

## Canopy quantum yield in a mesocosm study

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Received 12 March 1999; accepted 5 August 1999

### 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 ( $746 \mu\text{mol mol}^{-1}$ )  $\text{CO}_2$  concentrations. We continuously measured carbon flux during canopy development from which canopy quantum yield ( $\phi_C$ ) was estimated. The results indicated that the total daily carbon flux was similar between elevated and ambient  $\text{CO}_2$  treatments in the early stage of canopy development. After the canopy closed, carbon flux under elevated  $\text{CO}_2$  averaged 53% higher than that under ambient  $\text{CO}_2$ . Assimilation/incident irradiance (A/I) curves of leaves at different canopy positions were used to estimate leaf quantum yields ( $\phi_L$ ), and A/I curves of canopies at late development stages were used to estimate  $\phi_C$ . Elevated  $\text{CO}_2$  enhanced  $\phi_L$  by 24%. There was little difference in  $\phi_L$  at different canopy positions, averaging 0.0542 at ambient  $\text{CO}_2$  and 0.0671 at elevated  $\text{CO}_2$ . Canopy quantum yield ( $\phi_C$ ) was higher by 32% at elevated than ambient  $\text{CO}_2$ . 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  $\text{CO}_2$  and  $\phi_C = 0.01382 \text{ LAI}/(0.1129 + 0.1224 \text{ LAI})$  at elevated  $\text{CO}_2$ . 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  $\phi_C$  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.

**Keywords:** Carbon flux; Canopy; Leaf area index; Light use efficiency; Photosynthesis; Quantum yield; Radiation use efficiency; Scaling

### 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  $\text{CO}_2$ , and various pollutants. Photosynthesis, which determines the rate of  $\text{CO}_2$  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.

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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 CO<sub>2</sub> exchange (Baldocchi, 1993). Together with other experimental data (e.g. CO<sub>2</sub> flux from the soil surface and plant respiration), the net ecosystem CO<sub>2</sub> 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 ( $\phi$ ) 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 CO<sub>2</sub> is 8 mol photons, the maximum  $\phi$  is 0.125 mol CO<sub>2</sub> per quanta. In real plants, the quantum requirements are between 8.4 and 13.7 mol photon mol<sup>-1</sup> CO<sub>2</sub> as demonstrated by Ehleringer and Björkman (1977), Ku and Edwards (1978), and Farquhar and von Caemmerer (1982). Experimental measurements have indicated that  $\phi$  of CO<sub>2</sub> fixation under ambient CO<sub>2</sub> levels and moderate temperatures is similar in C<sub>3</sub> plants and C<sub>4</sub> plants. Other studies have confirmed that  $\phi$  is fairly insensitive to growth environments and species but varies with measurement temperature as well as CO<sub>2</sub> and O<sub>2</sub> concentration. The insensitivity of  $\phi$  to growth environment and interspecific variation within either C<sub>3</sub> or C<sub>4</sub> species has a very important implication for predicting relative C<sub>3</sub> and C<sub>4</sub> species distributions over global terrestrial ecosystems (Ehleringer, 1978; Ehleringer et al., 1997).

Canopy CO<sub>2</sub> fluxes have been studied in relation to solar radiation (see an extensive review by Ruimy et al., 1995). Measurements of canopy CO<sub>2</sub> 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 ( $\phi_C$ ) 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 CO<sub>2</sub> fluxes during the experimental period of 58 days to examine how canopy development and elevated CO<sub>2</sub> interactively affect ecosystem carbon fluxes. By combining these results with leaf-level measurements, we also compare  $\phi_C$  with leaf quantum yield ( $\phi_L$ ).

## 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 CO<sub>2</sub> conditions. Our previous (Griffin et al., 1996) and present studies indicate that canopy CO<sub>2</sub> 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 CO<sub>2</sub> ( $399 \pm 13 \mu\text{mol mol}^{-1}$ , mean  $\pm$  standard deviation) and elevated CO<sub>2</sub> ( $746 \pm 14 \mu\text{mol mol}^{-1}$ ), respectively. There were 108 plants in each EcoCELL. Sunflowers were used in this experiment because of (1) their typical CO<sub>2</sub> 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  $2.85 \times 3.90$ , equaling  $11.12 \text{ m}^2$ .)

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 a 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,  $\theta$  is the solar beam angle from true north measured in the horizontal plane (i.e. azimuth angle), and  $\beta$  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  $\theta$  and  $\beta$  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 ( $\phi_L$ ). Canopy gross photosynthetic CO<sub>2</sub> fluxes and incident irradiance in the morning from sunrise to noon (31 July–27 August, 1997) were used to derive canopy quantum yield ( $\phi_C$ ). 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

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

where  $P_n$  is net photosynthesis,  $P_g^*$  the maximal value of gross photosynthesis,  $\phi$  either leaf ( $\phi_L$ ) or canopy ( $\phi_C$ ) 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  $\phi_C$  by the rectangular hyperbolic model, we also used two other methods to compute  $\phi_C$ . 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  $\phi_C'$  is the canopy quantum yield estimated by the non-rectangular hyperbolic model and  $\theta$  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  $\phi_C''$  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  $\phi_L$  and  $\phi_C$  at ambient and elevated CO<sub>2</sub>. There was no replication of the CO<sub>2</sub> treatments. By definition, all the measurements made within each of the CO<sub>2</sub> treatments are pseudo-replicated (Hurlbert, 1984). Even if we have less statistical power to detect differences between CO<sub>2</sub> treatments, quantification of  $\phi_L$  and  $\phi_C$  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  $\text{CO}_2$  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  $\phi_L$  and  $\phi_C$  while comparison between the  $\text{CO}_2$  treatments was secondary.

