

Effect of the Long-Term Elevation of CO₂ Concentration in the Field on the Quantum Yield of Photosynthesis of the C₃ Sedge, *Scirpus olneyi*¹

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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 (ϕ_{abs}) 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 ϕ_{abs} and a portable chlorophyll fluorimeter was used to estimate the photochemical efficiency of photosystem II. When measured in an atmosphere with 10 millimoles per mole O₂ to suppress photorespiration, shoots showed a ϕ_{abs} 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 ϕ_{abs} 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 ϕ_{abs} , 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-limited conditions which would counteract the stimulation of photosynthetic CO₂ uptake otherwise expected through decreased photorespiration.

will increase A , through partial inhibition of photorespiration (19). Such observations suggest that the doubling of global CO₂ concentration projected to occur during the next century (28) would increase photosynthetic rates in C₃ plant communities. A number of studies have now shown, however, that growth at a c_a elevated to 600 to 700 $\mu\text{mol mol}^{-1}$ compared to the current atmospheric concentration of approximately 352 $\mu\text{mol m}^{-1}$ can depress photosynthetic capacity. Leaf photosynthetic rates of plants grown and measured in elevated CO₂ concentrations may be lower than those of plants grown in current ambient CO₂ concentrations (351 $\mu\text{mol m}^{-1}$) when both are measured in elevated concentrations (18, 22). Thus, development of photosynthetic organs in elevated CO₂ may result in acclimation, partially or wholly offsetting the increase that results from decreased photorespiration. Possible mechanisms of this acclimation of photosynthesis to elevated CO₂ include decreases in amounts of RuBP carboxylase/oxygenase (23), in the activation state of this enzyme, and in capacity for regeneration of the substrate RuBP (22). Most studies of the effects of growth at elevated c_a on photosynthetic CO₂ uptake have concerned effects on rates at or close to A_{sat} . Within a closed canopy many leaves will be shaded for most of the day and even exposed leaves will experience low light on cloudy days and at dawn and dusk. In these situations, light-limited rather than light-saturated rates of CO₂ uptake will be critical to the rate of photosynthetic carbon gain by plant canopies (3). The initial phase of the response curve of A to increase in the rate Q_{abs} is linear and represents the maximum efficiency of utilization of absorbed light in CO₂ fixation, *i.e.* ϕ_{abs} . It also provides a measure of photosynthetic capacity when light flux is limiting. Measurement of ϕ_{abs} is complicated by the need to ensure that calculations of slope are based on the initial linear portion

Temporary elevation of c_a^2 around the leaf of a C₃ plant

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² Abbreviations: c_a , the concentration of CO₂ in the ambient air ($\mu\text{mol mol}^{-1}$); A , rate of CO₂ uptake per unit of projected area of stem ($\mu\text{mol m}^{-2} \text{s}^{-1}$); RuBP, ribulose-1,5-bisphosphate; A_{sat} , A at light saturation ($\mu\text{mol m}^{-2} \text{s}^{-1}$); Q , photosynthetically active photon flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$); Q_{abs} , Q absorbed per unit of projected stem area; ϕ_{abs} , the maximum quantum yield, *i.e.* ratio of CO₂ molecules absorbed

per photon absorbed; Q_{wall} , Q on the wall of the Ulbricht sphere; F_v , variable component of F_m ; F_m , maximum emission of PSII chlorophyll fluorescence (arbitrary units); LCP, the light compensation point of photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$); $A_{\text{c,tot}}$, daily integral of net canopy photosynthetic CO₂ uptake ($\text{mol m}^{-2} \text{d}^{-1}$); Q_{tot} the photon flux accumulated over 1 d ($\text{mol m}^{-2} \text{d}^{-1}$); 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 ($\mu\text{mol m}^{-2} \text{s}^{-1}$); s , stem area index, *i.e.* stem surface area overlying a unit of ground area (dimensionless); α , the absorptance of the stem surface, *i.e.* the ratio of the absorbed flux to the incident flux (dimensionless).

of the response of A to Q_{abs} avoiding any subtle changes in linearity (24). Changes in surface absorptance will alter the quantum yield on an incident photon flux basis. To separate absorptance changes from changes in the efficiency of photosynthesis, Q_{abs} should be determined simultaneously with CO_2 uptake. A gas exchange cuvette incorporated into an integrating sphere enables such simultaneous measurements of A and Q_{abs} (15).

