development. The variation in CRUE is similar to other experimental and theoretical studies (Ruimy et al., 1995; Medlyn, 1998; Monje and Bugbee, 1998) but may not be consistent with the early observation. The early observation suggests that CRUE of a plant canopy under unstressed conditions is approximately constant with respect to changes in absorbed photosynthetically active radiation (Monteith, 1972, 1977). Monje and Bug-

bee (1998) have shown that CRUE varies with canopy development. The review by Ruimy et al. (1995) indicates that most canopy carbon fluxes observed in the field follow the curvilinear relationships with radiation availability. Medlyn (1998) used a mechanistic model to examine two of the three mechanisms that potentially transform the nonlinear relationship between leaf photosynthesis and light into a linear relationship between canopy carbon fluxes and radiation. Her study concluded that neither radiation distribution within canopy nor temporal integration of CRUE could result in the linear relationship between canopy carbon fluxes and radiation. Indeed, Hui et al. (1999), calculated CRUE, which varied from 0.019 μmol CO₂ μmol⁻¹ photon in early morning or late afternoon to 0.011 μmol CO₂ μmol⁻¹ photon at noon at ambient CO₂. At elevated CO₂, CRUE varied from 0.030 μmol CO₂ μmol⁻¹ photon in the early morning or later afternoon to 0.018 μmol CO₂ μmol⁻¹ photon at noon. However, the apparent deviation of experimental data from the typical hyperbolic function toward a more linear form when LAI is high (Figs. 5d and 6d) warrants more investigation into canopy gas exchange as related to radiation.

Leaf quantum yield (ϕ_L) generally does not vary with seasonal changes and canopy positions as shown in this as well as many other studies. Nilsen and Sharifi (1994) reported that there was no major difference in apparent ϕ_L between the spring and summer for two desert legumes (*Caes alponia virgata* and *Senna armata*). Webber et al. (1984) and Stirling et al. (1991) demonstrated that ϕ_L varied little during the development stage. Wang and Polglase (1995) suggested that estimates of ϕ_L are similar for leaves throughout closed canopies. Long and Drake (1991) found ϕ_L was remarkably uniform between replicates. On the other hand, there are several reports that ϕ_L varied with canopy position and measurement time. Lai and Edwards (1995) found that ϕ_L increased progressively from the basal section to the tip of the leaf of *Zea mays*. There was a significant decline in apparent ϕ_L for both CO₂ treatments between morning and afternoon (Kirschbaum and Farquhar, 1987; Eamus et al., 1993). In this study, we did not find any statistically significant difference in ϕ_L along canopy positions although ϕ_L increased from the bottom to the middle position and declined toward the top of canopy at both CO₂ treatments.

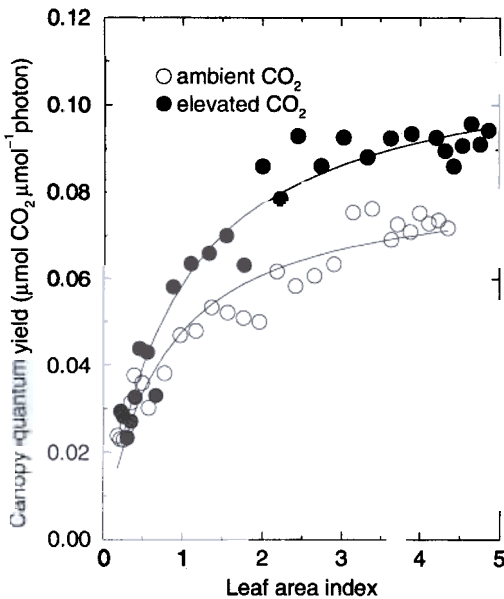


Fig. 7. Canopy quantum yield (ϕ_C) from 31 July to 27 August 1997 (Table 1) correlated with leaf area index (LAI). Circles represent observed ϕ_C at ambient CO₂ (O) and elevated CO₂ (●) with nonlinear regression equation $\phi_C = 0.0094 \text{ LAI} / (0.0829 + 0.1137 \text{ LAI})$, $r^2 = 0.992$ at ambient CO₂; and $\phi_C = 0.01382 \text{ LAI} / (0.1129 + 0.1224 \text{ LAI})$, $r^2 = 0.995$ at elevated CO₂, where r^2 is the determinant coefficient. See text for more explanation.

