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Photosynthesis–light relationships of a mixed culture of phytoplankton in fluctuating light

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Abstract

Rates of oxygen production and inorganic carbon uptake by a mixed culture of phytoplankton were determined in a highly variable light regime. Scatter diagrams of the results revealed a smoothly varying relationship between irradiance and photosynthetic oxygen release except when the rate of oxygen release was depressed by CO_2 depletion. There was no indication that the instantaneous rate of oxygen production depended on light intensities received in the recent (5–30 min) past. However, the net rate of inorganic carbon uptake exhibited large, transient fluctuations in response to rapid changes in light as CO_2 became depleted (<0.001 mg·liter^{-1}). Spectral analysis showed that the transient fluctuations in inorganic carbon exchange were related to the rate of change in irradiance. Enhanced transport of inorganic carbon into the cells at high pH may account for the highest rates of carbon uptake; diffusional loss of intracellular CO_2, photorespiration, or both may account for the highest rates of carbon release. Models derived from incubations at constant light intensities cannot account for the observed fluctuations in inorganic carbon uptake, indicating the importance of light variability, especially in systems that become depleted of CO_2.

Models for predicting rates of photosynthesis from measurements of light intensity are important tools for investigating the effects of environmental factors (light, temperature, nutrients, etc.) on the primary production of water bodies (Talling 1957; Vollenweider 1970; Schindler and Fee 1973; Bannister 1974; Platt and Jassby 1976). Measurements of photosynthesis by plankton in closed containers are frequently made under constant, artificial light. The photosynthesis–light (*P–I*) relationships derived from such experiments, and the empirical models used to represent them, contain no information about the response of the phytoplankton to a varying light field. We may characterize these experiments as "static experiments" and the corresponding empirical representations as "static models."

If we try to extrapolate static models to conditions under which light intensities are highly variable, we have to assume that the organisms respond to fluctuating light as if they had received independent exposures to all the different light intensities in the fluctuating regime. That is, it is assumed that the rate of photosynthesis at any time does not depend on light intensities received in the recent past. There is reason to believe that this assumption is not always justified (Harris 1973; Harris and Lott 1973; Harris and Piccinin 1977; Marra 1978*a*), and extrapolation of the static models is likely to incur errors in the prediction of integrals of production (Marra 1978*b*). The potential problems arising from the use of static models are of considerable importance in aquatic ecology, since organisms in the natural environment are only rarely, if ever, exposed to constant light for long periods (Harris and Piccinin 1977). In particular, the changes in irradiance due to fluctuations in cloud cover may be quite large, may contain many frequencies, and may be transmitted to considerable depths in the water (Dera and Gordon 1968). In situ incubations are intermediate between static experiments and the natural habitat, because in situ experiments integrate the fluctuations in incident light but ignore the fluctuations received by cells circulating in a vertical light gradient.

Several studies have indicated that the instantaneous rate of photosynthesis in a fluctuating light field depends, in part, on light intensities received in the recent

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(5–30 min) past (Harris 1973; Harris and Lott 1973; Falkowski and Owens 1978; Marra 1978*a*). In those studies, the rate of oxygen production was highest during the stepwise increasing portion of the light cycle and lowest during the falling portion (i.e. the rate was hysteretic). The rapid variations in light were artificially induced and were of fixed, predetermined durations. However, since the fluctuations in light received by photosynthetic organisms in nature occur within a broad and continuous range of frequencies, it is important to use an experimental and analytical approach that can deal with the photosynthetic response at different time scales.

We here examine the photosynthetic response to light fluctuations within a wide range of frequencies of ecological importance. We measured changes in rates of both oxygen and inorganic carbon exchange in cultures of phytoplankton exposed to rapidly varying light. By analyzing short term variations in the rates, we can test the validity of assumptions inherent in the application of static *P–I* models under conditions of rapidly varying light and thereby evaluate the importance of rapid light variations to the production ecology of aquatic systems.

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Methods and data analyses

The apparatus for growing phytoplankton consisted of a 38-liter (10 gallon) aquarium containing about 22 liters of water and mixed species of plankton (Fig. 1). It was partially submersed in a large tub (107 × 48 × 30 cm deep) of circulating tapwater to prevent extreme temperature excursions. A box-shaped cover of clear Plexiglas above the aquarium was open to the atmosphere at the bottom, but protected the system from rain and prevented strong gusts of wind from affecting the concentrations of dissolved gases. The apparatus was on the roof of a building at the University of Virginia; direct solar irradiance was not obstructed by buildings or trees at any time of day. Most of the time the culture was covered by a black, wire-mesh screen that reduced incident irradiance by about 60%. The data reported here were taken during a period (2–5 November 1977) of heavily overcast skies, and we removed the screen to increase the excursions in irradiance. Maximum irradiances with the screen in place for the 2 weeks preceding the experiments were <1,000 μEinst·m^{-2}·s^{-1}; maximum irradiances from 2–5 November with the screen removed were <800 μEinst·m^{-2}·s^{-1}.