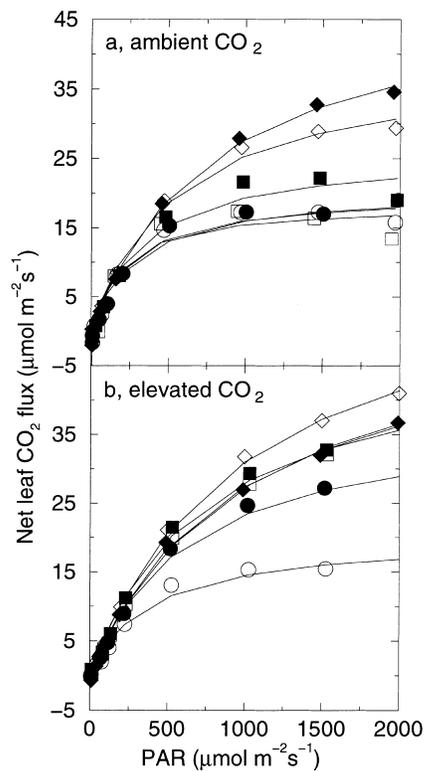


Fig. 1. Representative response curves of leaf assimilation with irradiance at different plant positions at ambient  $\text{CO}_2$  (a) and elevated  $\text{CO}_2$  (b). Symbols represent measured photosynthesis of Leaf 1 (the bottom leaf (O), Leaf 2 (●), Leaf 3 (□), Leaf 4 (■), Leaf 5 (◇), and Leaf 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  $\text{CO}_2$  (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  $\text{CO}_2$  flux changed from approximately 13 to  $36 \mu\text{mol m}^{-2} \text{s}^{-1}$  at ambient  $\text{CO}_2$  and from 15 to  $42 \mu\text{mol m}^{-2} \text{s}^{-1}$  at elevated  $\text{CO}_2$ . Elevated  $\text{CO}_2$  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

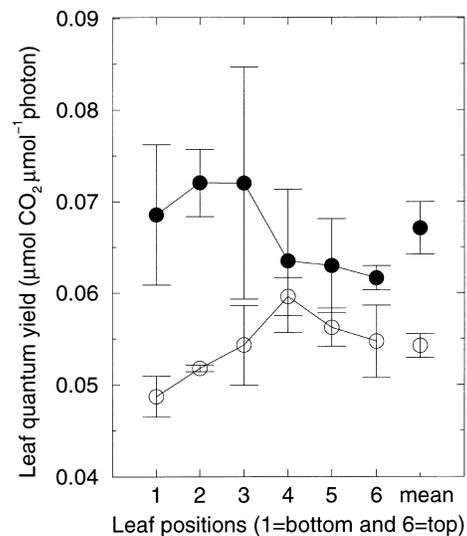


Fig. 2. Leaf quantum yield ( $\phi_L$ , mean  $\pm$  standard error) at six canopy positions from the bottom (Leaf 1) to the top (Leaf 6) of the canopy at ambient  $\text{CO}_2$  (O) and elevated  $\text{CO}_2$  (●). The averaged  $\phi_L$  (mean  $\pm$  standard error) from all the six positions within the canopy at ambient and elevated  $\text{CO}_2$  is plotted on the right side of figure for reference. The difference in  $\phi_L$  is not statistically significant between canopy positions at either ambient or elevated  $\text{CO}_2$ . The difference in  $\phi_L$  is statistically significant between the two  $\text{CO}_2$  treatments.

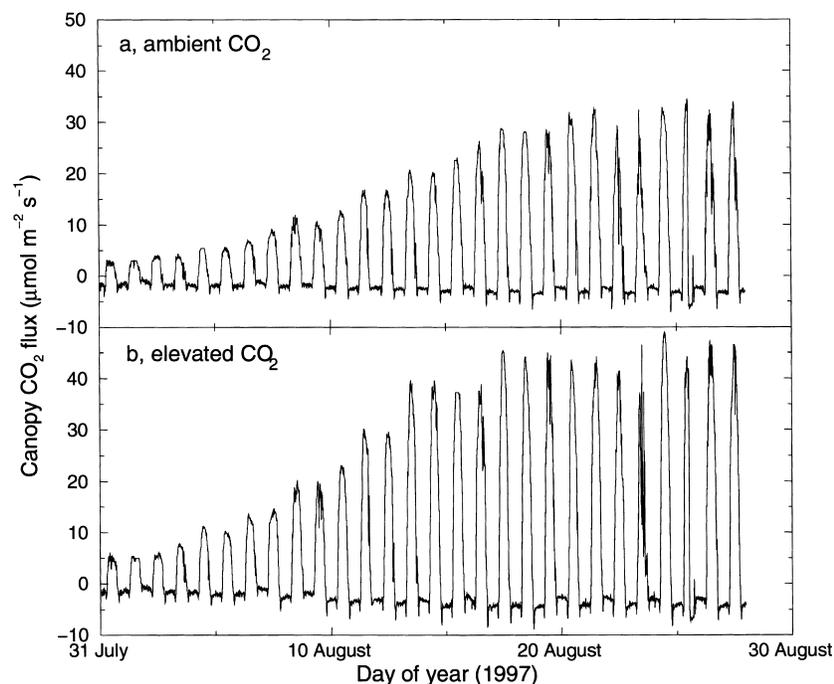


Fig. 3. Measured  $\text{CO}_2$  fluxes from 31 July to 27 August, 1997 at ambient  $\text{CO}_2$  (a) and elevated  $\text{CO}_2$  (b). Partially cloudy conditions prevailed on 9, 19, 16 and 24 August, 1997. Two EcoCELLs were completely covered with black sheets from 1200 to 1600, 26 August to measure daytime respiration.

