Effect of the Long-Term Elevation of CO₂ Concentration in the Field on the Quantum Yield of Photosynthesis of the C₃ Sedge, Scirpus olneyi¹

Stephen P. Long* and Bert G. Drake

Department of Biology, University of Essex, Colchester, CO4 3SQ, United Kingdom (S.P.L.), and Smithsonian Environmental Research Center, Edgewater, Maryland 21037 (B.G.D.)

ABSTRACT

CO₂ concentration was elevated throughout 3 years around stands of the C₃ sedge Scirpus olneyi on a tidal marsh of the Chesapeake Bay. The hypothesis that tissues developed in an elevated CO₂ atmosphere will show an acclimatory decrease in photosynthetic capacity under light-limiting conditions was examined. The absorbed light quantum yield of CO₂ uptake (ϕₘₐₓ) and the efficiency of photosystem II photochemistry were determined for plants which had developed in open top chambers with CO₂ concentrations in air of 680 micromoles per mole, and of 351 micromoles per mole as controls. An Ulbricht sphere cuvette incorporated into an open gas exchange system was used to determine ϕₘₐₓ and a portable chlorophyll fluorimeter was used to estimate the photosynthetic efficiency of photosystem II. When measured in an atmosphere with 10 millimoles per mole CO₂ to suppress photorespiration, shoots showed a ϕₘₐₓ of 0.093 ± 0.003, with no statistically significant difference between shoots grown in elevated or control CO₂ concentrations. Efficiency of photosystem II photochemistry was also unchanged by development in an elevated CO₂ atmosphere. Shoots grown and measured in 680 micromoles per mole of CO₂ in air showed a ϕₘₐₓ of 0.078 ± 0.004 compared with 0.065 ± 0.003 for leaves grown and measured in 351 micromoles per mole CO₂ in air; a highly significant increase. In accordance with the change in ϕₘₐₓ, the light compensation point of photosynthesis decreased from 51 ± 3 to 31 ± 3 micromoles per square meter per second for stems grown and measured in 351 and 680 micromoles per mole of CO₂ in air, respectively. The results suggest that even after 3 years of growth in elevated CO₂, there is no evidence of acclimation in capacity for photosynthesis under light-limiting conditions which would counteract the stimulation of photosynthetic CO₂ uptake otherwise expected through decreased photorespiration.

Temporary elevation of c₄² around the leaf of a C₃ plant

¹ Supported by a U.S. Department of Energy Project grant to B.D.G. at the Smithsonian Environmental Research Center and by a Visiting Research Fellowship to S.P.L. from the Smithsonian Institution, Washington, DC.

² Abbreviations: c₄, the concentration of CO₂ in the ambient air (μmol mol⁻¹); A, rate of CO₂ uptake per unit of projected area of stem (μmol m⁻² s⁻¹); RuBP, ribulose-1,5-bisphosphate; Aₘₐₓ, A at light saturation (μmol m⁻² s⁻¹); Q, photosynthetically active photon flux (μmol m⁻² s⁻¹); Qₘₐₓ, Q absorbed per unit of projected stem area; ϕₘₐₓ, the maximum quantum yield, i.e. ratio of CO₂ molecules absorbed per photon absorbed; Qₑ, Q on the wall of the Ulbricht sphere; Fᵥ, variable component of Fₘₐₓ; Fₘₐₓ, maximum emission of PSI chlorophyll fluorescence (arbitrary units); LCP, the light compensation point of photosynthesis (μmol m⁻² s⁻¹); Aₘₐₓ, daily integral of net canopy photosynthetic CO₂ uptake (mol m⁻² d⁻¹); Qₙₑ, the photon flux accumulated over 1 d (mol m⁻² d⁻¹); h, time between sunrise and sunset (s d⁻¹); k, canopy or foliar light extinction coefficient (dimensionless); R, dark respiration rate per unit of projected area of stem (μmol m⁻² s⁻¹); s, stem area index, i.e. stem surface area overlying a unit of ground area (dimensionless); φₑ, the absorbance of the stem surface, i.e. the ratio of the absorbed flux to the incident flux (dimensionless).
of the response of A to \( Q_{obs} \) avoiding any subtle changes in linearity (24). Changes in surface absorbance will alter the quantum yield on an incident photon flux basis. To separate absorbance changes from changes in the efficiency of photosynthesis, \( Q_{obs} \) should be determined simultaneously with CO₂ uptake. A gas exchange cuvette incorporated into an integrating sphere enables such simultaneous measurements of A and \( Q_{obs} \) (15).

