

IN SITU QUANTUM EFFICIENCY OF LAKE SUPERIOR PHYTOPLANKTON

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ABSTRACT. *In situ quantum efficiencies were measured in Lake Superior over a 4-day period in 1978 and on one occasion in 1980. In 1980, experimental artifacts caused by exposing deep phytoplankton to elevated irradiances were minimized by the use of SCUBA divers. The trends of quantum efficiency with depth agreed well with theory. In the nutrient-limited upper portion of the euphotic zone, quantum efficiencies increased with depth, whereas in the light-limited lower portion of the euphotic zone, quantum efficiencies were relatively constant. Maximum quantum efficiencies calculated with downwelling irradiances ranged from 0.041 to 0.069 moles C fixed • Einst abs⁻¹ with a mean maximum quantum efficiency of 0.0538 ± 0.0025 moles C fixed • Einst abs⁻¹. Maximum quantum efficiencies in morning experiments ranged from 0.041 to 0.053 moles C fixed • Einst abs⁻¹ and were slightly less than noon values, 0.057 to 0.067 moles C fixed • Einst abs⁻¹. Correction for scalar irradiance would reduce all quantum efficiencies by 25%.*

ADDITIONAL INDEX WORDS: *Primary productivity, light penetration, solar radiation, SCUBA diving.*

INTRODUCTION

The efficiency at which carbon is fixed by phytoplankton is of much concern to limnologists. This efficiency is generally expressed either as a light utilization efficiency (Dubinsky and Berman 1976) where the amount of carbon fixed is related to the total light assimilated by both phytoplankton and nonphytoplankton or as a quantum efficiency (Tyler 1975) where carbon fixed is related to the actual light used in photosynthesis. When the rate of photosynthesis is expressed as quantum efficiency or yield (moles C fixed • Einst abs⁻¹) the theoretical limit is 0.125 (Rabinowitch 1951) whereas the actual attainable limit is closer to 0.10 (Myers 1980). For various reasons such as nitrate reduction and less efficient sensitization of photosynthesis by accessory pigments, Bannister (1974)

suggested that the maximum yield for phytoplankton in lakes is a constant equal to ca. 0.06 moles C • Einst abs⁻¹. This value and its constancy have been debated (Dubinsky 1980, Bannister and Weidemann 1984). Field studies have found quantum maxima ranging from 0.02–0.12 moles C • Einst abs⁻¹ (Tyler 1975; Dubinsky and Berman 1976; Morel 1978; Dubinsky 1980; Bannister and Weidemann 1984; Dubinsky *et al.* 1984; Tilzer 1984 a,b). Furthermore, the exact trend in quantum efficiency with depth is still uncertain (Dubinsky 1980, Dubinsky *et al.* 1984). Theoretically quantum efficiency should be constant at low light (Bannister 1974), however, most *in situ* investigations have not found this trend (Tyler 1975; Dubinsky and Berman 1976, 1981; Morel 1978; Taguchi 1979; Tilzer 1984 a,b). In fact, all possible trends of quantum efficiency at low light have been found.

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The quantum efficiency of Great Lakes phytoplankton has not been measured. This study was conducted to determine the maximum quantum efficiency of Lake Superior phytoplankton and the trend in quantum efficiency with depth. Our results suggest that quantum efficiencies reach a plateau near the maximum yield at low light. However, the maximum value obtained in our profiles is not a constant but varied diurnally.

METHODS

Samples were collected at one station in Lake Superior on 15 to 20 August 1978, 47° 8' 36"N, 87° 54' 36"W, and at a nearby station on 12 August 1980, 46° 59' 53" N, 88° 11' 44"W. Incident photosynthetically active radiation (PAR) was measured with a recording and/or integrating quantum meter with a Licor model LI-129S quantum sensor. Cosine corrected diffuse downwelling irradiance was measured during each *in situ* primary production experiment with a Licor model LI-192S quantum sensor. Cosine corrected upwelling irradiance was also measured twice during the sampling period with a Licor model LI-192S quantum sensor. Spectral light measurements were taken by Dr. B. Premo at 5, 10, 15, and 20 m at 10-nm intervals with a scanning quantaspectrometer (QSM-2500) manufactured by Techtum Instruments. Temperature was measured with a mechanical bathythermograph.