yields ( $\phi_L$ ) 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  $\text{CO}_2$ . At elevated  $\text{CO}_2$ , the values of  $\phi_L$  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  $\phi_L$  values of middle leaves (Leaf 4 at ambient  $\text{CO}_2$  and Leaf 3 at elevated  $\text{CO}_2$ ) were slightly higher than those of lower and upper leaves. Analysis of variance (ANOVA), however, did not show significant difference in  $\phi_L$  between different leaf positions at either ambient ( $p=0.21$ ) or elevated  $\text{CO}_2$  ( $p=0.88$ ). Elevated  $\text{CO}_2$  resulted in an average of 24% higher  $\phi_L$  than ambient  $\text{CO}_2$ . The difference in  $\phi_L$  between the two  $\text{CO}_2$  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  $\text{CO}_2$ , 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  $\text{CO}_2$  treatments. At the early stage of canopy development, no substantial difference was observed between the two  $\text{CO}_2$  treatments. From 4 August, 1997 on, the canopy developed rapidly; and  $\text{CO}_2$  flux at elevated  $\text{CO}_2$  averaged 53% higher than that at ambient  $\text{CO}_2$ . Although this study lacks the statistical power to assert that the difference between the  $\text{CO}_2$  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  $\text{CO}_2$  treatments stimulated large differences in canopy carbon fluxes.

Within a single day, net canopy  $\text{CO}_2$  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

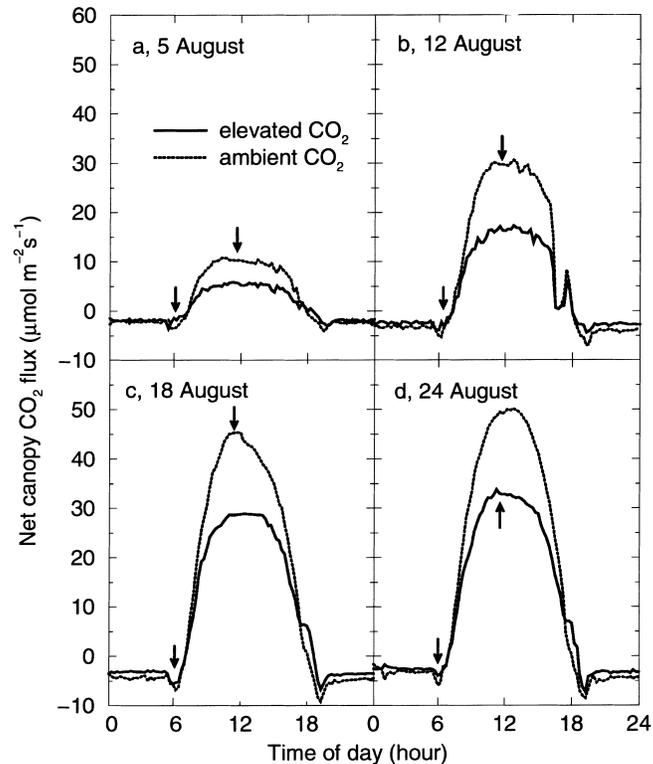


Fig. 4. Diurnal canopy  $\text{CO}_2$  fluxes measured at ambient  $\text{CO}_2$  (solid lines) and elevated  $\text{CO}_2$  (dotted lines) on (a) 5 August; (b) 12 August; (c) 18 August and (d) 24 August, 1997. High respiratory carbon release either in the early morning or late afternoon resulted from step changes between night ( $13^\circ\text{C}$ ) and day ( $28^\circ\text{C}$ ) temperature. The sudden decrease in net  $\text{CO}_2$  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,  $\text{CO}_2$  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  $\text{CO}_2$  fluxes changed from approximately  $6 \mu\text{mol m}^{-2} \text{s}^{-1}$  on 5 August to  $33 \mu\text{mol m}^{-2} \text{s}^{-1}$  on 24 August at ambient  $\text{CO}_2$  and from 11 to  $50 \mu\text{mol m}^{-2} \text{s}^{-1}$  at elevated  $\text{CO}_2$  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  $\text{CO}_2$ . The A/I curves derived from the four representative diurnal courses of  $\text{CO}_2$  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  $\phi_C$  and maximum photosynthetic capacity ( $P_g^*$ ). Data on 24 August, 1997, however, apparently deviated from equation 1 at both ambient and elevated  $\text{CO}_2$  (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  $\phi_C$  increased with canopy development, from  $0.024 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$  photon on 31 July, 1997 to  $0.072 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$  photon by the end of the experiment at ambient  $\text{CO}_2$  (Table 1).