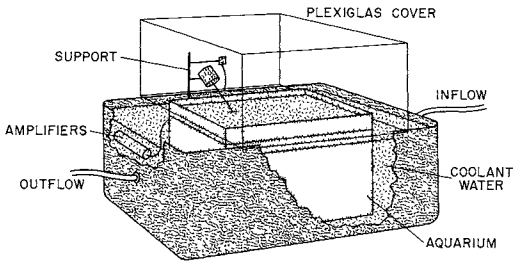

Fig. 1. Apparatus for growing phytoplankton outdoors. Ringstand supports stirring motor and quantum sensor. Output from amplifiers goes to magnetic tape recorder (not shown).

In early August 1977, water was collected from the Rivanna Reservoir near Charlottesville, Virginia, and enriched in the culturing apparatus with 0.15 g of KNO_3 and 0.15 g of KH_2PO_4, which produced a dense culture of mixed Chlorophyceae. The concentration of chlorophyll *a* (determined in triplicate by the SCOR-UNESCO procedure: Strickland and Parsons 1972) reached 0.13 (0.01 SD) mg·liter^{-1}. Typical diel excursions of pH were from about 8.7 to 10.2. The concentration of CO_2 [$=CO_2(aq) + H_2CO_3$] was rarely above air saturation, and was frequently <0.001 mg·liter^{-1}.

A thermistor (Fenwal), galvanic cell oxygen electrode (Electronic Instr. Ltd.) and a glass pH electrode (Sensorex) provided the data for calculating rates of photosynthesis and respiration. Flow for the oxygen electrode was provided by a

stirring motor, which also kept the cells well circulated and prevented thermal and chemical gradients from forming. Irradiance at the surface of the culture was measured by a Lambda Instruments PAR (photosynthetically active radiation) quantum sensor.

Signals from the sensors were amplified and recorded on magnetic tape cartridges every 9.2 s (details given by Kelly et al. 1974*b*). Digitized voltages from the cartridges were copied onto standard magnetic tape; the voltages were converted to actual values of temperature, oxygen concentration, pH, and irradiance and averaged at 1- and 5-min intervals.

Rates of oxygen production and inorganic carbon uptake were computed from the data by solving the mass balance equations for dissolved oxygen and inorganic carbon. The solution to the mass-balance equation for dissolved oxygen used here was presented by Gallegos et al. (1977), and the precision of the computations discussed in that paper and also by Gallegos (1979).

The equations for computing the net rate of inorganic carbon uptake are given in Table 1. We used the procedures of Kelly et al. (1974*a*) to calculate concentrations of total inorganic carbon (= $CO_3^{2-} + HCO_3^- + CO_2$) and CO_2 from measurements of pH and alkalinity, and to calculate the saturation concentration of CO_2 from measurements of temperature and barometric pressure.

The method for computing the net rate of inorganic carbon uptake is very similar to that of Gallegos et al. (1977); we present only an outline of the derivation here. Equation 1 (Table 1) indicates that changes in dissolved inorganic carbon in a well stirred container are caused by exchange with the atmosphere, photosynthesis, and respiration. CO_2 is the only form of inorganic carbon that exchanges with the atmosphere. The method requires no assumption about the species of inorganic carbon taken up during photosynthesis. We determine net inorganic carbon uptake from the function $F_c(t)$, formed from measured data according to Eq. 4, and obtain $h_c(\omega)$ from $F_c(t)$ (Eq. 6) by the fast Fourier transform algorithm. Once $h_c(\omega)$ is known, $g_c(\omega)$ can easily be determined by Eq. 5. Net inorganic carbon uptake is then determined from $g_c(\omega)$, again by the fast Fourier transform algorithm.

Table 1. Solution of mass-balance equation for dissolved inorganic carbon. C_T = total dissolved inorganic carbon (mol·liter^{-1}), $CO_2 = CO_2(aq) + H_2CO_3 \approx CO_2(aq)$ (mol·liter^{-1}), CO_{2s} = saturation concentration of CO_2 (mol·liter^{-1}), $K_c = CO_2$ reaeration coefficient (h^{-1}), $P_c - R_c$ = net inorganic carbon uptake (photosynthesis − respiration) (mol·liter^{-1}·h^{-1}), t = time (h).