Quantum yield calculated on an absorbed light basis (ϕ_{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 C_3 plants, a factor possibly reflected in the low interspecific variability in ϕ_{abs} within a photosynthetic type. At current atmospheric CO_2 concentrations, healthy C_3 plants show a ϕ_{abs} of approximately 0.055 at 30°C . In an atmosphere of 1% O_2 , ϕ_{abs} increases to 0.08 to 0.09 because of the inhibition of photorespiratory metabolism (4, 12, 20). In an atmosphere with an elevated CO_2 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 (CO_2/O_2), 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 c_a would seem unlikely. However, although ϕ_a 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 ϕ_a (3). Baker *et al.* (3) enumerated several potential causes of decreases in ϕ_{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 ϕ_{abs} (26). Furthermore, CO_2 concentration has been shown to modulate protein biosynthesis in photosynthetic cells (2). Thus, the possibility of change in photosynthetic capacity and ϕ_{abs} under light-limiting conditions, induced by development in elevated CO_2 atmospheres, cannot be dismissed.

The objective of this study was to determine whether *in situ* elevation of the CO_2 concentration to $680 \mu\text{mol mol}^{-1}$ around natural stands of the C_3 sedge *Scirpus olneyi* Gray (8) for 3 years resulted in acclimation of the maximum quantum yield of photosynthesis. This was assessed by measurement of ϕ_{abs} and the efficiency of PSII photochemistry.

MATERIALS AND METHODS

Plant Material

As part of a long-term investigation of the effects of elevated CO_2 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_a in one-half of these chambers has been maintained at $680 \pm 3 \mu\text{mol mol}^{-1}$ for the complete growing

seasons of the past 3 years (11). The remaining chambers were maintained at $c_a 351 \pm 1.3 \mu\text{mol mol}^{-1}$ 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 C_3 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 ϕ_{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 α of the sphere was determined with a black absorber $10 \text{ cm} \times 5 \text{ mm}$, 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 absorptance 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 α 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 $351 \mu\text{mol mol}^{-1}$ of CO_2 and 21 mmol mol^{-1} O_2 to represent current atmospheric conditions and the control CO_2 growth environment, (b) $680 \mu\text{mol mol}^{-1}$ CO_2 and 21 mmol mol^{-1} of O_2 in air to simulate the predicted "doubled CO_2 " atmosphere used in the elevated CO_2 growth environment, and (c) $351 \mu\text{mol mol}^{-1}$ CO_2 and 1 mmol mol^{-1} O_2 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 CO_2 concentration across the chamber and the absolute CO_2 concentration were measured with a two-channel infrared gas analyzer (Binos 2, Leybold-Heraeus, Hanau, FRG), calibrated against mixtures of CO_2 in air retained in aluminum cylinders

which had been previously cross-calibrated against a gravimetrically prepared CO₂ standard, traceable to a National Bureau of Standards reference (Matheson Gas Products, East Rutherford, NJ). Q_{wall} 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 $\pm 1.0\%$. Light fluxes within the sphere (Q_{wall}) in the range of 0 to 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ 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 $28^\circ\text{C} \pm 1.5^\circ\text{C}$ for all measurements of ϕ_{abs} . The projected stem surface area was determined with an area meter (LI-3100, Li-Cor). To determine ϕ_{abs} for any one stem in any one measuring gas composition, A was determined at 10 values of Q_{abs} from 5 to 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Within this range, the slope dA/dQ_{abs} was constant but began to decline above 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. An averaged ϕ_{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 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (25). Linearity over this range was indicated by the high r^2 values which exceeded 0.98 in all cases. Differences between the mean ϕ_{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_v 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_v . Induction of fluorescence emission was measured *in situ* on 20 stems from five control and 20 stems from five elevated CO₂ open-top chambers, using a portable fluorimeter (type PSM, BioMonitor S.C.I. AB, Malmö, Sweden). Measurements were made between 30 min and 1 h after sunset, to ensure that any short-term reductions in F_v/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 $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ and the kinetics of chlorophyll fluorescence monitored over the subsequent 10 s. Differences in mean F_v/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_v/F_m revealed no systematic deviation from the rankit line, suggesting that the assumption of normal

