Phytoplankton Productivity in Relation to Light Intensity: A Simple Equation

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A simple exponential equation is used to describe photosynthetic rate as a function of light intensity for a variety of unicellular algae and higher plants where photosynthesis is proportional to $(1 - e^{-\beta I})$. The parameter $\beta\ (= I_k^{-1})$ is derived by a simultaneous curve-fitting method, where **I** is incident quantum-flux density. The exponential equation is tested against a wide range of data and is found to adequately describe **P** *vs.* **I** curves. The errors associated with photosynthetic parameters are calculated. **A** simplified statistical model (Poisson) of photon capture provides a biophysical basis for the equation and for its ability to fit a range of light intensities. The exponential equation provides a non-subjective simultaneous curve fitting estimate for photosynthetic efficiency (a) which is less ambiguous than subjective methods: subjective methods assume that a linear region of the **P** *vs.* **I** curve is readily identifiable. Photosynthetic parameters β and a are used widely in aquatic studies to define photosynthesis at low quantum flux. These parameters are particularly important in estuarine environments where high suspended-material concentrations and high diffuse-light extinction coefficients are commonly encountered.

Introduction

Marine primary production is responsible for at least 30% of total global carbon fixation. As such, it occupies a key position in any assessment of the global carbon cycle or perturbations in that cycle. Photosynthesis consists of two basic reactions: a photochemical reaction whereby electromagnetic energy is converted to biochemical energy and a biochemical reaction whereby biochemical energy is utilized to synthesize reduced carbon compounds. Whereas the basic components of these reactions have been delineated, many of the specific reactions and aspects of the controlling mechanisms are as yet poorly known or understood. There is, however, wide ranging interest in developing mathematical models of photosynthesis in general (Farquhar & Caemmerer, 1983) and for marine and estuarine primary production in response to environmental variables in particular.

The three major environmental variables that control photosynthesis are light, temperature, and some function of nutrient availability. Perhaps the greatest attention has been given to light. For example, the rate of photosynthesis is a function of light over a

certain range of low to intermediate light intensities, but is essentially independent of light intensity over a second range of intermediate to high light intensities (which support maximal rates of photosynthesis), and can be photoinhibited at high light intensities. A number of empirical mathematical formulations, ranging from simple equations to complex multiparameter equations have been used to describe photosynthesis as a function of light intensity.

These equations have found broad applications ranging from describing crop production (Monteith, 1979; Band *et al.,* 1981) to estimating photosynthetic oxygen production or carbon assimilation by phytoplankton (Platt *et al.,* 1977; Woods & Onken, 1982).

In this paper, photosynthesis *vs.* light intensity *(P vs. I)* is described using a simple exponential equation of the form $(1 - e^{-\beta I})$, where the parameter β is empirically derived and Z is the incident quantum-flux density (light intensity). Various formulations of the equation have been used to describe the photosynthesis **of** trees (Webb *et al.,* 1974), algae associated with coral reefs (Chalker, 1981), calcification of corals in relation to light intensity (Grans & Macintyre, 1976), marine phytoplankton (Platt *et al.,* 1980), and estuarine phytoplankton where the photic depth is very shallow (Peterson *et al.,* in press). More complex higher order equations, with more variables, may provide better fits to *P vs. I* data. However, this exponential equation appears to be a close fit—with *so* few parameters—to a wide variety of data.

This paper describes the equation to fit *P vs. I* curves with a minimum number of parameters. The equation is tested against laboratory and field data from a wide variety of species and conditions to determine if, and how well, it accommodates such a range. The errors associated with the equation functions are computed for the calibration data. A physical model, based on photon capture, is described, The photon-incidence model (Poisson) suggests that there is a biophysical basis for the equation and that one exponential curve should adequately fit the whole range of light intensities (up to light-inhibition intensities). The use of a simple linear regression to determine the initial slope of the *P vs.* Z curve, the photosynthetic efficiency (**PSE**) or *a,* may actually underestimate light capture efficiency at low photon flux. Understanding photosynthetic responses to low light intensities is crucial to understanding estuarine photosynthesis and carbon flux because water-column light attenuation by suspended organic and inorganic particles is severe in many estuaries (cf. Peterson & Festa, 1984).

Methods and results

Empirical exponential equation describing P vs. I *curves*

The quantitative relation between gross rates of photosynthetic performance (oxygen production or carbon assimilation) and light intensity is described by the exponential equation:

$$P_G/P_{Gmax} = 1 - e^{-\beta I} \tag{1}$$

where P_{Gmax} is the maximum gross photosynthetic capacity, P_G is the photosynthetic performance at Z, Z is the incident light intensity, and β is a derived constant for the data set (see below). When respiration, **R,** is defined as negative carbon assimilation (i.e. $P_G = P_N - R$), the relationship may also be expressed, perhaps more usefully, as:

$$P_N = P_{Gmax} - P_{Gmax} e^{-\beta I} + (P_{Nmax} - P_{Gmax}) \tag{2a}$$

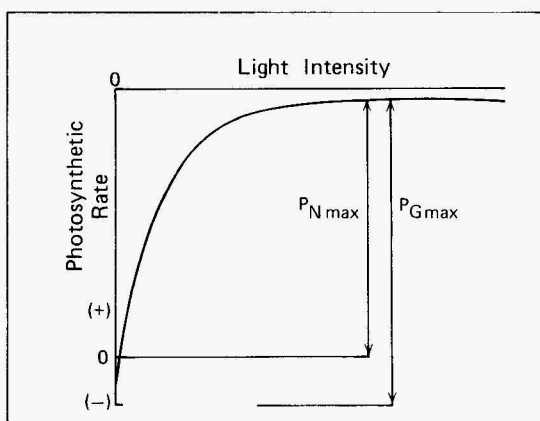$$\text{or, } P_N = P_{Nmax} - P_{Gmax} e^{-\beta I} \tag{2b}$$

Figure 1. Photosynthetic rate (in relative units) as a function of light intensity. Following equation (2), P_{Nmax} is the net photosynthesis and P_{Gmax} is the gross photosynthesis.

where P_N is now the observed or net productivity and an estimate of the respiration rate (or net loss of carbon) is incorporated as the difference in the derived constants $P_{Nmax} - P_{Gmax}$ (Figure 1). The constants P_{Nmax}, P_{Gmax}, and β, and their percentage relative standard errors were estimated using an exponential least squares method (see Appendix).

Using equation (2), the empirically observed values of net oxygen and carbon productivity were related to light intensity. Effects of light inhibition are not described by equations (1) and (2) and are not evaluated. In a few instances, lower productivity values were observed at higher light intensities than the intensity of maximum productivity, suggesting slight photoinhibition. These lower rates were set equal to the value of maximum productivity for this evaluation.

Relative standard error is the standard error divided by the value of the derived parameter and multiplied by 100 (the coefficient of variation, CV). Using the data of Irwin *et al.* (1975), the square of relative standard error $(CV)^2$ estimates of the parameter β were found to have a near-linear relation to R^2 (the ratio of the sum of the squares to total sum of the squares):

$$(CV)^2\beta = 1\cdot4 \times 10^4 - 1\cdot4 \times 10^4\,R^2 \tag{3}$$

It is also interesting to note that the frequency distribution in errors of the derived parameters P_{Nmax}, P_{Gmax}, and β, closely follow a·log-normal distribution for the data of Irwin *et al.* (1975). To minimize the number of figures this relation is only illustrated for errors in β (Figure 2). Too few sets of observations were made in the other studies reported to be able to complete a similar statistical analysis. However, with more observations, they would also be expected to follow a lognormal frequency distribution. Related examples of lognormal or approximately lognormal frequency distributions are apparent in the literature (cf. Malone & Neale, 1981, for P_{max} and PE; Senger & Fleishhacker, 1978a, algal cell size) and the sample frequency distribution in plankton abundance has been adequately described as lognormal (Aitchison & Brown, 1963). Implications of lognormal frequency distributions in studies of natural systems have been reviewed (Aitchison & Brown, 1963) but seem not to have been pursued for phytoplankton. For example, the lognormal frequency distribution in productivity (Figure 3) cannot be explained simply by physical factors (cf. Bencala & Seinfeld, 1976).
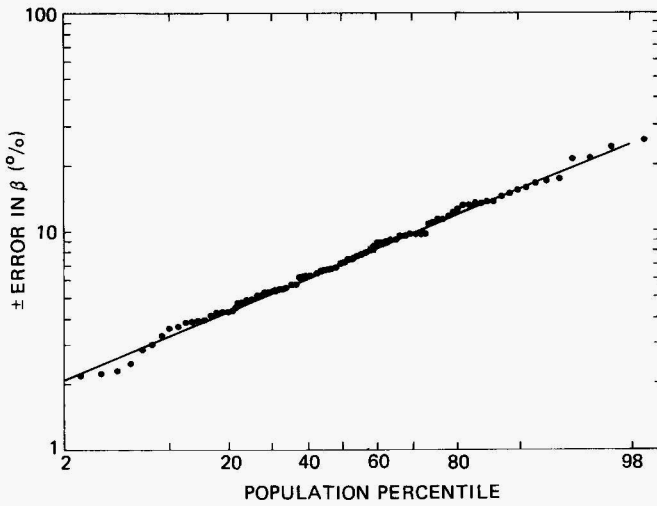
Figure 2. The frequency distribution of error for the parameter β is compared to a lognormal frequency distribution. Data are from Irwin *et al.* (1975) set B with 10 light-intensity determinations and 94 experiments (see Table 4).
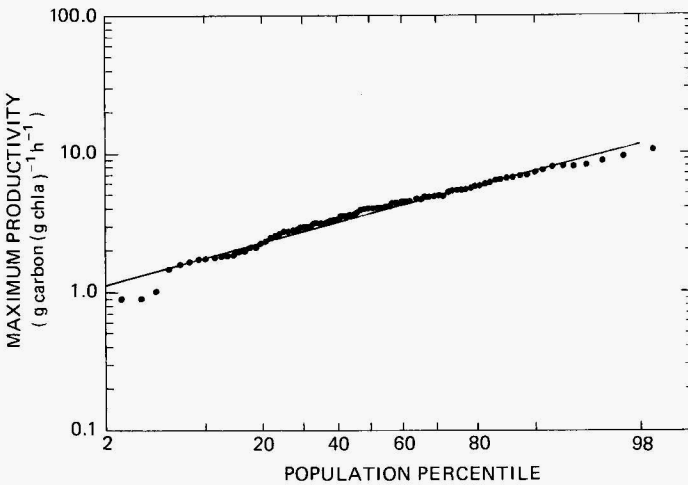

Figure 3. The frequency distribution of maximum productivity compared to a lognormal frequency distribution. Data are from Irwin *et al.* (1975) set B with 10 light-intensity determinations and 94 experiments (see Table 4).