Quantum yield calculated on an absorbed light basis (\( \phi_{abs} \)) is a function of (a) the efficiency of energy transduction into NADPH and ATP on the photosynthetic membrane and (b) the metabolic pathways in which this reducing and phosphorylating potential is utilized. Both of these characters show remarkable consistency within C₃ plants, a factor possibly reflected in the low interspecific variability in \( \phi_{abs} \) within a photosynthetic type. At current atmospheric CO₂ concentrations, healthy C₃ plants show a \( \phi_{abs} \) of approximately 0.055 at 30°C. In an atmosphere of 1% O₂, \( \phi_{abs} \) increases to 0.08 to 0.09 because of the inhibition of photorespiratory metabolism (4, 12, 20). In an atmosphere with an elevated CO₂ concentration, quantum yield would be expected to rise in proportion to the increase in the ratio of carboxylations of RuBP to oxygenations (13). This will be determined by the ratio of substrate concentrations (CO₂/O₂), and the \( V_{max} \) and \( K_m \) values for oxygenation and carboxylation (13). Because a change in the ratios of these kinetic constants would require a change within the structure of the enzyme, any adaptation to elevated CO₂ would seem unlikely. However, although \( \phi_{abs} \) is remarkably constant among healthy leaves of different species grown in controlled environments (4), leaves in suboptimal conditions in the field can show lower values of \( \phi_{abs} \) (3). Baker et al. (3) enumerated several potential causes of decreases in \( \phi_{abs} \) through changes in the composition and organization of the photosynthetic membrane induced by environmental perturbation. Marked heterogeneity of stomatal opening, induced by environmental treatments, can also produce apparent decreases in \( \phi_{abs} \) (26). Furthermore, CO₂ concentration has been shown to modulate protein biosynthesis in photosynthetic cells (2). Thus, the possibility of change in photosynthetic capacity and \( \phi_{abs} \) under light-limiting conditions, induced by development in elevated CO₂ atmospheres, cannot be dismissed.

The objective of this study was to determine whether in situ elevation of the CO₂ concentration to 680 \( \mu \)mol mol⁻¹ around natural stands of the C₃ sedge Scirpus olneyi Gray (8) for 3 years resulted in acclimation of the maximum quantum yield of photosynthesis. This was assessed by measurement of \( \phi_{abs} \) and the efficiency of PSIII photochemistry.

**MATERIALS AND METHODS**

**Plant Material**

As part of a long-term investigation of the effects of elevated CO₂ on vegetation of a tidal marsh, 30 open-top chambers were placed within the boundary of three mesohaline marsh community types of the Rhode River, a subestuary of the Chesapeake Bay in eastern Maryland (7). Via a computer-controlled system, \( c_c \) in one-half of these chambers has been maintained at 680 ± 3 \( \mu \)mol mol⁻¹ for the complete growing seasons of the past 3 years (11). The remaining chambers were maintained at \( c_c \) 351 ± 1.3 \( \mu \)mol mol⁻¹ to provide controls for the modification of plant microclimate produced by the presence of the chamber. Ten of these chambers are within a large monotypic stand of the C₃ sedge Scirpus olneyi. Plants in these chambers were used in the current investigation. The only photosynthetic organ of this species is its triangular stem. For the determination of \( \phi_{abs} \), mature stems were selected at random from within the open-top chambers, cut close to their base under distilled water, and immediately transferred to the assimilation chamber in a field laboratory adjacent to the site.

Measurements of chlorophyll fluorescence were made *in situ*.