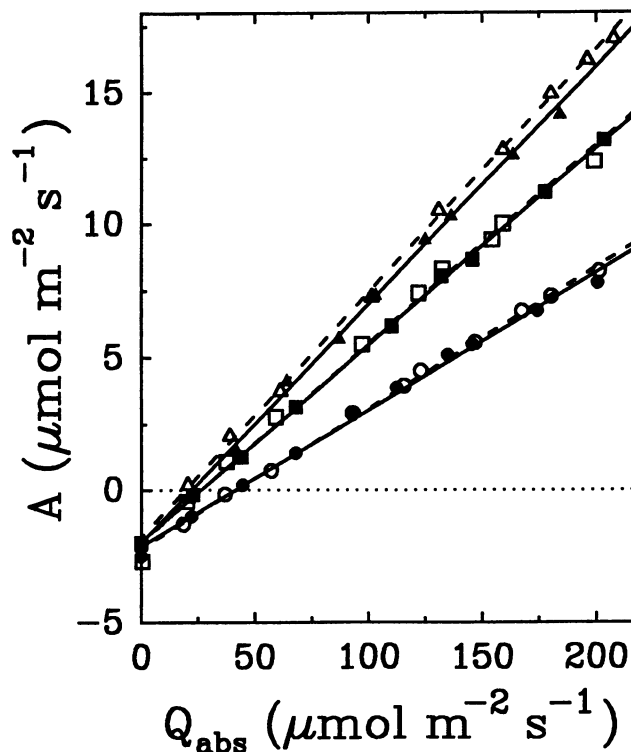


Figure 1. Response of A to Q_{abs} for a stem of *S. olneyi* grown in 351 $\mu\text{mol mol}^{-1}$ CO₂ in air (open symbols and broken lines) and a stem grown in 680 $\mu\text{mol mol}^{-1}$ CO₂ in air (closed symbols and solid lines). For both stems, the response of A to Q_{abs} was determined in three gas mixtures: 10 mmol mol⁻¹ O₂ and 351 $\mu\text{mol mol}^{-1}$ CO₂ (Δ , \blacktriangle), 210 mmol mol⁻¹ O₂ and 351 $\mu\text{mol mol}^{-1}$ CO₂ (\circ , \bullet), and 210 mmol mol⁻¹ O₂ and 680 $\mu\text{mol mol}^{-1}$ CO₂ (\square , \blacksquare). The balance of each mixture was N₂. All measurements were made at 28°C. Lines illustrate the best-fit relationship to the displayed data points determined by the least squares method.

frequency distributions of F_v/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_v/F_m after 10 min of dark adaptation or with an increase in the photon flux density of the actinic excitation beam above 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

RESULTS

The response of CO₂ uptake to absorbed photon flux (Q_{abs}) was linear up to approximately 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for all measuring gas compositions (Fig. 1). Although no attempt was made to select stems of uniform age or developmental stage, ϕ_{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 CO₂ environment. The slope is strongly influenced by the gas composition of the measuring atmosphere. This lack of influence of the growth environment on ϕ_{abs} is con-