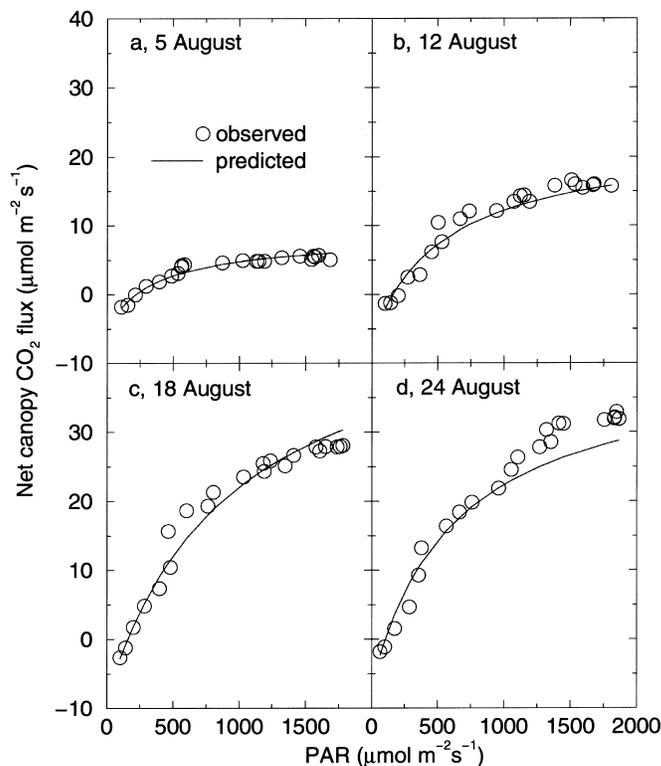


Fig. 5. Net canopy photosynthetic response to photosynthetically active radiation (PAR) on (a) 5 August; (b) 12 August; (c) 18 August and (d) 24 August, 1997 in ambient  $\text{CO}_2$ . Open circles represent observed  $\text{CO}_2$  fluxes, and the lines are the fitted A/I curves using the rectangular hyperbolic equation.

During the same period, the change in  $\phi_C$  was from 0.030 to 0.094  $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$  photon at elevated  $\text{CO}_2$ . Values of  $\phi_C$  were higher, on average of 28 points, by 31.5% at elevated  $\text{CO}_2$  than that at ambient  $\text{CO}_2$ . 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  $\text{CO}_2$  and 12.4 to 107.5  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$  at elevated  $\text{CO}_2$  (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  $\text{CO}_2$  and from 3.2 to 11.8  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$  at elevated  $\text{CO}_2$  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  $\phi_C$  and  $P_g^*$  are fairly sensitive to the estimates of daytime plant and soil respiration. In addition, we derived  $\phi_C$

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  $\text{CO}_2$  (Table 2). LAI was 0.66 on 5 August and 4.98 on 28 August, 1997 at elevated  $\text{CO}_2$ . There was very little difference in the total number of leaves between the two  $\text{CO}_2$  treatments (data not shown). This slight increase in canopy leaf area at elevated  $\text{CO}_2$  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  $\phi_C$  at both ambient and elevated  $\text{CO}_2$  treatments (Fig. 7). Canopy quantum yield ( $\phi_C$ ) increases with

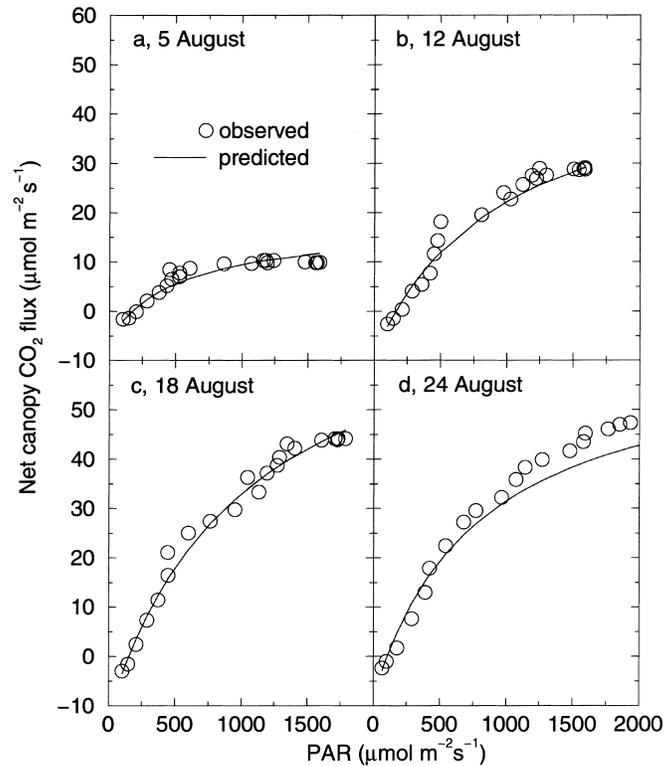


Fig. 6. Net canopy photosynthetic response to photosynthetically active radiation (PAR) on (a) 5 August; (b) 12 August; (c) 18 August; and (d) 24 August, 1997 in elevated CO<sub>2</sub>. Symbols are the same as in Fig. 5.

LAI and reached the values of leaf-level quantum yield ( $\phi_L$ ) at both ambient ( $\phi_L = 0.0542 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$ ) and elevated ( $\phi_L = 0.0671 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$ ) CO<sub>2</sub> treatments when LAI was approximately 1.5. When LAI approached 2.5–3.0,  $\phi_C$  gradually stabilized at  $0.073 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$  at ambient CO<sub>2</sub> and  $0.090 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$  at elevated CO<sub>2</sub>. 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  $\phi_C^*$  is the maximal value of  $\phi_C$ , we obtain  $a = 0.1137 \pm 0.0111$  (standard error) and  $\phi_C^* = 0.0829 \pm 0.0030$  at ambient CO<sub>2</sub>. At elevated CO<sub>2</sub>  $a = 0.1224 \pm 0.0099$  and  $\phi_C^* = 0.1129 \pm 0.0036$ . Statistical analysis indicated a significant difference in the  $\phi_C^*$  values between the two CO<sub>2</sub> treatment ( $p < 0.01$ ) but no significant difference in the  $a$  values between the CO<sub>2</sub> treatments ( $p > 0.10$ ).