Data base to test equation applicability

There are few calibration standards for evaluating the observations of *P vs. I* experiments. Partly for this reason, the performance of the equation was first examined against very precise and highly controlled laboratory observations of Bjorkman and co-workers (1971, 1975) for plant leaves, of Myers and Graham (1971) for the alga *Chlorella,* and of Perry *et al.* (1981) for a variety of marine phytoplankton. Analysis of natural assemblages includes experiments of Irwin *et al.* (1975) for Nova Scotian waters, Harding *et al.* (1981)

for California coastal phytoplankton, Peterson *et al.* (in press) for the San Francisco Bay estuary, Hass *et al.* (1981) for the York River Estuary, and Cole and Harmon (1981) for the Potomac estuary. For a complete description of the data, consult the original papers.

Data of Bjorkman et al. *(1971,1975).* Mean values of direct gas-exchange observations of plant-leaf photosynthesis are accurate relative to similar photosynthetic observations for phytoplankton. The leaf sample is typically much larger than for phytoplankton photosynthesis determinations, where values from the carbon-I4 method commonly used for phytoplankton photosynthesis may lie somewhere between gross and net assimilation rates (cf. Peterson, 1980).

The mean precision of derived parameters was found to be high (Table 1). Quantum yield, estimated by the equation $(P_{\text{Gmax}} \times \beta)$ (Absorbance)$-'$, is reasonable (Table 1), but this is not a thorough validation of this method of simultaneous curve-fitting for estimating quantum yield. The estimate depends largely on the number and accuracy of observations at low light intensities. However, the results are not unreasonable, indicating that the simultaneous method using the complete *P vs. Z* curve did not result in an obvious error, i.e. carbon-per-quantum values that were clearly too high or too low. To our knowledge this is the first time the simultaneous method has been tested against a known standard.

Data of Myers and Graham *(1971).* Algal cultures *(Chlorellapyrenoidosa)* were grown at six different light intensities to study the productivity (as measured by photosynthetic oxygen evolution) vs. light intensity curve. Absolute values of quantum **flux** for plant conditioning were not available. Each of the six different curves was quantitatively defined by 9–14 observations (Myers & Graham, 1971). The *P* vs. *Z* experiments were repeated four times for algae conditioned at two of the six different intensities, yielding growth rates of 2·4 and 0.78 day^{-1} (Table *2*, Myers & Graham, and unpublished data). Mean relative errors in the derived parameters in fitting equation *(2)* to observations of Myers and Graham (1971 and unpublished data) are small. The largest error lies in the parameter $\beta \pm 7.7\%$ (Table *2*).

Data of Perry et al. *(1981).* Cultures of seven species of marine phytoplankton, adapted to first high and then low light intensity, were harvested during the log phase of growth. *P vs. I* was determined by the carbon-14 method with *2.5* h incubations at 11 light intensities.

The precision estimates of the parameters derived were high (Table 3). All of the derived parameters $(P_{\text{Nmax}}, P_{\text{G max}},$ and $\beta)$ for the low growth-light phytoplankton showed a consistent difference from the parameters of the high growth-light phytoplankton with the exception of β for low growth-light *Thalassiosirapseudonana.*

Data of Irwin et al. *(1975).* The exponential equation is best illustrated for natural phytoplankton assemblages using the data of Irwin *et al.* (1975). One hundred and eighty five carbon-14 uptake incubation experiments were performed in duplicate with water samples collected at three coastal locations near Nova Scotia over a period from 1973 to 1975. In the earliest experiments, six different light intensities were used to define *P vs. Z* curves. Later the study was expanded to include up to 10 points on the curves. Duplicate experiments, presumably using different incubators, are arbitrarily labeled here as A and B (the A data set is taken from the left-hand page of their report, the B data set is taken from the right-hand page). Their 4-h incubations used artificial (tungsten) light. The initial nutrient concentrations were not determined. Although some variability in results might

TABLE 1. Photosynthetic parameters for plant leaves[a]