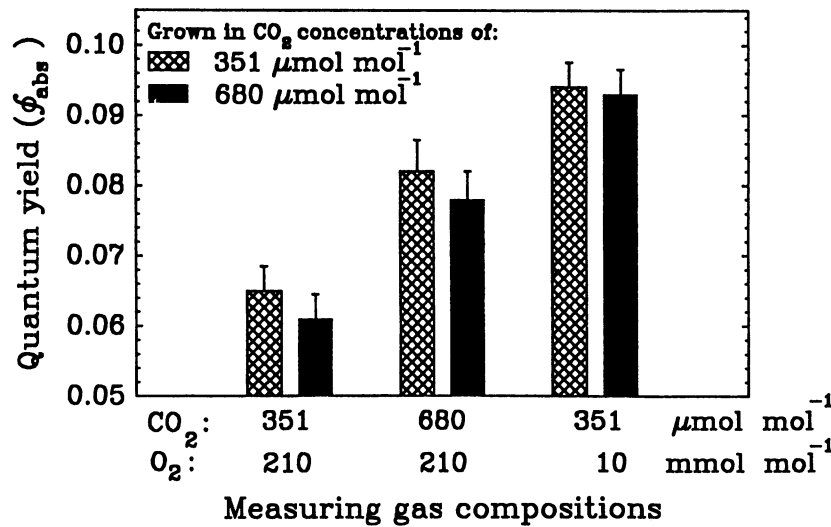


Figure 2. The mean ϕ_{abs} of 10 stems of *S. olneyi* grown in $680 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 10 stems grown in $351 \mu\text{mol m}^{-2} \text{s}^{-1}$. Vertical bars indicate +1 SE. ϕ_{abs} was determined for each stem in three measuring gas mixtures, as detailed in Figure 1.

firmed when the samples as a whole are considered. The mean ϕ_{abs} of the 10 stems developed in the control chambers and measured in an atmosphere of 21% O_2 and $351 \mu\text{mol mol}^{-1}$ CO_2 was 0.065 ± 0.003 . An increase in CO_2 concentration to $680 \mu\text{mol mol}^{-1}$ increased ϕ_{abs} to 0.080 ± 0.004 , whereas a decrease in O_2 concentration to 1% to eliminate photorespiration increased ϕ_{abs} to 0.093 ± 0.003 (Fig. 2). The difference in mean ϕ_{abs} between the three measurement gas mixtures was highly significant ($F = 26.26$). Although mean ϕ_{abs} values for plants grown in the elevated 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 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 $351 \mu\text{mol mol}^{-1}$ CO_2 with those developed and measured in $680 \mu\text{mol mol}^{-1}$ CO_2 . Here, elevated CO_2 is seen to lead to a statistically significant increase in ϕ_{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 absorptance calculated from the projected areas were 0.85 ± 0.02 and 0.84 ± 0.02 for stems developed in control and elevated CO_2 chambers, respectively. This indicates that quantum yield on an incident light basis would be increased in direct proportion with ϕ_{abs} .

It follows that, if ϕ_{abs} is increased for plants grown and measured in $c_a = 680 \mu\text{mol mol}^{-1}$ 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 $c_a = 680 \mu\text{mol mol}^{-1}$ CO_2 was $31 \pm 3 \mu\text{mol m}^{-2} \text{s}^{-1}$ compared to $51 \pm 3 \mu\text{mol m}^{-2} \text{s}^{-1}$ for stems grown and measured at $c_a = 351 \mu\text{mol mol}^{-1}$ CO_2 (Fig. 3). As in the case of ϕ_{abs} , LCP showed a highly significant difference between the measuring gas mixtures ($F = 55.5$) but no significant difference between the growth CO_2 concentrations ($F = 0.85$).

When ϕ_{abs} was determined in a decreased O_2 concentration (10 mmol mol^{-1}), ϕ_{abs} was almost identical regardless of whether the stems were grown in control or in elevated CO_2