A leaf chamber developed from the design of Ireland et al. (15) was incorporated into an open gas exchange system. The chamber was as described previously, except in the following aspects: (a) the sphere was constructed from aluminum to allow improved temperature control, (b) glass windows faced the inner gas exchange cuvette, (c) a 7.4-cm diameter and 4-mm thick white Teflon disc was placed below the light pipe to improve scattering of radiation on entry into the sphere, and (d) a paddle fan bridging the gas inlet and outlet was used to recirculate air within the chamber and raise the boundary layer conductance. The efficiency of diffusion of light within the sphere and the \( \alpha \) of the sphere was determined with a black absorber 10 cm × 5 mm, simulating a linear leaf or stem. The absorber was made by spraying a strip of paper with three coats of nonreflective black paint (Ultra Flat Black Lacquer, 32N282, Newark Electronics, Chicago, IL). The absorbance of the coated paper was determined at 0.952 using a Taylor integrating sphere (LI-1800–12, Li-Cor Inc., Lincoln, NE) following the procedure of Rackham and Wilson (21). When the absorber was turned through 360 degrees in 15-degree steps, the measured decrease in photon flux within the chamber varied by 4%, indicating a largely homogeneous distribution of light. The mean \( \alpha \) of the sphere surfaces was determined at 0.124 by the method of Idle and Proctor (14).

The quantum yield of each stem, 10 from each of the two growth treatments, was determined in three different gas mixtures: (a) air containing 351 \( \mu \)mol mol⁻¹ of CO₂ and 21 mmol mol⁻¹ O₂ to represent current atmospheric conditions and the control CO₂ growth environment, (b) 680 \( \mu \)mol mol⁻¹ CO₂ and 21 mmol mol⁻¹ of O₂ in air to simulate the predicted “doubled CO₂” atmosphere used in the elevated CO₂ growth environment, and (c) 351 \( \mu \)mol mol⁻¹ CO₂ and 1 mmol mol⁻¹ O₂ in air to provide an atmosphere in which photorespiration would be almost fully suppressed. Nitrogen provided the balance of these mixtures, supplied as compressed gases (Air Products Inc., Tamaqua, PA). The flow of dry gas from the cylinders to the leaf chamber was monitored with a mass flowmeter (type H-1K, Matheson Gas Products, East Rutherford, NJ), previously calibrated against a bubble flowmeter (16). Prior to entry into the chamber the air was humidified over distilled water at approximately 25°C. Air leaving the chamber was dried over anhydrous magnesium perchlorate (16) before entering the infrared gas analyzer. The change in CO₂ concentration across the chamber and the absolute CO₂ concentration were measured with a two-channel infrared gas analyzer (Binos 2, Leybold-Heraeus, Hanau, FRG), calibrated against mixtures of CO₂ in air retained in aluminum cylinders.
which had been previously cross-calibrated against a gravimetrically prepared CO\textsubscript{2} standard, traceable to a National Bureau of Standards reference (Matheson Gas Products, East Rutherford, NJ). \(Q_{abs}\) was determined with a miniature quantum sensor (QS 1, Delta-T Devices, Burwell, United Kingdom) which was cross-calibrated against a solarimeter (Precision Spectral Pyranometer, Eppley Lab, Inc., Newport, RI) in diffuse daylight using the conversion factors of Anderson (1). The quantum sensor was also cross-checked in daylight against a second quantum sensor (LI-191, Li-Cor) which had just been recalibrated by the manufacturer. The two were found to agree over a range of light levels to within ±1.0%. Light fluxes within the sphere (\(Q_{abs}\)) in the range of 0 to 250 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) were obtained by interposing neutral density filters between the quartz iodide source and light pipe entering the sphere. The quantity of light absorbed by the portion of stem within the chamber was determined as described previously (14). Stem surface temperature was 28°C ± 1.5°C for all measurements of \(\phi_{abs}\). The projected stem surface area was determined with an area meter (LI-3100, LI-Cor). To determine \(\phi_{abs}\) for any one stem in any one measuring gas composition, \(A\) was determined at 10 values of \(Q_{abs}\) from 5 to 200 \(\mu\)mol m\(^{-2}\) s\(^{-1}\). Within this range, the slope \(dA/dQ_{abs}\) was constant but began to decline above 200 \(\mu\)mol m\(^{-2}\) s\(^{-1}\). An averaged \(\phi_{abs}\) for each replicate was determined as the slope of the line (e.g. Fig. 1) fitted by least squares linear regression analysis of \(A\) to \(Q_{abs}\) between 0 and 200 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) (25). Linearity over this range was indicated by the high \(r^2\) values which exceeded 0.98 in all cases. Differences between the mean \(\phi_{abs}\) for stems from the two growth environments and for the three measuring gas compositions were analyzed by two-way analysis of variance and individual means were compared with an minimum statistically significant difference between two means calculated from Student’s \(t\) distribution (\(P = 0.05\)). Application of Bartlett’s homogeneity of variance statistic showed no significant differences between sample variances (\(P > 0.05\)), suggesting that application of a parametric analysis of variance was valid (25).