### 3.5. Comparison among three models

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

Table 1

Values of parameters  $\phi_C$  (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  $\text{CO}_2$

Date	Ambient $\text{CO}_2$				Elevated $\text{CO}_2$			
	$\phi_C$	$P_g^*$	$R$	$r^2$	$\phi_C$	$P_g^*$	$R$	$r^2$
31 July	0.0239	12.43	4.97	0.892	0.0294	13.68	4.16	0.912
1 August	0.0230	10.60	4.40	0.947	0.0283	12.80	3.58	0.946
2 August	0.0229	11.19	3.46	0.929	0.0234	12.39	2.51	0.929
3 August	0.0261	12.59	4.82	0.970	0.0271	22.06	4.36	0.965
4 August	0.0314	12.63	5.04	0.914	0.0326	26.37	4.49	0.988
5 August	0.0376	13.40	5.08	0.970	0.0439	23.34	5.72	0.945
6 August	0.0359	16.57	5.33	0.972	0.0431	28.51	5.25	0.958
7 August	0.0302	21.28	3.96	0.916	0.0330	40.72	3.15	0.879
8 August	0.0381	22.53	5.54	0.918	0.0581	36.57	7.12	0.925
9 August	0.0470	19.31	4.96	0.964	0.0634	32.85	5.60	0.960
10 August	0.0480	24.41	6.33	0.932	0.0658	47.00	8.45	0.968
11 August	0.0534	27.40	6.73	0.928	0.0698	61.64	9.33	0.987
12 August	0.0522	29.17	6.50	0.935	0.0631	61.35	8.87	0.969
13 August	0.0510	37.72	7.18	0.990	0.0862	73.06	10.53	0.976
14 August	0.0501	40.38	7.00	0.988	0.0787	83.40	9.40	0.964
15 August	0.0616	41.46	8.18	0.983	0.0931	76.73	12.10	0.971
16 August	0.0583	39.29	6.20	0.940	0.0863	68.33	9.67	0.967
17 August	0.0607	54.71	9.02	0.930	0.0928	79.71	12.04	0.970
18 August	0.0633	59.54	8.60	0.991	0.0883	91.05	11.83	0.984
19 August	0.0752	55.41	9.47	0.985	0.0926	89.32	12.43	0.981
20 August	0.0760	35.79	6.69	0.963	0.0936	41.03	7.78	0.948
21 August	0.0690	53.62	8.53	0.977	0.0928	70.90	11.67	0.976
22 August	0.0725	39.76	7.05	0.965	0.0897	51.28	8.34	0.975
23 August	0.0708	37.02	9.30	0.882	0.0862	45.65	11.14	0.885
24 August	0.0751	47.67	6.80	0.955	0.0909	71.46	8.50	0.968
25 August	0.0727	73.23	8.74	0.977	0.0959	107.54	11.18	0.973
26 August	0.0734	55.66	6.69	0.876	0.0913	97.72	8.82	0.956
27 August	0.0716	41.73	9.12	0.946	0.0944	57.02	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  $\phi_C$  is the highest as irradiance  $I$  approaches zero.

#### 4. Discussion

This study indicates that canopy quantum yield ( $\phi_C$ ) 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  $\text{CO}_2$  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  $\text{CO}_2$ . This range of  $\phi_C$  is generally comparable to estimates provided by Ruimy et al. (1995), who found  $\phi_C$  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  $\phi_C$  values larger than 0.100  $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$  photon and 84 have  $\phi_C$  values less than 0.054, the value of leaf-level quantum yield ( $\phi_L$ ) at ambient  $\text{CO}_2$  found in this study. In addition, our results showed that  $\phi_C$  increased by 31.5% at elevated  $\text{CO}_2$  compared to that at ambient  $\text{CO}_2$ . The  $\text{CO}_2$ -induced increase in  $\phi_C$  is similar to the stimulation reported by Monje and Bugbee (1998). Their study showed that  $\text{CO}_2$ -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 CO<sub>2</sub> (mean ± standard error). *p* is the probability that LAI is significantly different between the two CO<sub>2</sub> treatments. 28 August, 1997 was the last harvesting day

Date	Ambient CO <sub>2</sub>	Elevated CO <sub>2</sub>	<i>p</i>
7 August	0.59 ± 0.05	0.66 ± 0.05	0.36
15 August	2.19 ± 0.16	2.46 ± 0.15	0.26
21 August	3.64 ± 0.60	4.21 ± 0.14	0.39
28 August	4.48 ± 0.61	4.98 ± 0.68	0.60

(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 CO<sub>2</sub> μmol<sup>-1</sup> photon in early morning or late afternoon to 0.011 μmol CO<sub>2</sub> μmol<sup>-1</sup> photon at noon at ambient CO<sub>2</sub>. At elevated CO<sub>2</sub>, CRUE varied from 0.030 μmol CO<sub>2</sub> μmol<sup>-1</sup> photon in the early morning or later afternoon to 0.018 μmol CO<sub>2</sub> μmol<sup>-1</sup> 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 ( $\phi_L$ ) 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  $\phi_L$  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  $\phi_L$  varied little during the development stage. Wang and Polglase (1995) suggested that estimates of  $\phi_L$  are similar for leaves throughout closed canopies. Long and Drake (1991) found  $\phi_L$  was remarkably uniform between replicates. On the other hand, there are several reports that  $\phi_L$  varied with canopy position and measurement time. Lai and Edwards (1995) found that  $\phi_L$  increased progressively from the basal section to the tip of the leaf of *Zea mays*. There was a significant decline in apparent  $\phi_L$  for both CO<sub>2</sub> 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  $\phi_L$  along canopy positions although  $\phi_L$  increased from the bottom to the middle position and declined toward the top of canopy at both CO<sub>2</sub> treatments.