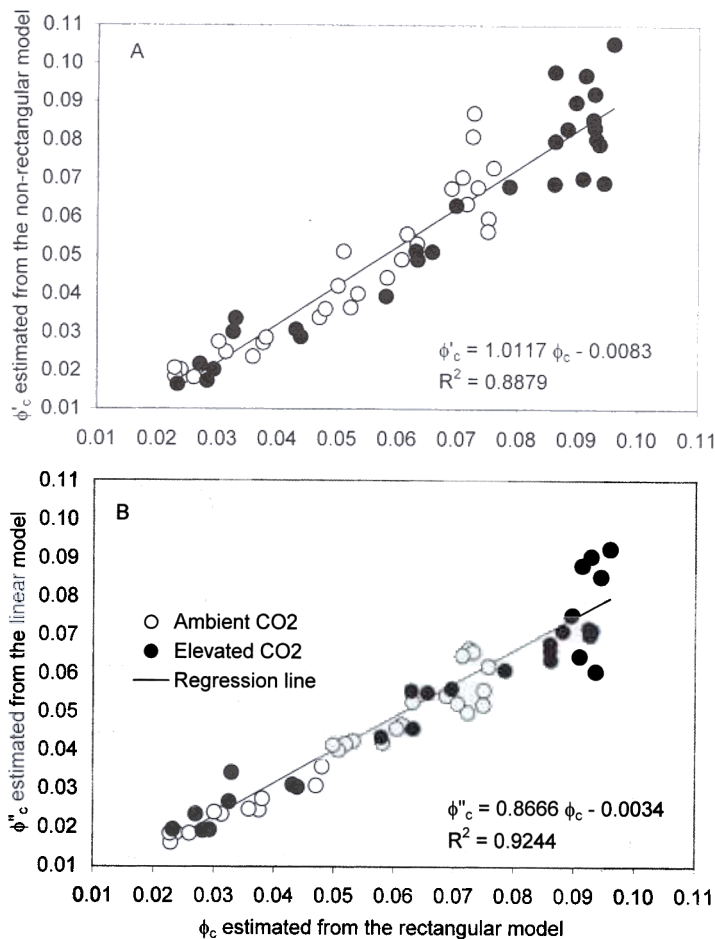


Fig. 8. Comparison of estimated canopy quantum yield among the rectangular hyperbolic, non-rectangular hyperbolic, and linear models. Circles represent quantum yield at ambient CO₂ (○) and elevated CO₂ (●). The rectangular hyperbolic model is the primary model used in this study.

It has generally been reported that ϕ_L increases at elevated CO₂ (Chen and Sung, 1990; Teramura et al., 1990; Ziska et al., 1991; Eamus et al., 1993; Wang et al., 1995). However, a decrease of ϕ_L in Siberian white birch and Japanese white birch was found by Koike et al. (1996) and no difference in ϕ_L was reported by Delgado et al. (1994). Our results suggest that elevated CO₂ increased ϕ_L of sunflower plants by 24%. The increase is slightly smaller than the theoretical value predicted by Farquhar and von Caemmerer (1982).

A comparison of leaf with canopy A/I curves (Fig. 1 versus Figs. 5 and 6) suggests different mechanisms in controlling leaf versus canopy photosynthetic responses to light availability. Leaves with different

photosynthetic capacity respond similarly to an increase in light availability at the low level until photosynthesis reaches a light saturating point. The higher the leaf photosynthetic capacity is, the larger the light saturating point with similar initial slopes of A/I curves. Thus, leaf-level quantum yield (ϕ_L) is not correlated with photosynthetic capacity (P_g^*). Unlike the leaf A/I responses, we did not observe any apparent light saturating points for canopy photosynthetic responses to light. Observed ϕ_C appears to be correlated with canopy P_g^* (Table 1).

In summary, leaf quantum yield was found in this study not significantly different at different positions within the canopy but increased by 24% at elevated

CO₂ compared with that at ambient CO₂ (0.0671 versus 0.0542 μmol CO₂ μmol⁻¹ photon). Canopy quantum yield strongly varied with canopy development, varying from 0.0229 to 0.0959 μmol CO₂ μmol⁻¹ photon over LAI changes from 0.5 to 5.0. CO₂ enrichment resulted in a 31.5% increase in the canopy quantum yield. In addition, examination of relationship between canopy quantum yield and incident PAR suggested that canopy radiation use efficiency (CRUE) varied with light levels. Variability in CRUE demonstrated in this and other studies warrants further investigation into the notion drawn from earlier studies that CRUE under non-stressed conditions is approximately constant.

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