Mass-balance equation:

$$\frac{dC_T}{dt} = K_c(CO_{2s} - CO_2) - (P_c - R_c). \quad (1)$$

Represent $(P_c - R_c)$ by a Fourier integral:

$$(P_c - R_c) \equiv (2\pi)^{-\frac{1}{2}} \int_{-\infty}^{\infty} g_c(\omega) e^{i\omega t}\, d\omega. \quad (2)$$

Substitute Eq. 2 into 1 and integrate:

$$C_T(t + \delta) \cong C_T(t) - S_c(t,\delta) + (2\pi)^{-\frac{1}{2}} \int_{-\infty}^{\infty} \frac{g_c(\omega)(1 - e^{i\omega\delta})}{i\omega} e^{i\omega t}\, d\omega, \quad (3)$$

where $S_c(t,\delta) \equiv K_c \int_t^{t+\delta} (CO_{2s} - CO_2)\, dt.$

Define:

$$F_c(t) \equiv C_T(t + \delta) - C_T(t) - S_c(t,\delta) \quad (4)$$

and

$$h_c(\omega) \equiv g_c(\omega) \cdot \frac{1 - e^{i\omega\delta}}{i\omega}. \quad (5)$$

Substitute Eq. 4 and 5 into 3:

$$F_c(t) = (2\pi)^{-\frac{1}{2}} \int_{-\infty}^{\infty} h_c(\omega) e^{i\omega t}\, d\omega. \quad (6)$$

Variations in O_2 production and C uptake over the lighted portion of the day were computed from 5-min averages of the data on dissolved O_2 and inorganic C. This produced time series of about 120 values, from which we formed photosynthesis-light curves based on O_2 production or carbon uptake, using 40 points chosen at random. We refer to these plots as "static" *P–I* plots because they are formed as if each point represented an independent determination of photosynthesis at a fixed light intensity. The applicability of static models to describe the *P–I* relationships was judged by inspection of the plots. We can identify three potential sources of scatter in the

P–I plots formed in this manner: the noise generated by imprecise estimates of O_2 and C exchange, the effects of variables other than light, and the time-dependence of the photosynthetic response to light. By time-dependence, we mean the dependence of photosynthesis on past as well as present light intensities, for example, time lags in the photosynthetic response, hysteresis, or attenuation or amplification of the response due to high frequency fluctuations in light. In a fluctuating light field composed of a continuous spectrum of frequencies, time-dependence causes a wide range of photosynthetic rates to be associated with a single light intensity on a static *P–I* plot. We investigated time-dependence by means of cross-spectral analysis. Gain, phase, and coherence spectra (or transfer functions) were computed with the BMD autocovariance and power spectrum analysis program (Dixon 1968). Procedures for identifying forms of time-dependence from estimates of the gain and phase spectra are given by Jenkins and Watts (1968) and Bendat and Piersol (1971) and an example of the technique applied to photosynthesis-light relationships by Gallegos et al. (1977).

Results

In Fig. 2 are time-series plots of irradiance, net oxygen production, and net inorganic carbon uptake (computed from 5-min averages of the data) for 2–5 November 1977. The figure shows that short term changes in both oxygen production and inorganic carbon uptake can be detected and that the changes are associated with fluctuations in irradiance (*see also Fig.* 3). On 3 and 4 November (Fig. 2b, c), photosynthetic oxygen production was depressed from about 1200 to 1600 hours. The afternoon depression was characterized by a period of declining rate of O_2 release (while irradiance remained high) followed by a period when the mean rate of O_2 production was nearly constant, and the sensitivity to short term changes in light was reduced (*see especially Fig. 2b*).

The patterns of inorganic C uptake in Fig. 2 differed from those for O_2 production. During the morning (0730 to ≈1030 hours), changes in net inorganic C uptake rose smoothly with changes in light (Fig. 2b–d). However in the late morning and afternoon, there were large, rapid fluctuations in the net rate of inorganic C uptake, often so large as to obscure any smooth, diurnal trend in the rate of C uptake.

We first investigated the adequacy of static *P–I* models by making scatter diagrams between irradiance and rates of oxygen and carbon exchange. As expected from the time-series plots, oxygen production (Fig. 3) varied smoothly with light. The afternoon depression of O_2 production on 3 and 4 November 1977 caused hysteresis in the *P–I* plots for those days (Fig. 3b, c), resulting in several points falling on a horizontal line (at about 0.25 mg $O_2 \cdot \text{liter}^{-1} \cdot \text{h}^{-1}$) to the right of the light-dependent portion of the curve. Otherwise, there was no indication of time-dependence in the response of instantaneous net oxygen productivity to short term changes in available light.

In Fig. 4 are static *P–I* plots based on rates of inorganic carbon uptake. Correlation coefficients were calculated for the early morning (0730–1000 hours) and late morning and afternoon (1000–1730 hours) periods separately, and are reported in Table 2. During the early morning, inorganic C uptake and irradiance were highly correlated (Fig. 4b–d). During the late morning and afternoon, the large fluctuations in net inorganic C uptake caused wide scatter in the *P–I* plots of Fig. 4, and the correlation between irradiance and C uptake was reduced (Table 2).