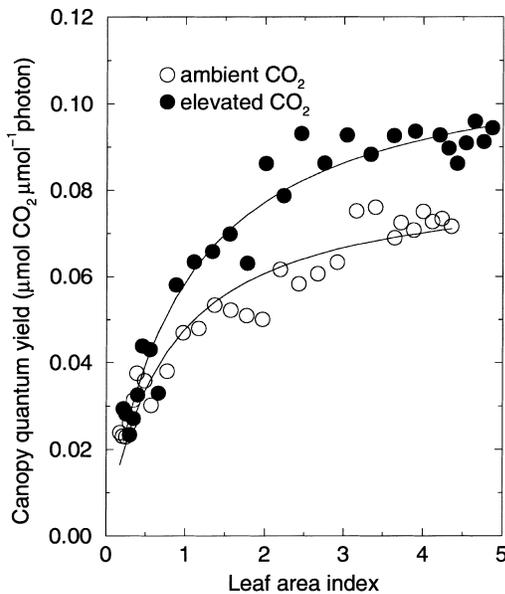


Fig. 7. Canopy quantum yield ( $\phi_C$ ) from 31 July to 27 August 1997 (Table 1) correlated with leaf area index (LAI). Circles represent observed  $\phi_C$  at ambient CO<sub>2</sub> (O) and elevated CO<sub>2</sub> (●) with nonlinear regression equation  $\phi_C = 0.0094 \text{ LAI} / (0.0829 + 0.1137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

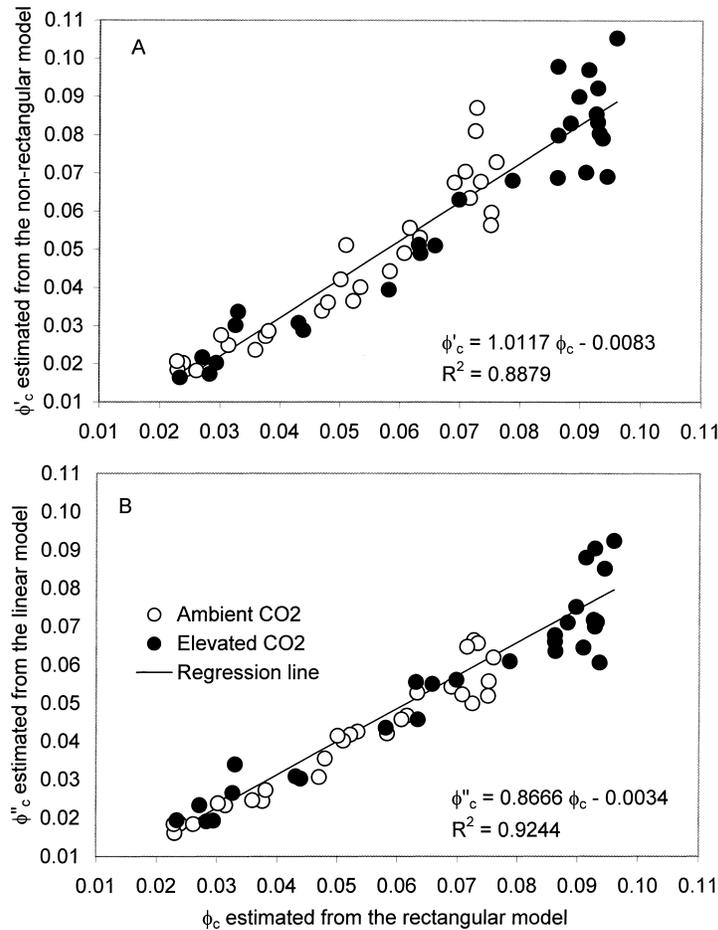


Fig. 8. Comparison of estimated canopy quantum yield among the rectangular hyperbolic, non-rectangular hyperbolic, and linear models. Circles represent quantum yield at ambient CO<sub>2</sub> (○) and elevated CO<sub>2</sub> (●). The rectangular hyperbolic model is the primary model used in this study.

It has generally been reported that  $\phi_L$  increases at elevated CO<sub>2</sub> (Chen and Sung, 1990; Teramura et al., 1990; Ziska et al., 1991; Eamus et al., 1993; Wang et al., 1995). However, a decrease of  $\phi_L$  in Siberian white birch and Japanese white birch was found by Koike et al. (1996) and no difference in  $\phi_L$  was reported by Delgado et al. (1994). Our results suggest that elevated CO<sub>2</sub> increased  $\phi_L$  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 ( $\phi_L$ ) 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  $\phi_C$  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

CO<sub>2</sub> compared with that at ambient CO<sub>2</sub> (0.0671 versus 0.0542 μmol CO<sub>2</sub> μmol<sup>-1</sup> photon). Canopy quantum yield strongly varied with canopy development, varying from 0.0229 to 0.0959 μmol CO<sub>2</sub> μmol<sup>-1</sup> photon over LAI changes from 0.5 to 5.0. CO<sub>2</sub> 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.

### Acknowledgements

The authors thank D. Schorran, E. Sotoodeh, V. Yturiaga, and W. Liu for technical support and two anonymous reviewers for useful suggestions. This study would not be possible without the conception and construction of EcoCELLs led by Dr. J.T. Ball. Preparation of this paper was partially supported by the NSF/DOE/NASA/USDA/EPA/NOAA Interagency Program on Terrestrial Ecology and Global Change (TECO) by DOE under DE-FG03-98ER62676 to YL.