**Photochemical Efficiency of PSII**

The maximal quantum yield of photochemistry at PSII is proportional to the ratio of \(F_a\) and \(F_m\) of dark-adapted tissue (5). This interpretation assumes that PSII is fully oxidized at the point of addition of saturating light to induce the rise in fluorescence to \(F_a\). Induction of fluorescence emission was measured in situ on 20 stems from five control and 20 stems from five elevated CO\textsubscript{2} open-top chambers, using a portable fluorimeter (type PSM, BioMonitor S.C.I. AB, Malmo, Sweden). Measurements were made between 30 min and 1 h after sunset, to ensure that any short-term reductions in \(F_a/F_m\), that might result from exposure to high light during the day (5) would be removed. After 10 min of dark adaptation, the stem was excited with light of 400 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) and the kinetics of chlorophyll fluorescence monitored over the subsequent 10 s. Differences in mean \(F_a/F_m\) between the two growth treatments were tested by Student’s \(t\) test. For both populations, examination of graphical plots of ranked normal derivatives (rankits) against \(F_a/F_m\) revealed no systematic deviation from the rankit line, suggesting that the assumption of normal frequency distributions of \(F_a/F_m\) over the range of values examined here, was valid (25). The period of dark adaptation and the excitation flux used were chosen after preliminary measurements. Using a range of dark adaptation periods and excitation light levels, we found that these measurements showed no significant increase in \(F_a/F_m\) after 10 min of dark adaptation or with an increase in the photon flux density of the actinic excitation beam above 400 \(\mu\)mol m\(^{-2}\) s\(^{-1}\).

**RESULTS**

The response of CO\textsubscript{2} uptake to absorbed photon flux (\(Q_{abs}\)) was linear up to approximately 200 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) for all measuring gas compositions (Fig. 1). Although no attempt was made to select stems of uniform age or developmental stage, \(\phi_{abs}\) was remarkably uniform between replicates, with SE values ranging from 4.2 to 7.3% of the means (Fig. 2). Figure 1 illustrates that, for one stem from each of the chamber types, the slope of the response of \(A\) to \(Q_{abs}\) appears unaffected by whether the stem developed in a control or an elevated CO\textsubscript{2} environment. The slope is strongly influenced by the gas composition of the measuring atmosphere. This lack of influence of the growth environment on \(\phi_{abs}\) is con-
firmed when the samples as a whole are considered. The mean \( \phi_{\text{abs}} \) of the 10 stems developed in the control chambers and measured in an atmosphere of 21% \( \text{O}_2 \) and 351 \( \mu \text{mol m}^{-1} \) \( \text{CO}_2 \) was 0.065 ± 0.003. An increase in \( \text{CO}_2 \) concentration to 680 \( \mu \text{mol m}^{-1} \) increased \( \phi_{\text{abs}} \) to 0.080 ± 0.004, whereas a decrease in \( \text{O}_2 \) concentration to 1% to eliminate photorespiration increased \( \phi_{\text{abs}} \) to 0.093 ± 0.003 (Fig. 2). The difference in mean \( \phi_{\text{abs}} \) between the three measurement gas mixtures was highly significant \( (F = 26.26) \). Although mean \( \phi_{\text{abs}} \) values for plants grown in the elevated \( \text{CO}_2 \) chambers were slightly lower (Fig. 2) than those for plants grown in the control chambers, when both were measured in the same gas mixture, these differences were not statistically significant \( (F = 1.18) \) nor was there any significant interaction between the \( \text{CO}_2 \) concentration of the growth environment and the composition of the measurement gas mixture \( (F = 1.75) \). The key comparison is between stems that had developed in and were measured in 351 \( \mu \text{mol m}^{-1} \) \( \text{CO}_2 \) with those developed and measured in 680 \( \mu \text{mol m}^{-1} \) \( \text{CO}_2 \). Here, elevated \( \text{CO}_2 \) is seen to lead to a statistically significant increase in \( \phi_{\text{abs}} \) of 20%, from 0.065 ± 0.003 to 0.078 ± 0.004 (minimum statistically significant difference between two means = 0.008, \( P = 0.05 \)). The absorbance calculated from the projected areas were 0.85 ± 0.02 and 0.84 ± 0.02 for stems developed in control and elevated \( \text{CO}_2 \) chambers, respectively. This indicates that quantum yield on an incident light basis would be increased in direct proportion with \( \phi_{\text{abs}} \).