We then performed cross-spectral analysis between time series of irradiance and net inorganic carbon uptake (computed from 1-min averages of the data). Transfer functions (gain and phase spectra) between time series of irradiance and inorganic C uptake are shown in Fig. 5. Squared coherencies between the series (which are frequency-dependent coefficients of determination) are reported in Table 3.

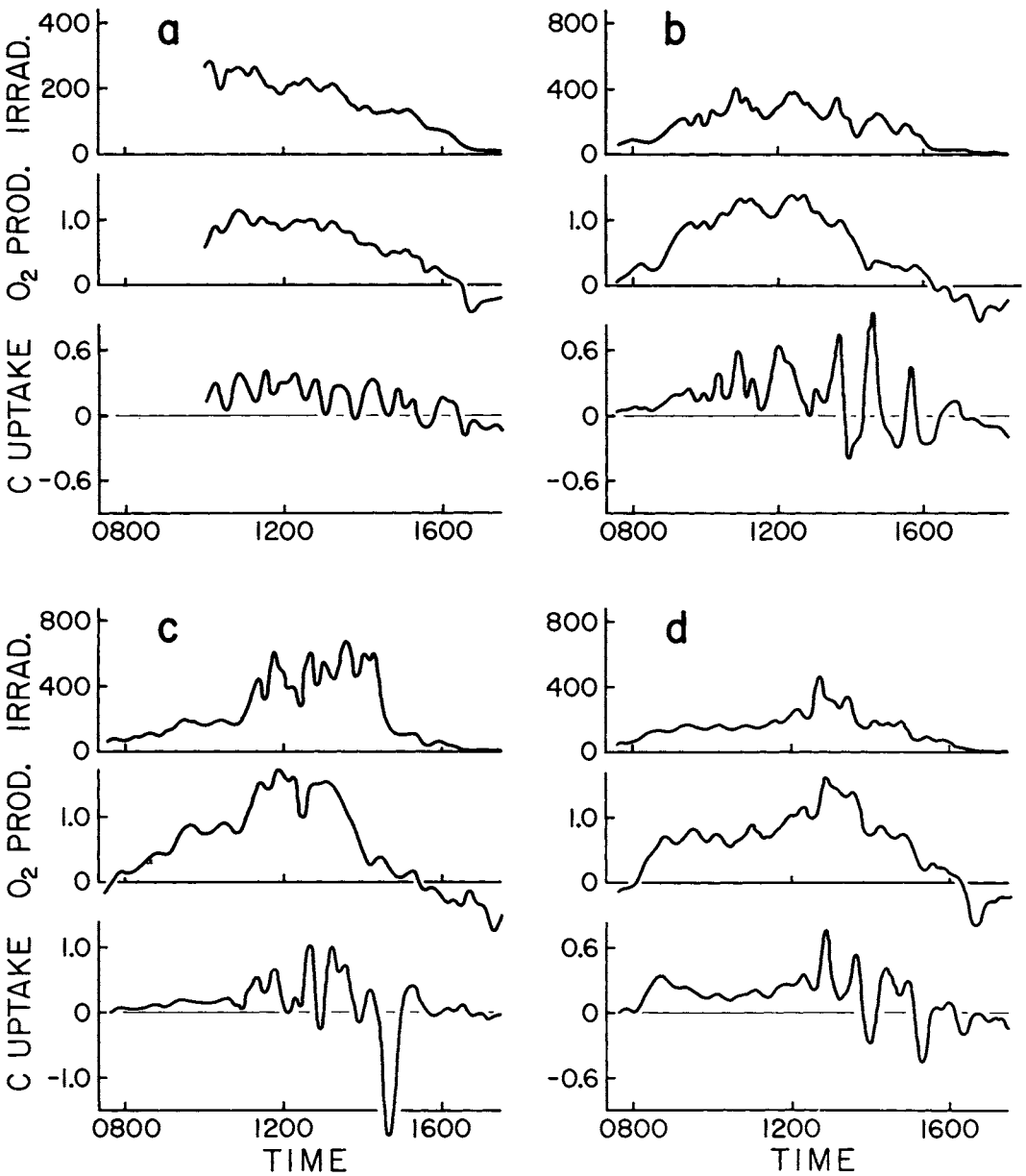

Fig. 2. Time series of irradiance (μEinst·m^{-2}·s^{-1}), net oxygen production (mg O_2·liter^{-1}·h^{-1}) and net inorganic carbon uptake (mg C·liter^{-1}·h^{-1}), computed from 5-min averages of data. All figures: a—2 November 1977; b—3 November 1977; c—4 November 1977; d—5 November 1977.