Chlorophyll concentrations were determined from samples extracted with 90% acetone in 1980 and by *in vivo* fluorescence in 1978. *In vivo* fluorescence was measured with a pump sampling system (Moll and Stoermer 1982) and calibrated with extracted chlorophyll samples taken from the fluorometer exhaust.

Phytoplankton samples from 1978 were preserved and prepared for identification and enumeration as described in Stoermer and Tuchman (1979). Phytoplankton samples from 1980 were preserved with Lugol's solution (Vollenweider 1974) and permanent slides were prepared (Dozier and Richerson 1975). Phytoplankton were counted under oil immersion at 1250X with a Leitz Ortholux microscope.

Primary production was measured *in situ* by the ¹⁴C technique (Vollenweider 1974). Two or three light bottles and one dark bottle were incubated at each depth. Procedures used in 1978 and 1980 were similar with one exception. A decontamination procedure (Lean and Burnison 1979) was used in

1980 but not in 1978. Low production rates may be difficult to determine without the use of a decontamination procedure (Williams *et al.* 1972). To produce greater compatibility between 1978 and 1980 techniques all light bottle uptake rates in 1978 that were less than the average dark bottle rates were excluded from this study.

Prior to the start of production incubations, extreme care was taken to protect the bottles from elevated irradiances. In 1978 all light bottles were covered with a black shield that was removed when the bottles were 1 to 2 m below the surface. In 1980 the black shields were removed by SCUBA divers at 10 to 15 m or at shallower *in situ* depths.

Quantum yields at depth *Z* were calculated over the interval of the incubation (*t*₁-*t*₂) with the equation:

$$\delta_z = \frac{\bar{P}_z}{12\bar{a}_c C_z \int_{t_1}^{t_2} I_z(t) dt} \quad (1)$$

where δ_z = quantum yield (moles C fixed • Einst abs⁻¹), \bar{P}_z = carbon fixed (gC • m⁻³), I_z = quanta received (Einst m⁻² sec⁻¹), C_z = chlorophyll concentration (mg Chl • m⁻³), and \bar{a}_c = mean absorption coefficient (m³ • mg Chl⁻¹). To solve the integral in equation (1) Beer's law was used:

$$I_z(t) = I_0(t)e^{-\epsilon z} \quad (2)$$

where ϵ = extinction coefficient (m⁻¹) and I_0 = quanta received at the surface. The extinction coefficient was determined at each depth by simultaneous measurements of I_0 and I_z during each incubation period.

The mean absorption coefficient (\bar{a}_c) is the most difficult parameter in equation (1) to determine. The procedure used to estimate \bar{a}_c considers the light absorption spectra of the dominant alga, as well as the spectral quality of light (Morel 1978, Atlas and Bannister 1980). During these experiments diatoms, particularly small species of *Cyclotella*, dominated the phytoplankton assemblage. Therefore, to estimate \bar{a}_c , underwater spectral irradiances measured at 5, 10, 15, and 20 m were combined with the relative absorption spectrum for the diatom, *Navicula minima*, taken from Lattimer and Rabinowitch (1959). The value of a_c (675nm) was assumed to be 0.022 m² • mg Chl⁻¹ (Morel and Bricaud 1981). The following equation was used to calculate \bar{a}_c :

$$\bar{a}_c = [\sum a_c(\lambda) i(\lambda)] / [\sum i(\lambda)] \quad (3)$$

where \bar{a}_c = mean absorption coefficient ($m^2 \cdot mg \text{ Chl}^{-1}$), i = quanta received at wavelength λ , and a_c = absorption coefficient at wavelength λ .

RESULTS

Thermal stratification was present during all sampling (Fig. 1). The surface temperature ranged from 15 to 16.5°C in 1978 and was 17°C in 1980. The depth of the epilimnion was quite variable in 1978, ranging from less than 5 m on 16 August to greater than 10 m on 19 August. The extent of the euphotic zone (1% light level) was between 25 and 30 m. Vertical chlorophyll distributions were also quite variable, with subsurface maxima located between 20 and 25 m (Fig. 1). Chlorophyll concentrations at the maximum were 2 to 3 times surface concentrations (Fig. 1). Phytoplankton species

composition was similar throughout the water column in 1978 and 1980 and was dominated by small *Cyclotella* species, such as *C. stelligera*, *C. comensis*, and *C. ocellata*.