Species	$\bar{I}$[b] (quantum cm^{-2} s^{-1})	P_{Nmax} (μmol C m^{-2} s^{-1})	P_{Gmax}	β (quanta^{-1} cm^2 s)	$P_{Gmax}\beta$ (carbon quanta^{-1})	Assumed[c] absorptance (%)	Quantum efficiency[d] (mole C/mole absorbed light)	Data source
Atriplex[e] *triangularis*	3.7×10^{16}	34.3 (1.3%)[f]	37.6 (1.2%)	2.9×10^{-17} (3.5%)	0.065	85	0.071	Björkman *et al.* (1971)
Atriplex triangularis	3.5×10^{16}	24.2 (0.6%)	26.2 (0.7%)	4.5×10^{-17} (1.9%)	0.071	82	0.086	Björkman *et al.* (1971)
Atriplex triangularis	3.7×10^{15}	6.5 (1.4%)	7.0 (2.3%)	1.8×10^{-16} (6.5%)	0.074	80	0.092	Björkman *et al.* (1971)
Tidestromia oblongifolia	7.0×10^{16}	51.8 (5.0%)	54.9 (4.4%)	1.6×10^{-17} (10.0%)	0.048			Björkman (1975)
Atriplex nastata	3.0×10^{16}	24.0 (1.9%)	26.7 (2.1%)	4.3×10^{-17} (5.9%)	0.068			Björkman (1975)
Alicasia macrorrhiza	2.0×10^{14}	3.3 (5.2%)	3.7 (7.7%)	4.3×10^{-16} (17.0%)	0.110			Björkman (1975)
Mean		(2.6%)	(3.1%)	(7.4%)			0.083[g]	

[a] Estimated by simultaneous exponential least-squares fit of all *P vs. I* experimental data to $P = P_{Nmax} - P_{Gmax} e^{-\beta I}$.

[b] Daily-mean PAR of the growth-light regime.

[c] cf. Björkman (1981: 66) for PAR absorbance of plant leaves: approximately 0.73 (250 mg chl m^{-2}) to 0.87 (759 mg chl m^{-2}); high-, intermediate-, and low-light growth plants.

[d] Calculated from $P_{Gmax} \beta$ (% absorbance)$^{-1}$.

[e] Note that each of the *Atriplex triangularis* experiments consisted of nine data points with only two in the light-intensity range 0–55 μ Em^{-2} s^{-1} for high-light grown and three in that range for intermediate and low-light grown plants.

[f] See text and Appendix for definition of relative standard error in derived parameters.

[g] All three values were actually 0.081 based on a linear fit to four quantum efficiency observations made in the range 0–<55 μEm^{-2} s^{-1} monochromatic light at 654 nm (Björkman *et al.*, 1971: 117, Figure 19).

TABLE 2. Photosynthetic parameters from *P vs. I* curves for *Chlorella pyrenoidosa*; data of Myers and Graham (1971 and unpublished). In some instances, photosynthetic rates of highest intensities indicated slight light-inhibition effects, and these values were assumed to be equivalent to the maximum values observed at a lower light intensity

Specific growth rate (days^{-1})	P_{Nmax}	P_{Gmax}	β
	[moles O$_2$ (mol chl $a+b$)$^{-1}$ h^{-1}]		($\times 10^{-16}$ quantum^{-1} cm^2 s)
2·40	418·1 ($\pm 1\cdot 2\%$)	433·1 ($\pm 1\cdot 5\%$)	0·62 ($\pm 4\cdot 7\%$)
2·40	490·3 ($\pm 1\cdot 8\%$)	506·0 ($\pm 2\cdot 8\%$)	0·58 ($\pm 6\cdot 8\%$)
2·40	436·8 ($\pm 1\cdot 5\%$)	455·0 ($\pm 2\cdot 1\%$)	0·58 ($\pm 6\cdot 8\%$)
2·40	406·1 ($\pm 1\cdot 1\%$)	424·0 ($\pm 2\cdot 1\%$)	0·57 ($\pm 5\cdot 2\%$)
2·30	293·1 ($\pm 2\cdot 3\%$)	309·2 ($\pm 2\cdot 6\%$)	0·58 ($\pm 11\%$)
1·80	198·7 ($\pm 1\cdot 2\%$)	212·2 ($\pm 2\cdot 8\%$)	1·19 ($\pm 5\cdot 8\%$)
1·30	165·6 ($\pm 1\cdot 8\%$)	178·8 ($\pm 2\cdot 8\%$)	1·49 ($\pm 7\cdot 3\%$)
0·78	142·5 ($\pm 2\cdot 9\%$)	161·7 ($\pm 4\cdot 2\%$)	1·74 ($\pm 11\%$)
0·78	153·1 ($\pm 2\cdot 8\%$)	166·0 ($\pm 4\cdot 0\%$)	1·45 ($\pm 11\%$)
0·78	157·5 ($\pm 1\cdot 7\%$)	173·0 ($\pm 2\cdot 7\%$)	1·65 ($\pm 7\cdot 2\%$)
0·78	153·5 ($\pm 1\cdot 1\%$)	181·0 ($\pm 5\cdot 5\%$)	1·78 ($\pm 8\cdot 4\%$)
0·35	107·5 ($\pm 1\cdot 6\%$)	118·4 ($\pm 3\cdot 3\%$)	2·08 ($\pm 7\cdot 6\%$)
Mean relative error	$\pm 1\cdot 7\%$	$\pm 3\cdot 0\%$	$\pm 7\cdot 7\%$

TABLE 3. Photosynthetic parameters for seven species of cultured marine phytoplankton using simultaneous curve-fitting method (data from Perry *et al.*, 1981)