It follows that, if \( \phi_{\text{abs}} \) is increased for plants grown and measured in \( c_\text{a} = 680 \mu \text{mol m}^{-1} \) \( \text{CO}_2 \), but respiration is unchanged, then the LCP of photosynthesis should decrease, as indicated in Fig. 1. LCP for stems grown and measured at \( c_\text{a} = 680 \mu \text{mol m}^{-1} \) \( \text{CO}_2 \) was 31 ± 3 \( \mu \text{mol m}^{-2} \text{~s}^{-1} \) compared to 51 ± 3 \( \mu \text{mol m}^{-2} \text{~s}^{-1} \) for stems grown and measured at \( c_\text{a} = 351 \mu \text{mol m}^{-1} \) \( \text{CO}_2 \) (Fig. 3). As in the case of \( \phi_{\text{abs}} \), LCP showed a highly significant difference between the measuring gas mixtures \( (F = 55.5) \) but no significant difference between the growth \( \text{CO}_2 \) concentrations \( (F = 0.85) \).

When \( \phi_{\text{abs}} \) was determined in a decreased \( \text{O}_2 \) concentration (10 \( \mu \text{mol m}^{-1} \)), \( \phi_{\text{abs}} \) was almost identical regardless of whether the stems were grown in control or in elevated \( \text{CO}_2 \).
chambers (Figs. 1 and 2). This suggests that, under conditions in which photorespiration is virtually eliminated, there is no difference in the maximum efficiency with which these stems utilize absorbed photons in maximum efficiency. This lack of difference in \( \phi_{\text{abs}} \) is paralleled by the observation that \( F_0/F_\infty \) was 0.851 ± 0.004 for plants grown in elevated CO\(_2\) chambers and 0.846 ± 0.004 for plants growing in control chambers, suggesting that the maximum quantum yield of PSII photochemistry was also unchanged.

**DISCUSSION**

Björkman and Demmag (4), in a survey of a range of vascular plants, showed a mean absorbed light quantum yield for \( O_2 \) evolution of 0.105 measured in approximately 10 mmol mol\(^{-1}\) CO\(_2\). Given the fact that some of the products of non-cyclic electron transport will be used in processes other than CO\(_2\) fixation, a lower \( \phi_{\text{abs}} \) for CO\(_2\) uptake would be expected. When the CO\(_2\) concentration was lowered to 10 mmol mol\(^{-1}\) to inhibit photorespiration, \( \phi_{\text{abs}} \) was 0.093. Although approximately 12% less than the value suggested for \( O_2 \) evolution (4), it is among the highest values of \( \phi_{\text{abs}} \) that have been determined (19, 24). These values suggest that the features of organization and composition of the photosynthetic apparatus which are critical to the efficiency of photosynthesis under light-limiting conditions are unaffected by development in an elevated CO\(_2\) atmosphere in the field.