### References

- Amthor, J.S., 1994. Scaling CO<sub>2</sub>-photosynthesis relationships from the leaf to the canopy. *Photosyn. Res.* 39, 353–359.
- Baker, N.R., McKiernan, M., 1988. Modifications to the photosynthetic apparatus of higher plants in response to changes in the light environment. *Biol. J. of the Linnean Society* 34, 193–203.
- Baldocchi, D., 1993. Scaling water vapor and carbon dioxide exchange from leaves to a canopy: Rules and tools. In: Ehleringer J.R., Field, C.B. (Eds.), *Scaling Physiological Processes: Leaf to Global*. Academic Press, London, pp 77–114.
- Campbell, G.S., Norman, J.M., 1998. *An Introduction to Environmental Biophysics*. 2nd ed. Springer, New York.
- Charles-Edwards, D.A., 1982. *Physiological Determinants of Crop Growth*. Academic Press, Sydney.
- Chen, J.J., Sung, J.M., 1990. Crop physiology and metabolism. Gas exchange rate and yield responses of virginia-type peanut to carbon dioxide enrichment. *Crop Sci.* 30, 1085–1089.
- Cheng, W., Sims, D.A., Luo, Y., Johnson, D.W., Ball, J.T., Coleman, J., 1999. Demonstration of Complete Carbon Budgeting in Plant-Soil Mesocosms under Elevated CO<sub>2</sub>: Locally Missing Carbon? *Global Change Biology* (in press).
- Delgado, E., Mitchell, R.A.C., Parry, M.A.J., Driscoll, S.P., Mitchell, V.J., Lawlor, D.W., 1994. Interacting effects of CO<sub>2</sub> concentration, temperature and nitrogen supply on the photosynthesis and composition of winter wheat leaves. *Plant, Cell and Environ.* 17, 1205–1213.
- de Pury, D.G.G., Farquhar, G.D., 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell and Environ.* 20, 537–557.
- Eamus, D., Berryman, C.A., Duff, G.A., 1993. Assimilation, stomatal conductance, specific leaf area and chlorophyll responses to elevated CO<sub>2</sub> of *Maranthus corymbosa*, a tropical monsoon rain forest species. *Austr. J. Plant Physiol.* 20, 741–755.
- Ehleringer, J.R., 1978. Implications of quantum yield differences on the distributions of C<sub>3</sub> and C<sub>4</sub> grasses. *Oecologia* 31, 255–267.
- Ehleringer, J.R., Björkman, O., 1977. Quantum yield for CO<sub>2</sub> uptake in C<sub>3</sub> and C<sub>4</sub> plants. *Plant Physiol.* 59, 86–90.
- Ehleringer, J.R., Cerling, T.E., Helliker, B.R., 1997. C<sub>4</sub> photosynthesis, atmospheric CO<sub>2</sub>, and climate. *Oecologia* 112, 285–299.
- Ehleringer, J.R., Pearcy, R.W., 1983. Variation in quantum yield for CO<sub>2</sub> uptake among C<sub>3</sub> and C<sub>4</sub> plants. *Plant Physiol.* 73, 555–559.
- Emerson, R., 1958. The quantum yield of photosynthesis. *Annu. Rev. Plant Physiol.* 9, 1–4.
- Farquhar, G.D., von Caemmerer, S., 1982. Modelling of photosynthetic response to environmental conditions. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), *Physiological Plant Ecology II*. (Encyclopedia of Plant Physiology, NS, vol. 12B). Springer, Berlin New York, pp 549–587.
- Farquhar, G.D., von Caemmerer, S., Berry, J.A., 1980. A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* 149, 78–90.
- Field, C.B., Ball, J.T., Berry, J.A., 1991. Photosynthesis: Principles and field techniques. In: Pearcy, R.W., Ehleringer, J.R., Mooney, H.A., Rundel, P.W. (Eds.), *Plant Physiological Ecology: Field Methods and Instrumentation*. Chapman & Hall London, pp 209–253.
- Griffin, K.L., Ross, P.D., Sims, D.A., Luo, Y., Seemann, J.R., Fox, C.A., Ball, J.T., 1996. EcoCELLs: Tools for mesocosm scale measurements of gas exchange. *Plant Cell and Environ.* 19, 1210–1221.
- Harley, P.C., Thomas, R.B., Reynolds, J.F., Strain, B.R., 1992. Modelling photosynthesis of cotton grown in elevated CO<sub>2</sub>. *Plant, Cell and Environ.* 15, 271–282.
- Hirose, T., Ackerly, D.D., Traw, M.B., Ramseier, D., Bazzaz, F.A., 1997. CO<sub>2</sub> elevation, canopy photosynthesis, and optimal leaf area index. *Ecology* 78, 2339–2350.
- Hui, D., Luo, Y., Cheng, W., Coleman, J.S., Johnson, D.W., Sims, D.A., 1999. Canopy radiation and water use efficiencies of as affected by elevated [CO<sub>2</sub>]. *Global Change Biology* (submitted).
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54, 187–211.
- Kaharabata, S.K., Schuepp, P.H., Ogunjemiyo, S., Shen, S., Leclerc, M.Y., Desjardins, R.L., MacPherson, J.I., 1997.