The gain spectra for each of the 4 days were flat or positively sloped in the range of frequencies from 0.8 to 5·h^{-1}; there was no significant tendency for variations in net inorganic carbon uptake to be damped at any frequency within that range. Squared coherencies (Table 3) remain high within that frequency range, indicating that the temporal fluctuations in C uptake were well correlated with

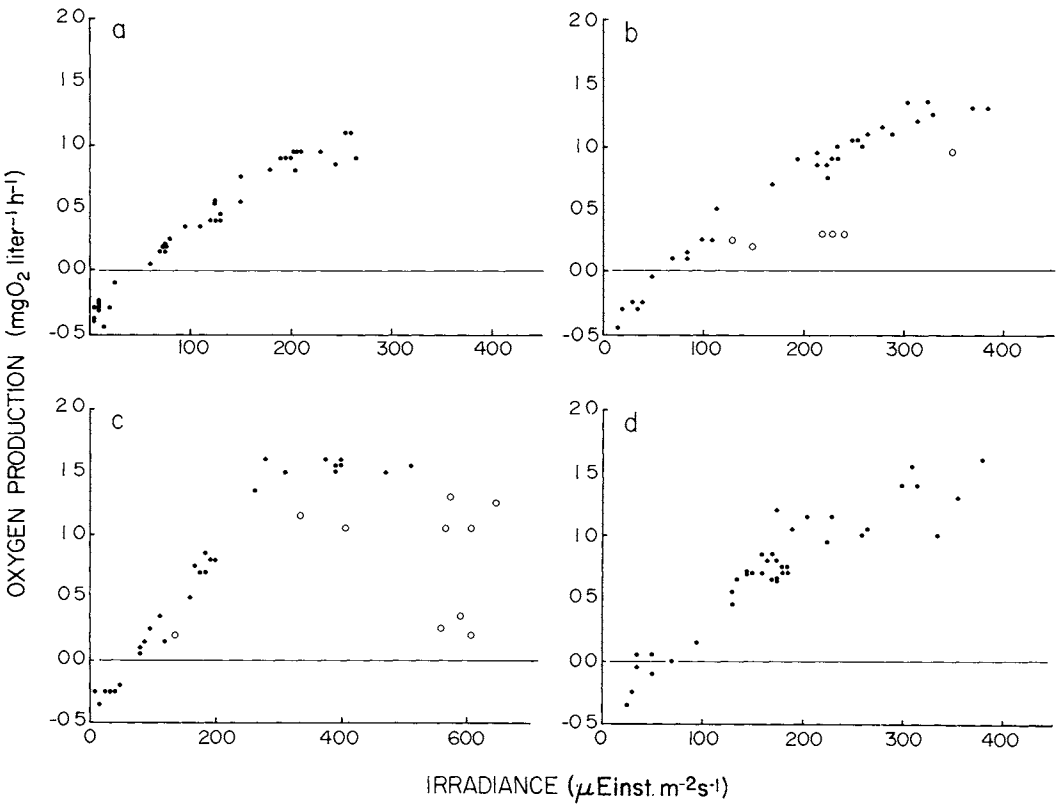

Fig. 3. Net rate of oxygen production plotted against irradiance. O—Affected by afternoon depression.

light, and that therefore the scatter in the *P–I* plots in Fig. 4 was not due to measurement noise in the rates of C uptake. The practical limit of detection of high frequency fluctuations in rates of C exchange in this system was in the range of frequencies from 6 to $10 \cdot h^{-1}$ (Gallegos 1979), and thus we must confine our discussion to the range of frequencies from <1 to $\approx 10 \cdot h^{-1}$.

The upward sloping gain spectra suggest that the sensitivity of net inorganic carbon uptake to changes in light was enhanced at high frequencies. This is supported by the phase spectra in Fig. 5, which show a phase lead between inorganic C uptake and light. This behavior results when a system responds to the rate of change of the independent variable (Jenkins and Watts 1968). The effect of such a response was that the rates of inorganic C uptake were highest in rapidly increasing light and lowest in rapidly decreasing light (*see especially Fig. 2c*). This form of time-dependence can cause scatter in *P–I* plots and indicates the limitations of static models to describe the response.

Discussion

In fluctuating light, we could detect short term changes in rates of both oxygen production and inorganic carbon uptake; however the types of response for inorganic carbon uptake were quite different from those for oxygen production.