A number of studies have suggested that growth in elevated CO\(_2\) can lead to an acclimatory decrease in photosynthetic capacity (reviewed in Ref. 17). The results show that, despite 3 years of growth in elevated CO\(_2\), there is no evidence of acclimation with respect to either the maximum quantum yield of CO\(_2\) assimilation or the quantum yield of photochemistry at PSII inferred from chlorophyll fluorescence. In the absence of any significant acclimation, \( \phi_{\text{abs}} \) would be expected to benefit fully from the potential decrease in photorespiration with elevation of \( c_s \). This is clearly evident when plants grown and measured at \( c_s = 351 \) μmol mol\(^{-1}\) are compared to those grown and measured at \( c_s = 680 \) μmol mol\(^{-1}\) (Fig. 2). What significance might these increases in \( \phi_{\text{abs}} \) have to plants in the doubled CO\(_2\) environment predicted for the next century?

Charles-Edwards (6) suggested a simple equation for examining the consequences of change in leaf photosynthetic parameters to canopy CO\(_2\) uptake. This is adapted here for use with photon flux and \( \phi_{\text{abs}} \) (Eq. 1). This equation assumes a rectangular hyperbolic response of the rate of CO\(_2\) uptake to photon flux over the full range of light levels, an exponential decline in light with depth into the canopy, and a diurnal course of incident photon flux described by a sine function:

\[
A_{\text{tot}} = \frac{\alpha\phi_{\text{abs}}Q_{\text{tot}}h(A_{\text{sat}} + R(1 - e^{-\alpha t}))}{k\alpha\phi_{\text{abs}}Q_{\text{tot}} + h(A_{\text{sat}} + R)} - 8.64 \times 10^4 (Rt)
\]

where terms are as defined previously\(^2\) and 8.64 \times 10\(^4\) is the number of seconds in a day.

Table I gives the values for \( A_{\text{tot}} \) calculated from Equation 1 using \( A_{\text{sat}} \) and \( s \) determined for plants in the control and elevated CO\(_2\) chambers during June 1988 (29). Values of \( \phi_{\text{abs}} \) and \( \alpha \) were as determined in this study. In a previous year, the loss of light from the top to the base of this community canopy in June, \( i.e. \) the proportion of incident light absorbed determined at 0.80 (27). Combining this with the values of \( s \) determined in June 1988 (9) would give a \( k \) of 0.27 (6). There was no significant difference in stem respiration between the two growth treatments, which averaged 1.17 μmol m\(^{-2}\) s\(^{-1}\) (calculated from data in Ref. 10). On June 12, 1988, \( Q_{\text{tot}} \) at the site was 58.9 mol m\(^{-2}\) s\(^{-1}\) during the 15.5 h of daylight and the temperature was 29.5\(^\circ\)C (9), \( i.e. \) close to the temperature at which \( \phi_{\text{abs}} \) was measured in this study. Substituting these values into Equation 1 yields \( A_{\text{tot}} \) = 0.63 and 1.06 mol m\(^{-2}\) s\(^{-1}\) for the control and elevated CO\(_2\) chambers, respectively, on June 12 (Table I). These values are remarkably close to those measured for these whole canopies on the same day (9). Given the many assumptions implicit in Equation 1, the close agreement of predicted and measured values is clearly fortuitous; however, it does suggest that the model correctly indicates the proportionate change in \( A_{\text{tot}} \) with