The spectral irradiance measurements exhibited a band of maximum penetration at ca. 510 nm. The mean absorption coefficient, \bar{a}_c , exhibited little change with depth (Table 1). Because the variability among depths was less than 5% of the mean, differences may have resulted from variability in underwater light measurements. Furthermore, our mean absorption coefficients decreased slightly with depth while the absorption coefficients determined by Jerome *et al.* (1983) for Lake Superior using the absorption spectrum for chlorophyll and spectral light measurements increased slightly. Therefore, an average \bar{a}_c of $0.017 m^2 \cdot mg \text{ Chl}^{-1}$ was used for all determinations of quantum yield. All quantum yield determination were made with downwelling irradiance measurements. Since measurements of upwelling irradiance were also made, it is possible to estimate scalar irradiance (Kirk 1981). Estimated scalar irradiance is approximately 25% higher than downwelling irradiance.

TABLE 1. Calculated mean spectral absorption coefficients, \bar{a}_c ($m^2 \cdot mg \text{ Chl a}^{-1}$).

Depth (m)	\bar{a}_c
5	0.0173
10	0.0175
15	0.0168
20	0.0167

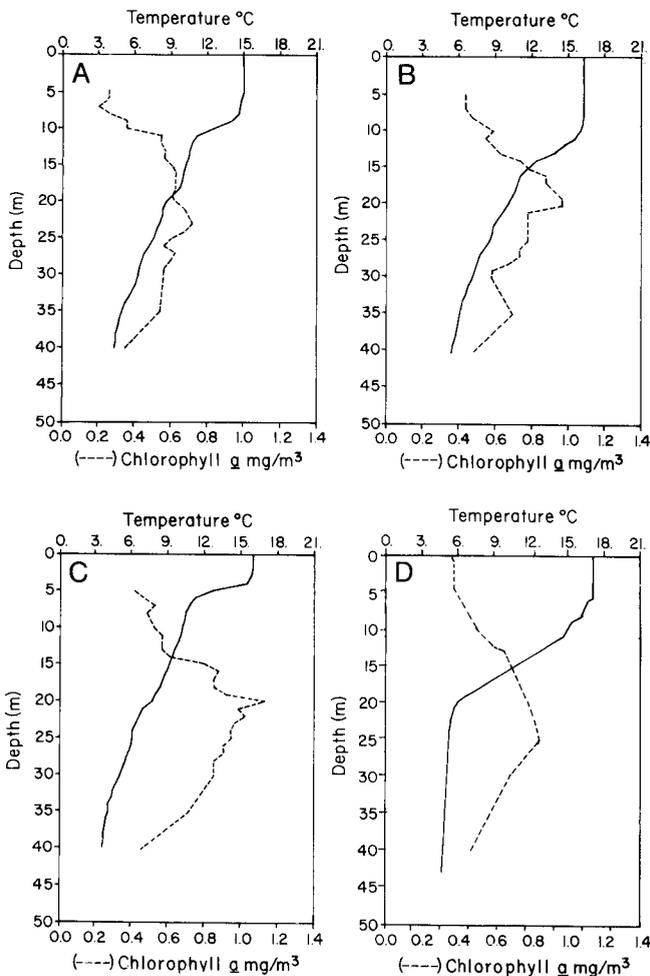


FIG. 1. Temperature and chlorophyll profiles from A) 16 August 1978, B) 17 August 1978, C) 19 August 1978, and D) 12 August 1980.

Quantum yields increased with depth reaching a maximum of ca. 0.07 moles C • Einst abs⁻¹ with one higher value (Fig. 2). Because of differences in irradiance at similar depths in the composite data set, trends in quantum yields are presented for individual profiles that represent a cloudy day (Fig. 3a), partly cloudy day (Fig. 3b), and 2 sunny days (Figs. 3c and 3d). In all profiles, quantum yields increased with depth (Fig. 3). Maximum yields (moles C • Einst abs⁻¹) determined from the mean (± 1 S.D.) of light bottles in these three profiles are: 0.069 ± 0.013 at 15 m (Fig. 3a), 0.058 ± 0.004 at 20 m and 0.059 ± 0.002 at 25 m (Fig. 3b), 0.067 ± 0.002 at 25 m and 0.060 ± 0.010 at 30 m (Fig. 3c), and 0.043 ± 0.007 at 20 m and 0.041 ± 0.008 at 25 m (Fig. 3d and Table 2). Maximum