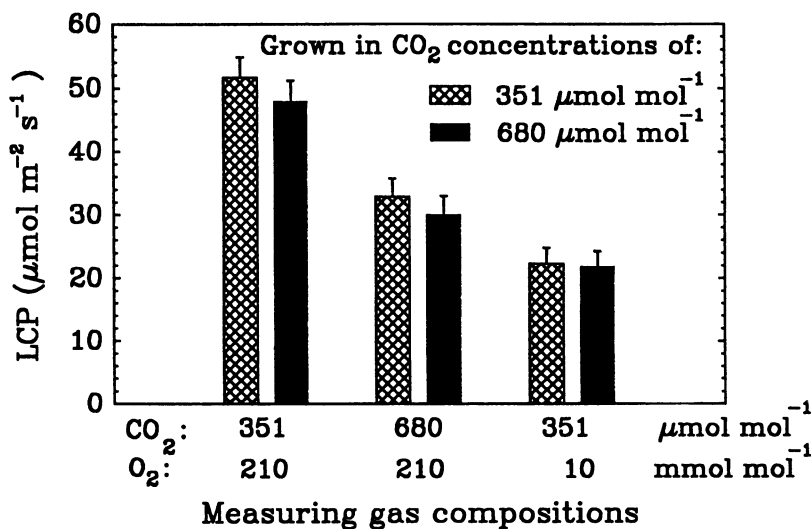


Figure 3. The mean LCP for 10 stems of *S. olneyi* grown in $680 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 10 stems grown in $351 \mu\text{mol m}^{-2} \text{s}^{-1}$. Vertical bars indicate +1 SE. LCP was determined for each stem in three measuring gas mixtures, as detailed in Figure 1.

Table 1. Estimation of $A_{c,tot}$ from Equation 1 for *S. olneyi* stands growing in 351 and 680 $\mu\text{mol mol}^{-1}$ of CO₂ in air

Columns 1 and 2 use values measured for the 351 and 680 $\mu\text{mol mol}^{-1}$ CO₂ concentration chambers, respectively, to calculate $A_{c,tot}$ following Equation 1 for June 12, 1988. In column 3, $A_{c,tot}$ is recalculated using the values of column 2 but assuming no increase in ϕ_{abs} with CO₂ elevation. Columns 4 and 5 examine the effects of an approximately 65% decrease in Q_{tot} on the estimated $A_{c,tot}$ using the measured parameters for the two chamber types.

	1	2	3	4	5
c_a ($\mu\text{mol mol}^{-1}$)	351	680	680	351	680
k (dimensionless) ^a	0.27	0.27	0.27	0.27	0.27
α (dimensionless) ^b	0.85	0.85	0.85	0.85	0.85
ϕ_{abs} (dimensionless) ^b	0.065	0.078	0.065	0.065	0.078
A_{sat} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) (29)	12.5	19.8	19.8	12.5	19.8
s (dimensionless) (9)	5.93	6.78	6.78	5.93	6.78
Q_{tot} ($\text{mol m}^{-2} \text{s}^{-1}$) (9)	58.9	58.9	58.9	20.0	20.0
R ($\mu\text{mol m}^{-2} \text{s}^{-1}$) ^c	1.17	1.17	1.17	1.17	1.17
$A_{c,tot}$ ($\text{mol m}^{-2} \text{s}^{-1}$) ^d	0.63	1.06	0.90	0.04	0.17
$A_{c,tot}$ ($\text{mol m}^{-2} \text{s}^{-1}$) ^e (9)	0.61	1.07			

^a Calculated from Refs. 27 and 9. ^b Parameter determined in this study. ^c Calculated from data from Refs. 9 and 10. ^d Estimated value of $A_{c,tot}$. ^e Measured value of $A_{c,tot}$.

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 CO₂ fixation. This lack of difference in ϕ_{abs} is paralleled by the observation that F_v/F_m was 0.851 ± 0.004 for plants grown in elevated CO₂ 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 Demmig (4), in a survey of a range of vascular plants, showed a mean absorbed light quantum yield for O₂ evolution of 0.105 measured in approximately 10 mmol mol⁻¹ CO₂. Given the fact that some of the products of non-cyclic electron transport will be used in processes other than CO₂ fixation, a lower ϕ_{abs} for CO₂ uptake would be expected. When the O₂ concentration was lowered to 10 mmol mol⁻¹ to inhibit photorespiration, ϕ_{abs} was 0.093. Although approximately 12% less than the value suggested for O₂ evolution (4), it is among the highest values of ϕ_{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 CO₂ atmosphere in the field.