Species	$\bar{I}^a$ (quantum cm^{-2} s^{-1})	P_{Nmax}	P_{Gmax}	β
		[g carbon (g chl a)$^{-1}$ h^{-1}]		($\times 10^{-16}$ quantum^{-1} cm^2 s)
Chaetoceros danicus	$1\cdot 8 \times 10^{16}$	4·7 ($\pm 2\cdot 8\%$)	5·6 ($\pm 3\cdot 8\%$)	1·8 ($\pm 9\cdot 3\%$)
Chaetoceros gracilis	$1\cdot 8 \times 10^{16}$	8·0 ($\pm 4\cdot 8\%$)	9·1 ($\pm 5\cdot 1\%$)	1·4 ($\pm 14\%$)
Thalassiosira fluviatilis	$1\cdot 8 \times 10^{16}$	6·7 ($\pm 4\cdot 6\%$)	7·5 ($\pm 4\cdot 9\%$)	1·4 ($\pm 13\%$)
Thalassiosira pseudonana	$2\cdot 8 \times 10^{16}$	7·0 ($\pm 3\cdot 3\%$)	8·2 ($\pm 4\cdot 0\%$)	1·5 ($\pm 10\%$)
Skeletonema costatum	$1\cdot 8 \times 10^{16}$	5·0 ($\pm 5\cdot 0\%$)	6·2 ($\pm 5\cdot 5\%$)	1·6 ($\pm 15\%$)
Isochrysis galbana	$1\cdot 8 \times 10^{16}$	8·5 ($\pm 4\cdot 1\%$)	9·1 ($\pm 4\cdot 2\%$)	1·2 ($\pm 10\%$)
Dunaliella euchlora	$1\cdot 8 \times 10^{16}$	5·1 ($\pm 3\cdot 5\%$)	5·7 ($\pm 3\cdot 9\%$)	1·3 ($\pm 11\%$)
Chaetoceros danicus	$2\cdot 4 \times 10^{14}$	1·2 ($\pm 2\cdot 1\%$)	1·3 ($\pm 7\cdot 0\%$)	4·0 ($\pm 11\%$)
Chaetoceros gracilis	$2\cdot 4 \times 10^{14}$	2·5 ($\pm 1\cdot 8\%$)	3·0 ($\pm 3\cdot 5\%$)	3·7 ($\pm 7\cdot 6\%$)
Thalassiosira fluviatilis	$2\cdot 4 \times 10^{14}$	2·1 ($\pm 1\cdot 1\%$)	2·8 ($\pm 2\cdot 8\%$)	5·6 ($\pm 5\cdot 4\%$)
Thalassiosira pseudonana	$2\cdot 4 \times 10^{14}$	3·0 ($\pm 4\cdot 0\%$)	3·2 ($\pm 5\cdot 3\%$)	1·9 ($\pm 14\%$)
Isochrysis galbana	$2\cdot 4 \times 10^{14}$	2·3 ($\pm 3\cdot 0\%$)	2·8 ($\pm 6\cdot 9\%$)	4·8 ($\pm 14\%$)
Dunaliella euchlora	$2\cdot 4 \times 10^{14}$	1·4 ($\pm 0\cdot 6\%$)	1·7 ($\pm 1\cdot 4\%$)	5·1 ($\pm 3\%$)
Mean relative error		($\pm 3\cdot 1\%$)	($\pm 5\cdot 1\%$)	($\pm 11\%$)

^{a}Daily-mean PAR of the growth-light regime.

be due to low initial nutrient concentrations, this complication is not considered a serious problem in interpreting the results for the purposes of this study.

The large number of discrete observations (3106) are reduced by considering the relative percentage error in the parameter β rather than illustrating results for all parameters as

TABLE 4. Lognormal distribution[a] statistics of the percentage relative error in β for data sets with 6, 9, and 10 experimental determinations of the phytoplankton productivity–light intensity curves; data from Irwin *et al.* (1975)

Number of determinations along the productivity–light curve in each experiment	Data set	No. of experiments	Relative error of β population percentile (%)			Standard deviation of the logarithm of the data
			10	50	90	
6	A	62	$\leqslant 4 \cdot 9$	$\leqslant 11 \cdot 0$	$\leqslant 24 \cdot 0$	0.27
	B	57	$\leqslant 4 \cdot 9$	$\leqslant 12 \cdot 0$	$\leqslant 28 \cdot 0$	0.29
9	A	18	$\leqslant 4 \cdot 3$	$\leqslant 7 \cdot 7$	$\leqslant 14 \cdot 0$	0.10
	B	22	$\leqslant 6 \cdot 6$	$\leqslant 10 \cdot 0$	$\leqslant 16 \cdot 0$	0.15
10	A	100	$\leqslant 4 \cdot 0$	$\leqslant 7 \cdot 9$	$\leqslant 16 \cdot 0$	0.23
	B	94	$\leqslant 3 \cdot 3$	$\leqslant 7 \cdot 1$	$\leqslant 15 \cdot 0$	0.26

[a] $\dfrac{1}{\sqrt{2\overline{x}s^2}} \exp \dfrac{(\log x - \overline{x})^2}{2x^2}$, where $\overline{x}$ is the log of the 50% population percentile and s is the standard deviation of the logarithm of the data, x.