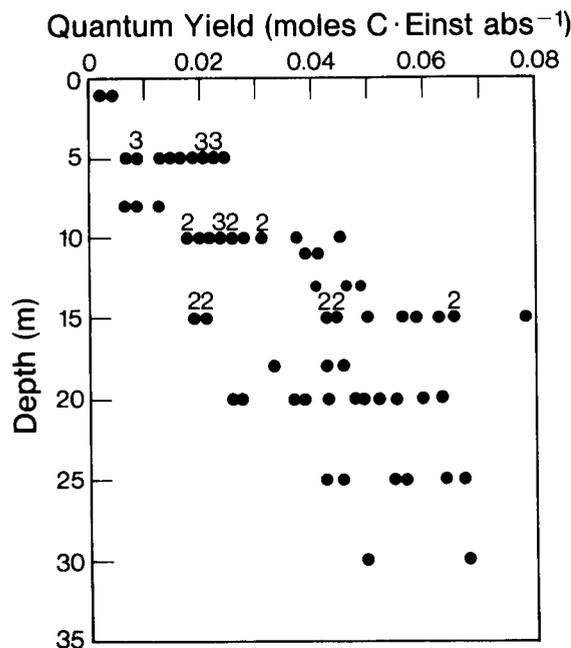


FIG. 2. Composite data set (1978 and 1980) of quantum efficiency and depth. Each point represents a single light bottle while numbers represent additional bottles.

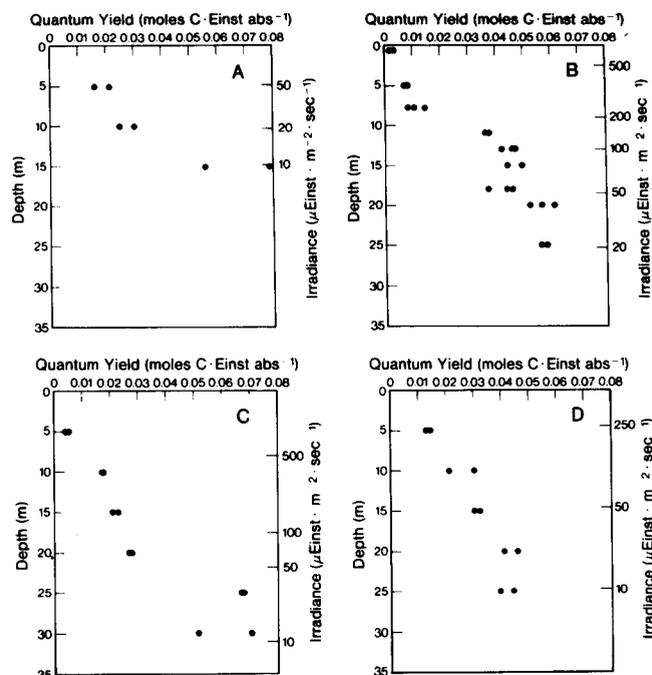


FIG. 3. Individual profiles of quantum efficiency, depth and irradiance which represent (A) cloudy day 16 August 1978(n), (B) partly cloudy day 12 August 1978(n), (C) sunny day 17 August 1978(n), and (D) sunny day 16 August 1978(m).

TABLE 2. Summary of all in situ profiles with dates and periods of day (m = morning, n = noon, a = afternoon), average surface irradiances during incubation ($\mu\text{Einst} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$), depth(s) and maximum quantum efficiencies determined from the mean of light bottles (moles C fixed $\cdot \text{Einst abs}^{-1}$), and the highest light levels at which the maximum quantum yields were achieved ($\mu\text{Einst} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$).

Date	Surface irradiance	Depth(s) and maximum quantum efficiencies (± 1 S.D.)	Light Level at quantum maximum
16 August 1978 (m)	622	20 m-0.043 \pm 0.007 25 m-0.041 \pm 0.008	22.2
16 August 1978 (n)	283	15 m-0.062 \pm 0.002 20 m-0.057 \pm 0.003	21.6
16 August 1978 (a)	122	15 m-0.069 \pm 0.013	9.8
17 August 1978 (m)	471	15 m-0.053 \pm 0.009	27.8
17 August 1978 (n)	1,832	25 m-0.067 \pm 0.002 30 m-0.060 \pm 0.010	36.4
17 August 1978 (a)	760	15 m-0.048 \pm 0.020 20 m-0.051 \pm 0.014	26.4
19 August 1978 (m)	157	15 m-0.046 \pm 0.002	12.5
12 August 1980 (n)	731	20 m-0.058 \pm 0.004 25 m-0.059 \pm 0.002	35.0

quantum yields for all eight profiles ranged from 0.041 to 0.069 moles C • Einst abs⁻¹ (Table 2) with a mean (± 1 S.E.) of 0.0538 ± 0.0025 . Although not statistically significant, a diurnal trend of maximum quantum yields was evident. Maximum quantum yields from morning profiles (0.041 to 0.053 moles C • Einst abs⁻¹) were less than from noon profiles (0.057 to 0.067 moles C • Einst abs⁻¹). These quantum yield maxima were achieved at low light, 9.8 to 36.4 Einst • m⁻² • sec⁻¹ (Table 2).