- Footprint consideration in BOREAS. *J. Geophys. Res.* 102, 29113–29124.
- Kirschbaum, M.U.F., Farquhar, G.D., 1987. Investigation of the CO<sub>2</sub> dependence of quantum yield and respiration in *Eucalyptus pauciflora*. *Plant Physiol.* 83, 1032–1036.
- Koike, T., Lei, T.T., Maximov, T.C., Tabuchi, R., Takahashi, K., Ivanov, B.I., 1996. Comparison of the photosynthetic capacity of Siberian and Japanese birch seedlings growth in elevated CO<sub>2</sub> and temperature. *Tree Physiol.* 16, 381–385.
- Ku, S.B., Edwards, G.E., 1978. Oxygen inhibition of photosynthesis. III. Temperature dependence of quantum yield and its relation to O<sub>2</sub>/CO<sub>2</sub> solubility ratio. *Planta* 140, 1–6.
- Kubiske, M.E., Pregitzer, K.S., 1996. Effects of elevated CO<sub>2</sub> and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiol.* 16, 351–358.
- Lai, A., Edwards, G.E., 1995. Maximum quantum yields of O<sub>2</sub> evolution in C<sub>4</sub> plants under high CO<sub>2</sub>. *Plant Cell Physiol.* 36, 1311–1317.
- Lawlor, D.W., 1995. Photosynthesis, productivity and environment. *J. Exp. Bot.* 46, 1449–1461.
- Lee, X.H., 1997. On micrometeorological observation of surface-air exchange over tall vegetation. *Agric. For. Meteorol.* 91, 39–49.
- Long, S.P., Drake, B.G., 1991. Effect of the long-term elevation of CO<sub>2</sub> concentration in the field on the quantum yield of photosynthesis of the C<sub>3</sub> sedge, *Scirpus olneyi*. *Plant Physiol.* 96, 221–226.
- McNaughton, K.G., 1994. Effective stomatal and boundary-layer resistances of heterogeneous surfaces. *Plant, Cell and Environ.* 17, 1061–1068.
- Medlyn, B.E., 1998. Physiological basis of the light use efficiency model. *Tree Physiol.* 18, 167–176.
- Monje, O., Bugbee, B., 1998. Adaption to high CO<sub>2</sub> concentration in an optimal environment: Radiation capture, canopy quantum yield and carbon use efficiency. *Plant, Cell and Environ.* 21, 315–324.
- Nilsen, E., Sharifi, M.R., 1994. Seasonal acclimation of stem photosynthesis in woody legume species from the Mojave and Sonoran Deserts of California. *Plant Physiol.* 105, 1385–1391.
- Norman, J.M., 1993. Scaling processes between leaf and canopy levels. In: Ehleringer J.R., Field, C.B. (Eds.), *Scaling Physiological Processes: Leaf to Global*. Academic Press, London, pp. 41–76.
- Raupach, M.R., Finnigan, J.J., 1988. Single-layer models of evaporation from plant canopies are incorrect but useful, whereas multilayer models are correct but useless: Discuss. *Austr. J. Plant Physiol.* 15, 705–716.
- Reich, P.B., Ellsworth, D.S., Kloeppel, B.D., Fownes, J.H., Gower, S.T., 1990. Vertical variation in canopy structure and CO<sub>2</sub> exchange of oak–maple forests: influence of ozone, nitrogen, and other factors on simulated canopy carbon gain. *Tree Physiol.* 7, 329–345.
- Ruimy, A., Jarvis, P.G., Baldocchi, D.D., Saugier, B., 1995. CO<sub>2</sub> fluxes over plant canopies and solar radiation: A review. *Adv. Ecol. Res.* 26, 1–68.
- Sims, D.A., Cheng, W., Luo, Y., Seemann, J.R., 1999. Photosynthetic acclimation to elevated CO<sub>2</sub> in a sunflower canopy. *J. Exp. Bot.* 50, 645–653.
- Stirling, C.M., Nie, G.Y., Aguilera, C., Nugawela, A., Long, S.P., Baker, N.R., 1991. Photosynthetic productivity of an immature maize crop: changes in quantum yield of CO<sub>2</sub> assimilation conversion efficiency and thylakoid proteins. *Plant, Cell and Environ.* 14, 947–954.
- Teramura, A.H., Sullivan, J.H., Ziska, L.H., 1990. Interaction of elevated ultraviolet-B radiation and CO<sub>2</sub> on productivity and photosynthetic characteristics in wheat, rice and soybean. *Plant Physiol.* 94, 470–475.
- Wang, K., Kellomaki, S., Laitinen, K., 1995. Effects of needle age long-term temperature and CO<sub>2</sub> treatments on the photosynthesis of Scots pine. *Tree Physiol.* 15, 211–218.
- Wang, Y.P., Polglase, P.J., 1995. Carbon balance in the tundra, boreal forest and humid tropical forest during climate change: Scaling up from leaf physiology and soil carbon dynamics. *Plant, Cell and Environ.* 18, 1226–1244.
- Waring, R.H., Law, B.E., Goulden, M.L., Bassow, S.L., McCreight, R.W., Wofsy, S.C., Bazzaz, F.A., 1995. Scaling gross ecosystem production at Harvard Forest with remote sensing: A comparison of estimates from a constrained quantum use efficiency model and eddy correlation. *Plant, Cell and Environ.* 18, 1201–1213.
- Webber, A.N., Baker, N.R., Platt-Aloia, K., Thomson, W.W., 1984. Appearance of a state 1-state 2 transition during chloroplast development in the wheat leaf: Energetic and structural considerations. *Physiol. Plant* 60, 171–179.
- Whitehead, D., Hinckley, T.M., 1991. Models of water flux through forest stands: Critical leaf and stand parameters. *Tree Physiol.* 9, 35–57.
- Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.M., Bakwin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A., 1993. Exchange of CO<sub>2</sub> in a mid-latitude forest. *Science* 260, 1314–1317.
- Ziska, L.H., Hongan, K.P., Smith, A.P., Drake, B.G., 1991. Growth and photosynthetic responses of nine tropical species with long term exposure to elevated carbon dioxide. *Oecologia* 86, 383–389.