TABLE 5. Diel variation in photosynthetic parameters of California coastal phytoplankton; data derived from Harding, *et al.* (1981)

Sampling period	Number of experiments	P_{max} (gC gchl a^{-1} h^{-1})	(quantum^{-1} cm^2 s)
Daylight 11:00 a.m.–7:00 pm	19	8·8	$2 \cdot 7 \times 10^{-16}$
Night 10:15 p.m.–8:45 a.m.	10	3·9	$4 \cdot 3 \times 10^{-16}$

per data of Myers and Graham (Table 2). Because the frequency distribution of percentage relative error closely followed a lognormal distribution (Figure 2), the data were characterized using lognormal statistics (Table 4). Sets with only six observations showed a larger range in error than for 9 and 10 observations.

Data of Harding et al. *(1981)*. Subsamples of California coastal marine phytoplankton were collected, through a diurnal period, approximately every 4 h and incubated shipboard for 1·5–2 h. Photosynthesis was determined by the carbon-14 method.

The precision of the shipboard short-term incubation parameters was not as good as the approximately 4-h laboratory incubations of Irwin *et al.* (1975). The mean standard error estimate of β is $\pm 29\%$. The primary purpose here was to identify the possible diel variability in the parameter β (Table 5) as was done for the parameters P_{max} and a (estimated in Harding *et al.*, 1981). This data base also provided an example of the application of the exponential equation in evaluating the discrepancy in a by subjective and simultaneous methods noted by Harding *et al.* (1981). (See Discussion.)

Data of Peterson et al. *(in press)*. Daylight and 24-h *in situ* incubations were performed for natural phytoplankton assemblages in the San Francisco Bay (under high nutrient concentrations) and in the Potomac River estuaries. Photosynthesis was determined by
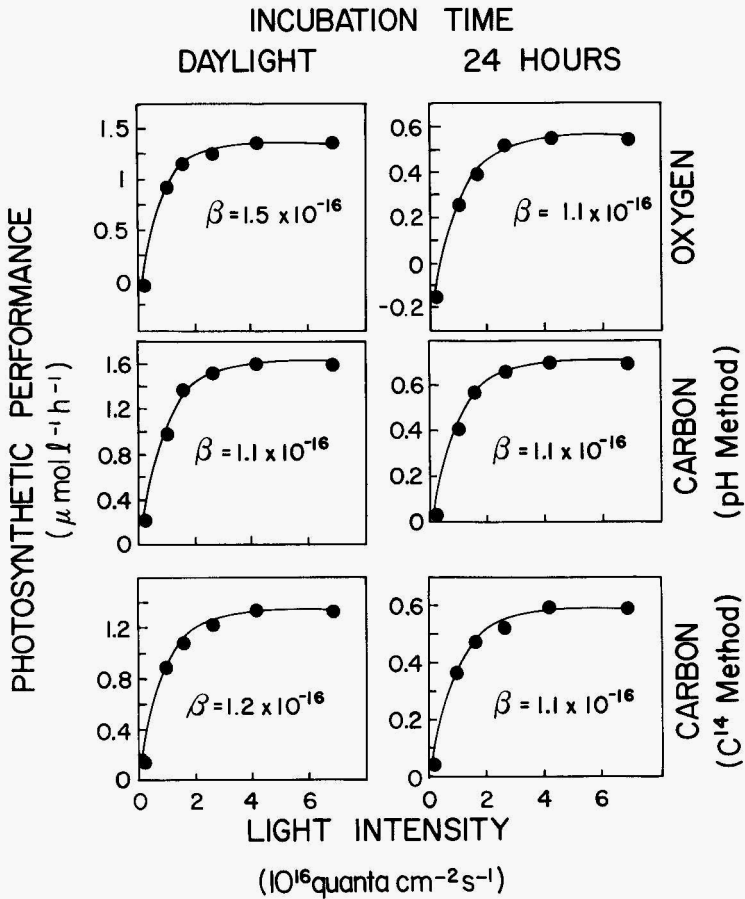
INCUBATION TIME

DAYLIGHT   24 HOURS

Figure 4. Photosynthetic rate was determined for San Francisco Bay phytoplankton using three different methods. Two incubation periods in relation to light intensity were used. Both estimates of β used mean-daylight light intensity, but with corresponding mean-daylight and mean 24-h productivity. Data are from San Francisco Bay, 16 September 1976 (Cole & Herndon, 1979). All observations at highest light intensities indicated slight effects of light inhibition. For calculation purposes, these are set equal to the highest rate at lower intensities.

oxygen, pH, and carbon-14 methods (Cole & Herndon, 1979; Hager *et al.* 1979; Cole & Harmon, 1981).

Precision of daylight and 14-h *in situ* incubations was similar to results of Irwin *et al.* (1975) using the average values of duplicate or triplicate observations at each depth interval. Application of the exponential equation appears to be appropriate for describing *P vs. I* in relatively long incubation and multispecies experiments (cf. Figure 4).