The short term variations in oxygen production were superimposed on the long term, diurnal trend. When we used the data averaged at 5-min intervals, we could recover a smooth relationship between irradiance and rates of oxygen pro-

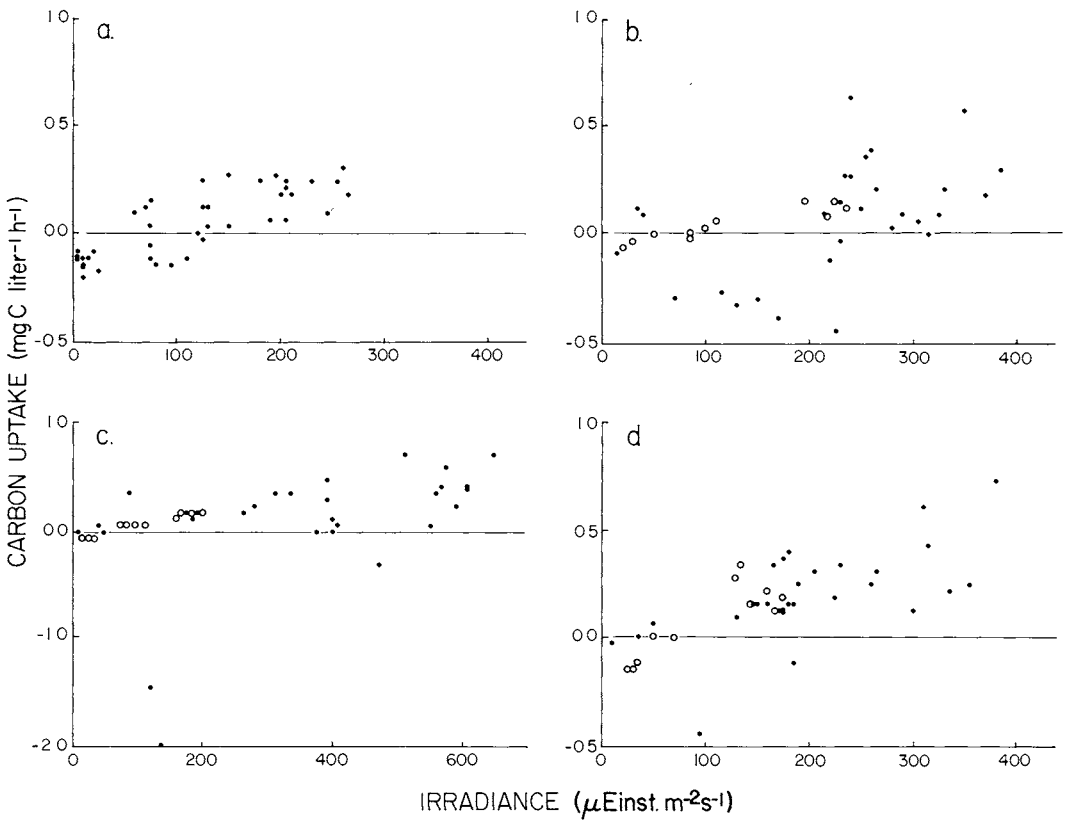

Fig. 4. Net rate of inorganic carbon uptake plotted against irradiance (○—0730–1000 hours; ●—1005–1730 hours).

duction, even in fluctuating light. The *P–I* plots made with data averaged every 5 min exhibited diurnal changes in the steady state relationship, such as the afternoon depression on 3 and 4 November 1977 (Fig. 3b, c). The afternoon depression of oxygen production in this system was apparently caused by CO_2 depletion (*see below*) and thus the excessive scatter in Fig. 3c can be attributed to the effects of a variable other than light. Otherwise, we conclude that, in this system, static *P–I* models based on instantaneous rates of oxygen production and instantaneous values of irradiance chosen at random times throughout the day also describe the response of minute-to-minute changes in oxygen exchange to changes in light induced by variations in cloud cover. Thus, the *P–I* relationship for O_2 production on time scales from 10–30 min was identical to the relationship for variations in light and O_2 production on time scales of ≈10 h. This is consistent with other data showing a lack of time-dependence in the linear range of the *P–I* curve (Harris 1973; Harris and Piccinin 1977). Our failure to observe time-dependence in rates of oxygen production may

Table 2. Correlation coefficients (r) between irradiance and net inorganic carbon uptake for early morning and late morning and afternoon periods separately. n is number of points for each correlation coefficient.

	0730–1000 hours		1005–1730 hours	
	r	n	r	n
3 Nov	0.95	11	0.49	29
4 Nov	0.99	11	0.46	29
5 Nov	0.86	11	0.64	29