The depth of the maximum quantum efficiency increased with the amount of surface irradiance, i.e., the shallowest maximum when cloudy and deepest when sunny (Fig. 3). In three of the four profiles presented, quantum yields reached a maximum at low light and then appeared to remain constant (Figs. 3b, 3c, and 3d). This trend is found in all profiles where quantum yields were measured at more than three depths. In the rest of the profiles, data were obtained at only three depths and no trend could be determined at low light (e.g., Fig. 3a) since in these profiles usually only one measurement was made in the light-limited region of the euphotic zone.

DISCUSSION

The maximum efficiency of phytoplankton photosynthesis in lakes is an important parameter in describing phytoplankton growth (Laws and Bannister 1980, Kiefer and Mitchell 1983). The value of this parameter is generally assumed to be 0.06 mole C fixed • Einst abs⁻¹ (Bannister 1974). Recently, Bannister and Weidemann (1984) suggested that the maximum *in situ* quantum efficiency is 0.03 to 0.07 moles C • Ein abs⁻¹. The range of maximum quantum efficiencies found in this study, 0.041 to 0.069 moles C • Ein abs⁻¹ (0.031 to 0.052 moles C • Ein abs⁻¹ if scalar irradiance is used) is consistent with Bannister and Weidemann. However, the idea of a constant maximum quantum efficiency has to be questioned since the range of maximum quantum efficiencies observed in our study appears to be related to the diurnal cycle.

Trends of quantum efficiency with depth in aquatic environments have also received much attention. All *in situ* quantum yields (Tyler 1975; Dubinsky and Berman 1976, 1981; Morel 1978; Taguchi 1979; Bannister and Weidemann 1984; Dubinsky *et al.* 1984; Tilzer 1984a, b; present study) increased with depth as predicted by theory

(Bannister 1974, Kiefer and Mitchell 1983). However, near the base of the euphotic zone, previously observed trends of *in situ* quantum yield were not always consistent with the expectation that quantum yields reach maximum values at low light and then remain constant with depth. Most *in situ* quantum yields increased with depth with no apparent leveling off at low light. Our results produced quantum yields that are maximal and plateau at low light.

Some of the observed variability in quantum yields at low light can be related to two experimental problems: measuring photosynthesis at low light levels and determining light absorption by phytoplankton. Spurious primary production rates can be caused by exposing phytoplankton obtained from deep in the water column to elevated surface and near-surface irradiances. When experimental artifacts of this kind are eliminated, as in this study, quantum yields were found to level off at low light. The possibility of this artifact (Dubinsky 1980) could not be dismissed from most previous *in situ* quantum efficiency studies (Tyler 1975; Dubinsky and Berman 1976, 1981; Morel 1978; Taguchi 1979; Bannister and Weidemann 1984; Dubinsky *et al.* 1984; Tilzer 1984a, b).

The second, and probably more difficult, problem is obtaining reliable measurements of light absorption (mean absorption coefficient). Subtle changes in light absorption with depth can affect quantum yields at low light (Dubinsky 1980). These changes can be directly related to phytoplankton by species composition changes with depth, by "photoadaptation" of a specific population (Falkowski 1980, Prezelin 1981), or by a spectral shift in light quality with depth (Atlas and Bannister 1980). Most previous *in situ* quantum yield investigations assumed that light absorption did not change with depth. This assumption is certainly less troublesome than measurements of actual light absorption but all too often has not and probably could not be justified.