A number of studies have suggested that growth in elevated CO₂ can lead to an acclimatory decrease in photosynthetic capacity (reviewed in Ref. 17). The results show that, despite 3 years of growth in elevated CO₂, there is no evidence of acclimation with respect to either the maximum quantum yield of CO₂ assimilation or the quantum yield of photochemistry at PSII inferred from chlorophyll fluorescence. In the absence of any significant acclimation, ϕ_{abs} would be expected to benefit fully from the potential decrease in photorespiration with elevation of c_a . This is clearly evident when plants grown and measured at $c_a = 351 \mu\text{mol mol}^{-1}$ are compared to those

grown and measured at $c_a = 680 \mu\text{mol mol}^{-1}$ (Fig. 2). What significance might these increases in ϕ_{abs} have to plants in the doubled CO₂ 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 CO₂ uptake. This is adapted here for use with photon flux and ϕ_{abs} (Eq. 1). This equation assumes a rectangular hyperbolic response of the rate of CO₂ 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:

$$A_{c,tot} = \frac{\alpha\phi_{abs}Q_{tot}h(A_{sat} + R)(1 - e^{-kx})}{k\alpha\phi_{abs}Q_{tot} + h(A_{sat} + R)} - 8.64 \times 10^4 (Rs) \quad (1)$$

where terms are as defined previously² and 8.64×10^4 is the number of seconds in a day.

Table I gives the values for $A_{c,tot}$ calculated from Equation 1 using A_{sat} and s determined for plants in the control and elevated CO₂ chambers during June 1988 (29). Values of ϕ_{abs} and α 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 calculated 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 $1.17 \mu\text{mol m}^{-2} \text{s}^{-1}$ (calculated from data in Ref. 10). On June 12, 1988, Q_{tot} at the site was $58.9 \text{ mol m}^{-2} \text{s}^{-1}$ during the 15.5 h of daylight and the temperature was 29.5°C (9), *i.e.* close to the temperature at which ϕ_{abs} was measured in this study. Substituting these values into Equation 1 yields $A_{c,tot} = 0.63$ and $1.06 \text{ mol m}^{-2} \text{s}^{-1}$ for the control and elevated CO₂ 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 $A_{c,tot}$ with

growth in elevated CO₂. What significance for $A_{c,tot}$ might the increase of ϕ_{abs} from 0.065 for plants growing in $c_a = 351 \mu\text{mol mol}^{-1}$ to a ϕ of 0.078 for plants growing in $c_a = 680 \mu\text{mol mol}^{-1}$ have? This may be estimated by recalculating $A_{c,tot}$ for the elevated CO₂ chambers but assuming an unchanged ϕ_{abs} of 0.065. This predicts an $A_{c,tot}$ of $0.90 \text{ mol m}^{-2} \text{ s}^{-1}$ (Table I), suggesting that 39% of the increase in $A_{c,tot}$ in the elevated CO₂ chambers results from the increase in ϕ_{abs} . June 12 was a day with clear skies. For a cloudy day, Q_{tot} would be substantially reduced. In Table I recalculations of $A_{c,tot}$ from the parameters of columns 1 and 2, but assuming a 65% decrease in Q_{tot} , are given in columns 4 and 5. Under these conditions the increase in $A_{c,tot}$ attributable to the increase in ϕ_{abs} with increase in the CO₂ concentration is 86%. This increased importance of ϕ_{abs} with decrease in Q_{tot} 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 ϕ_{abs} demonstrated in this study assumes particular significance for canopy photosynthetic CO₂ uptake with increasing atmospheric CO₂ levels.

In conclusion, long-term growth in elevated CO₂ has not produced significant acclimation in photosynthetic capacity under light-limiting conditions. These results, therefore, suggest that increasing CO₂ levels will result in an increase in the photosynthetic efficiency of *S. olneyi* at low light levels, irrespective of any acclimation of photosynthetic response in saturating light.

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