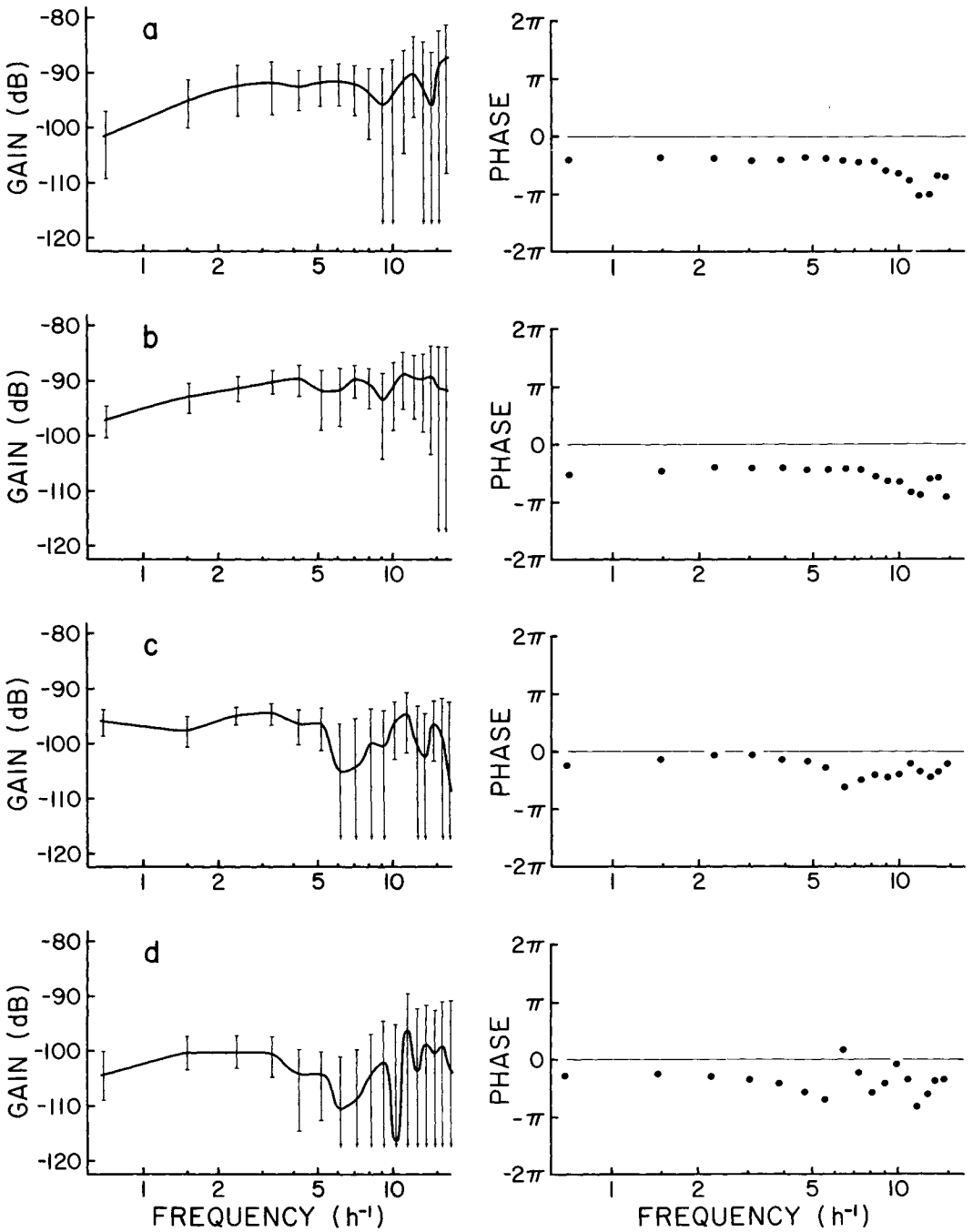

Fig. 5. Gain and phase spectra between time series of irradiance (independent variable) and net inorganic carbon uptake (dependent variable). Gain has units of net inorganic carbon uptake per unit of irradiance. Decibel scale defined as 20 $\log_{10}$ (●). A negative phase lag indicates that net inorganic C uptake leads irradiance. Error bars—95% confidence intervals (those with downward arrowheads denote gain estimates not significantly different from zero).

Table 3. Squared coherencies between time series of irradiance and net inorganic carbon uptake, as a function of frequency.

Frequency (h^{-1})	Squared coherence			
	2 Nov	3 Nov	4 Nov	5 Nov
0.86	0.388*	0.675*	0.611*	0.566*
1.72	0.515*	0.692*	0.674*	0.668*
2.57	0.467*	0.755*	0.848*	0.685*
3.43	0.513*	0.782*	0.782*	0.569*
4.28	0.595*	0.663*	0.618*	0.293*
5.14	0.612*	0.416*	0.526*	0.296*
6.00	0.569*	0.410*	0.054	0.047
6.86	0.485*	0.640*	0.053	0.045
7.72	0.356*	0.559*	0.133	0.045
8.57	0.133	0.281*	0.143	0.071
9.43	0.116	0.328*	0.404*	0.014
10.28	0.237*	0.415*	0.381*	0.136
11.14	0.230*	0.385*	0.192	0.001
12.00	0.090	0.333*	0.100	0.144
12.86	0.045	0.230*	0.390*	0.146
13.72	0.173	0.106	0.116	0.083
14.57	0.205	0.097	0.009	0.010

* Values significantly different from zero at 95% confidence level.

be the result of the previous growth of the organisms at high irradiances (Harris 1978).