One of the best ways to determine the mean absorption coefficient, \bar{a}_c , is to combine the *in situ* light absorption spectrum of the phytoplankton at each depth (Kiefer and SooHoo 1982) with the spectral quality of light (Morel and Bricaud 1981). In our investigation, the observed spectral quality of underwater light was combined with an assumed absorption spectrum of diatoms, the dominant phytoplankton. Thus, our trend of quantum yields at low light is correct only if the absorption coefficient did not change in the lower euphotic zone, or

at depths ranging from 15 to 30 m. We do not think absorption coefficient changed because phytoplankton composition was uniform in this region and opportunity for "adaptation" was minimized. Over the short time period of the study the system was highly variable in terms of both thermocline location (Fig. 1) and incident irradiation (Table 2). This environmental variability probably did not allow the phytoplankton in the 15 to 30-m region sufficient time to reach different degrees of "adaptation" (Jorgensen 1964, Falkowski 1980, Prezelin and Matlick 1980; Côté and Platt 1983). Furthermore, slopes of photosynthesis and irradiance versus depth in the lower euphotic zone are similar (Table 3), suggesting that the absorption coefficient is constant (Bannister and Weidemann 1984). Therefore our trend of constant quantum efficiency at low light is probably correct. It should be noted, however, that Jerome *et al.* (1983), using light data from Lake Superior and absorption spectrum for chlorophyll taken from Prieur and Sathyendranath (1981), found light absorption by the phytoplankton should increase slightly in the lower euphotic zone. The increases they found would have little effect on our trends but point to the importance of determinations of *in situ* light absorption in Lake Superior.

Our results suggest that quantum efficiencies in Lake Superior increase with depth and reach a maximum at low light and then remain relatively constant. Support for this pattern can be found outside theoretical considerations (Bannister 1974, Kiefer and Mitchell 1983). In laboratory studies of sun and shade adapted plants, maximum quantum yields determined at low light were similar (Bjorkman *et al.* 1972, Gauhl 1969, Senger and Fleischhacker 1978). Senger and Fleischhacker found that light "adaptation" had no influence on the maximum quantum efficiency of the alga,

Scenedesmus obliquus. Tilzer *et al.* (1975) found that light utilization efficiencies were relatively constant throughout the region of light limitation in Lake Tahoe while Tilzer (1984a, b) found some profiles which exhibited relatively constant quantum yields at low light at periods of weak or no thermal stratification. Tilzer *et al.*'s (1975) results are particularly interesting since they took phytoplankton from one depth and incubated them throughout the euphotic zone, thus ensuring that the light absorption capabilities of the phytoplankton were similar. Provided the spectral quality of light did not change significantly in the lower euphotic zone, which seems probable given dominance of diatoms (Goldman 1980) and the blue water (Atlas and Bannister 1980), then Tilzer's trends at low light should reflect trends in quantum yields.

The apparent variability in quantum efficiency at low light appears to be real and should be expected based on information from previous studies. The maximum quantum efficiency at low light will depend on factors of varying importance in different environments. Maximum quantum efficiency can be influenced by nutrient availability (Kok 1948, Welschmeyer and Lorenzen 1981), chromatic adaptation (Bordy and Emerson 1959), phytoplankton size (Taguchi 1980), and diel cycle (Tilzer 1984b, present study). Therefore, trends in maximum quantum efficiency diverging from theory and laboratory studies may be found in some environments, particularly in highly stratified eutrophic environments where strong gradients in nutrient supply and spectral light quality exist.

Obtaining information on *in situ* quantum efficiency with depth can be important in understanding the environmental control of primary production. Dugdale (1967) proposed that the euphotic zone can be divided into two regions, an upper

TABLE 3. Slopes of log transformed, normalized primary production and irradiance versus depth for samples from the lower euphotic zone in Figures 3b-d.

Date		Slopes \pm S.E.
12 August noon (Fig. 3b)	Production	- 0.12 \pm 0.02
	Irradiance	- 0.14 \pm 0.01
17 August noon (Fig. 3c)	Production	- 0.12 \pm 0.02
	Irradiance	- 0.16 \pm 0.01
16 August morning (Fig. 3d)	Production	- 0.17 \pm 0.03
	Irradiance	- 0.14 \pm 0.01

nutrient-limited region and a lower light-limited region. Theoretically, in some environments these regions can be related to patterns of quantum efficiency with depth. The region where quantum efficiency increases with depth is the region where light is saturating or inhibiting and coincides with Dugdale's nutrient-limited region, and the region where quantum efficiency is relatively constant is the region where light is limiting and coincides with Dugdale's light-limited region (Bannister 1974, Tilzer *et al.* 1975). This information can also be used to determine the possibility of nutrient-light interactions (Rhee and Gotham 1981).

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