<table>
<thead>
<tr>
<th>( c_s ) (μmol mol(^{-1}))</th>
<th>351</th>
<th>680</th>
<th>680</th>
<th>351</th>
<th>680</th>
</tr>
</thead>
<tbody>
<tr>
<td>( k ) (dimensionless)*</td>
<td>0.27</td>
<td>0.27</td>
<td>0.27</td>
<td>0.27</td>
<td>0.27</td>
</tr>
<tr>
<td>( \alpha ) (dimensionless)*</td>
<td>0.85</td>
<td>0.85</td>
<td>0.85</td>
<td>0.85</td>
<td>0.85</td>
</tr>
<tr>
<td>( \phi_{\text{abs}} ) (dimensionless)*</td>
<td>0.065</td>
<td>0.078</td>
<td>0.065</td>
<td>0.065</td>
<td>0.078</td>
</tr>
<tr>
<td>( A_{\text{sat}} ) (μmol m(^{-2}) s(^{-1})) (29)</td>
<td>12.5</td>
<td>19.8</td>
<td>19.8</td>
<td>12.5</td>
<td>19.8</td>
</tr>
<tr>
<td>( s ) (dimensionless) (9)</td>
<td>5.93</td>
<td>6.78</td>
<td>6.78</td>
<td>5.93</td>
<td>6.78</td>
</tr>
<tr>
<td>( Q_{\text{tot}} ) (mol m(^{-2}) s(^{-1})) (9)</td>
<td>58.9</td>
<td>58.9</td>
<td>58.9</td>
<td>20.0</td>
<td>20.0</td>
</tr>
<tr>
<td>( R ) (μmol m(^{-2}) s(^{-1}))</td>
<td>1.17</td>
<td>1.17</td>
<td>1.17</td>
<td>1.17</td>
<td>1.17</td>
</tr>
<tr>
<td>( A_{\text{tot}} ) (mol m(^{-2}) s(^{-1}))</td>
<td>0.63</td>
<td>1.06</td>
<td>0.90</td>
<td>0.04</td>
<td>0.17</td>
</tr>
<tr>
<td>( A_{\text{tot}} ) (mol m(^{-2}) s(^{-1})) (9)</td>
<td>0.61</td>
<td>1.07</td>
<td>0.61</td>
<td>1.07</td>
<td>0.61</td>
</tr>
</tbody>
</table>

* Calculated from Refs. 6 and 7. ** Parameter determined in this study. * Measured value of \( A_{\text{tot}} \).
growth in elevated CO$_2$. What significance for $A_{\text{act}}$ might the increase of $\phi_{\text{act}}$ from 0.065 for plants growing in $c_\text{i} = 351 \mu\text{mol mol}^{-1}$ to a $\phi$ of 0.078 for plants growing in $c_\text{i} = 680 \mu\text{mol mol}^{-1}$ have? This may be estimated by recalculating $A_{\text{act}}$ for the elevated CO$_2$ chambers but assuming an unchanged $\phi_{\text{act}}$ of 0.065. This predicts an $A_{\text{act}}$ of 0.90 mol m$^{-2}$ s$^{-1}$ (Table 1), suggesting that 39% of the increase in $A_{\text{act}}$ in the elevated CO$_2$ chambers results from the increase in $\phi_{\text{act}}$. June 12 was a day with clear skies. For a cloudy day, $Q_{\text{tot}}$ would be substantially reduced. In Table 1 recalculation of $A_{\text{act}}$ from the parameters of columns 1 and 2, but assuming a 65% decrease in $Q_{\text{act}}$, are given in columns 4 and 5. Under these conditions the increase in $A_{\text{act}}$ attributable to the increase in $\phi_{\text{act}}$ with increase in the CO$_2$ concentration is 86%. This increased importance of $\phi_{\text{act}}$ with decrease in $Q_{\text{act}}$ results from the increased proportion of the canopy which will be light limited on a cloudy day. Thus, under low photon fluxes in the field the increase in $\phi_{\text{act}}$ demonstrated in this study assumes particular significance for canopy photosynthetic CO$_2$ uptake with increasing atmospheric CO$_2$ levels.

In conclusion, long-term growth in elevated CO$_2$ has not produced significant accumulation in photosynthetic capacity under light-limiting conditions. These results, therefore, suggest that increasing CO$_2$ levels will result in an increase in the photosynthetic efficiency of $S.$ olenyi at low light levels, irrespective of any accumulation of photosynthetic response in saturating light.

ACKNOWLEDGMENTS

The Ulbricht sphere leaf chamber used in these studies was constructed in collaboration with Dr. K. J. Parkinson of PP Systems Ltd. (Hitchin, United Kingdom). We thank Dr. D. W. Lawlor for his constructive criticism of the manuscript in draft.

LITERATURE CITED