The same conclusion about the use of static models does not apply to C uptake; large transient responses were observed, even within the range of light intensities for which the *P–I* plots based on O_2 production were linear (cf. Figs. 3d, 4d). Spectral analysis indicated that the transient fluctuations of inorganic C exchange were important on time scales from ≈10 min to 1 h (Fig. 5, Table 3). However, Harris and Piccinin (1977) found agreement between short term measurements of O_2 release (using an O_2 electrode) and short term (10 min) measurements of ^{14}C fixation at low light intensities. If our results are to be compatible with theirs, we must assume either that the transient fluctuations of inorganic C exchange did not occur in the system they studied or that our data show transient exchanges of inorganic carbon not detected by the ^{14}C technique.

Since a typical light-saturation curve does not describe the fluctuations in inorganic carbon exchange under highly variable light, some other explanation is needed for the transient changes observed here. Although our experiments were not designed to determine physiological mechanisms, it is worthwhile to speculate because of the implications for the interpretation of measurements of C exchange. The transient changes in net inorganic C uptake might be due to photorespiration, if the light-dependent respiratory carbon release responded more slowly to changes in light than did photosynthetic C uptake. Photorespiration could then account for large temporal fluctuations and enhanced rates of carbon release. Conditions in the culture were highly conducive to photorespiration. The afternoon depression of oxygen production in Figs. 2 and 3 occurred as CO_2 fell below 0.0005 mg·liter^{-1} and as pH rose above 10.1. It is possible that photorespiration contributed to the reduced rate of oxygen production and the high rates of carbon release on the afternoons of 3, 4, and 5 November. However, certain observations cannot be entirely explained by photorespiration. Peak rates of inorganic C uptake in Fig. 2b, c were in the afternoon (1400–1500 hours) and were higher than those at comparable light intensities before 1200 hours. Whereas cessation of photorespiration during brief periods of reduced light could possibly restore the rate of C uptake to the levels observed before the onset of photorespiration, we would not expect the rates of C uptake in the afternoon to be higher. Also, rates of oxygen exchange did not exhibit the types of transients normally associated with photorespiration (Harris and Piccinin 1977; Harris 1978).

Transient changes in inorganic carbon exchange could also result from exchanges of carbon between the cell and its environment from a cellular pool of inorganic C. Lehman (1978) postulated that HCO_3^- entered *Chlamydomonas* cells at high pH and was converted to CO_2 at a lower intracellular pH, keeping the intracellular concentration of CO_2 higher than the external values. A similar mechanism could explain our results if the rate of entry of HCO_3^- were a function of light intensity and if some of the

intracellular CO_2 escaped to the medium by passive diffusion. In rapidly increasing light, the net rate of uptake would be high initially, but would decrease as intracellular CO_2 built up and diffusion back to the medium increased. Similarly, with rapidly decreasing light, the net rate of carbon release would initially be high as uptake declined and diffusional loss of CO_2 continued; the rate of release would decrease as the intracellular concentration of CO_2 approached steady state with the lower rate of uptake. Thus in a fluctuating light field, the intracellular concentration of CO_2 would be kept higher at high than at low light intensities.

Substantially the same results could be obtained if the uptake of inorganic carbon were by a light-dependent β-carboxylation into C_4 compounds, followed by decarboxylation to release CO_2 (i.e. the C_4 pathway: Beardall et al. 1976). The high rates of carbon release shown in Fig. 2 could then be due to a temporary continuation of decarboxylation at a high rate after a reduction in light intensity.

The two hypotheses to account for the transient fluctuations of inorganic carbon uptake (photorespiration or enhancement of intracellular CO_2 levels) have different implications for the functioning of the organisms at low concentrations of CO_2. In the first case, the transients are an unavoidable result of photorespiration at low CO_2 and high pH; in the second, the transients are viewed as part of a mechanism for minimizing or avoiding photorespiration. Species differ in their abilities to survive and carry out photosynthesis at high pH and low CO_2 (Talling 1976). It would be interesting to find out whether the presence of transient fluctuations of inorganic C uptake in a fluctuating light field and at low CO_2 is correlated with the differential abilities of species to survive in such environments.

Regardless of the mechanisms responsible for the observed transients, the analysis of short term variations in oxygen and carbon exchange has shown that, not only light *availability*, but light *variability* is an important factor in the production ecology of aquatic systems. As pointed out earlier, models of photosynthetic activity assume that the *P–I* relationship determined under constant light applies in fluctuating light as well. This assumption seems to be valid for oxygen production on diurnal and shorter time scales but is not always correct for carbon uptake on short time scales. Carbon uptake as measured in this study can only be modeled by a time-dependent approach, and, more important, this time-dependent uptake does not necessarily measure the final reduction of CO_2 into organic compounds.

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