Data of Haas et al. *(1981)*. Incubations (2 h) of natural phytoplankton populations were made with fluorescent light using the carbon-14 method. The parameters (Table 6) were consistent with the stratification, destratification, stratification sequence as explained in Haas *et al.* (1981), and the effects of light history on the photosynthetic parameters as explained in Perry *et al.* (1981).

TABLE 6. Variation in photosynthetic parameters for an estuarine water column under stratified, mixed, and restratified conditions; derived from data of Haas *et al.* (1981)

		Water depth			
		1 m		8 m	
Date	Description	P_{max} (gC gchl^{-1} h^{-1})	β (quantum^{-1} cm^2 s)	P_{max} (gC gchl a^{-1} h^{-1})	β (quantum^{-1} cm^2 s)
Aug. 10	Stratified	19	4.1×10^{-16} ($\pm 30\%$)	10·0	7.1×10^{-16} ($\pm 15\%$)
Aug. 22	Mixed	10	5.2×10^{-16} ($\pm 5.0\%$)	8·6	5.8×10^{-16} ($\pm 3.2\%$)
Aug. 27	Stratified	16	3.2×10^{-16} ($\pm 22\%$)	7·2	7.2×10^{-16} ($\pm 2.8\%$)
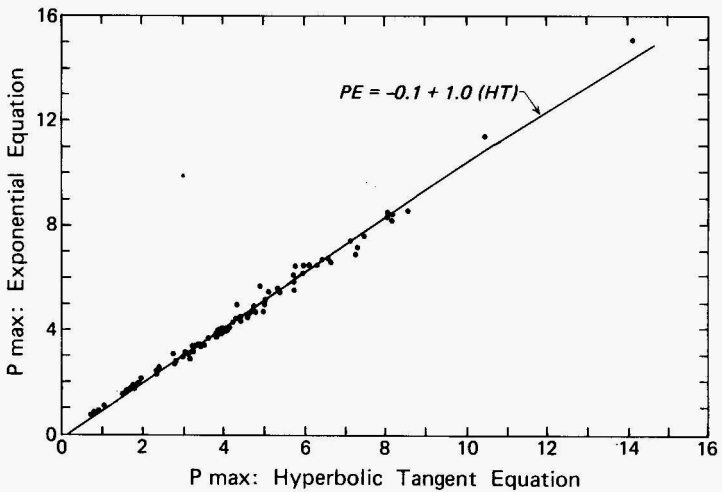
Figure 5. The mean value of maximal photosynthesis (P_{max}) in grams carbon per gram chlorophyll *a* per hour was estimated from the exponential equation (PE) and the hyperbolic tangent equation (HT) (Platt & Jassby, 1976). Data are from Irwin *et al.* (1975) sets A and B, with 10 light intensity determinations (see Table 4).

Discussion

Estimation of photosynthetic parameters

A simple exponential equation is not traditionally used for describing *P vs. I* curves. Partly for this reason and partly because of the complexity of photosynthesis, the close fit of the exponential equation against a variety of high-precision *P vs. I* observations (Tables 1 and 2) was unexpected.

Our results with the well-defined data sets indicate that this simple exponential equation, with a minimal number of parameters, fits a wide variety of data very well. The relative error estimates are lowest for net maximum productivity, P_{Nmax}, slightly greater for gross maximum productivity, P_{Gmax}, and are the highest for the parameter β. Although the exponential equation is relatively precise, these precision estimates refer to the derived parameters of the data set, and do not necessarily reflect experimental accuracy or precision (Peterson, 1980; Lederman & Tett, 1981; McCree, 1981). Furthermore, note that in all experiments the mean relative errors in both net and gross maximum productivity are quite small. It is easily shown that the differences are small between two estimates of P_{Nmax} made with different equations (and methods) but using the same empirical observations (Figure 5). However, differences are large between two estimates
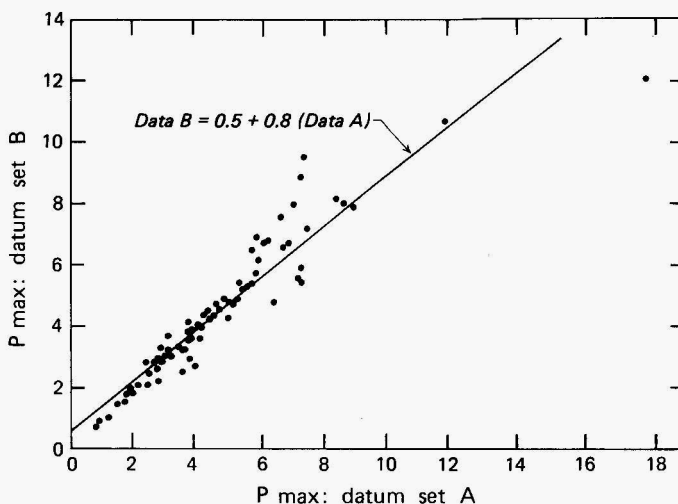
Figure 6. Maximal photosynthesis (P_{max}) was estimated by the exponential equation for data sets A and B from Irwin *et al.* (1975) for 10 light determinations (Table 4). The units are grams carbon per gram chlorophyll *a* per hour.

of P_{Nmax} made with replicate experiments but using the same equation (Figure 6). The relative error in respiration ($R = P_{Nmax} - P_{Gmax}$) is large ($\pm 100\%$) (Platt & Jassby, 1976; Malone & Neale, 1981) because it is typically estimated as a small difference between two large numbers (cf. Figure 1).

The exponential equation performs well in curve-fitting and estimating various parameters of photosynthesis for a wide selection of plants, environments, and time scales. Although other higher-order equations may perform equally well (cf. Lederman & Tett, 1981; Field & Effler, 1982) or even slightly better, an advantage of the exponential equation is that it provides a highly simplified model of photosynthesis over the near-linear light-dependent part of the photosynthesis curve. This region of the curve is used to calculate PSE. In estuarine studies, PSE is an especially important parameter as plankton productivity in estuaries is often light limited. Despite the importance of this parameter in production models, the precision estimates of PSE are generally lower than for P_{max} or β alone.

Photosynthetic efficiency

Photosynthetic efficiency (PSE), also designated as *a* in aquatic literature, is one of the important parameters used to describe and predict photosynthesis (Platt & Jassby, 1976; Malone & Neale, 1981). PSE is, by definition, the initial slope of the *P vs. I* curve for incident light, assuming linearity of the initial part of the curve. Quantum efficiency is, in contrast, photosynthesis normalized per quantum of light *absorbed* by photosynthetic pigments.

Calculated estimates of both PSE and quantum efficiency ultimately decrease as the range in experimental light intensity increases (cf. Table 7), indicating that light intensity is no longer the rate-limiting factor for this reaction (cf. Schwartz, 1957). Then other processes, such as electron transport or enzyme activity and, for higher terrestrial plants, the partial pressure of CO_2 in the atmosphere (cf. Farquhar & Caemmerer, 1983), become rate limiting.

TABLE 7. Comparison of the initial slope of *P vs. I* curves computed by a subjective linear method (PSE_L) for different ranges of light incubation intensities and a comparison of their values with the simultaneous curve-fitting value (PSE_S); data from Irwin *et al.* (1955) and from Platt and Jassby (1976)

Experiment	IL^a ($\mu E\,m^{-2}\,s^{-1}$)	n	$\left(\dfrac{PSE_L}{\dfrac{g\,C\,(g\,chl\,a)^{-1}\,h^{-1}}{\mu E\,m^{-2}\,s^{-1}}}\right)$	R^{2b}	$PSE_L\,(PSE_S)^{-1}$	$I_K(I_L)^{-1}$
BB-5M	230	14	0·024	0·800	0·25	0·24
	100	12	0·050	0·980	0·52	0·56
	50	10	0·065	0·995	0·67	1·10
	25	8	0·072	0·995	0·74	2·20
SMB-10M	280	15	0·018	0·95	0·47	0·54
	130	13	0·026	0·98	0·70	1·20
	62	11	0·033	0·99	0·98	2·40
	34	9	0·028	0·95	0·76	4·40
	19	7	0·035	0·92	0·95	7·90
CH-5M	164	14	0·043	0·90	0·60	0·61
	76	12	0·072	0·98	1·00	1·30
	42	10	0·067	0·98	0·93	2·40
	23	8	0·070	0·97	0·97	4·30

[a]Light intensity corresponding to the upper limit or maximal photosynthetic rate for the assumed linear part of the curve. Note the decrease in PSE_L with increasing I_L.
[b]Ratio of sum of squares to total sum of squares.

Generally, PSE and quantum efficiency are measured at light intensities below approximately $55\,\mu\,E\,m^{-2}\,s^{-1}$ (cf. Bjorkman *et al.*, 1971; Platt & Jassby, 1976; Welschmeyer & Lorenzen, 1981; Richardson *et al.*, 1983). A difficulty in estimating PSE is the possible bias in choice of the linear or apparent linear range in light intensities. This uncertainty is minimized by simultaneously curve-fitting all observations during parameter estimation (Lederman & Tett, 1981). [Note that this procedure of simultaneous curve fitting is not followed for measuring quantum efficiency (Ehleringer & Bjorkman, 1977; Bjorkman *et al.*, 1971; Senger & Fleischhacker, 1978a) because these curve-fitting methods utilize observations at all light intensities.]

The discrepancies between PSE calculated by simultaneous curve-fitting and subjective methods are recognized (Harding *et al.*, 1981). A comparison of the differences in the two methods was made for some of the data used to test the equation (Table 7). Two major problems with the subjective method are (1) the decision of how far the linear portion of the curve extends, and (2) the increased error associated with restricting observation points to a small number. We attempt to illustrate these problems with the following statistical model of photon capture at low quantum flux densities.

The Poisson model

The Poisson model assumes that the photosynthetic response of a natural assemblage of phytoplankton follows a Poisson probability function with respect to light intensity. This is described by the Poisson equation (Haight, 1967):

$$P_x(\lambda) = \frac{e^{-\lambda}(\lambda)^x}{x!} \qquad x = 0, 1, 2, \ldots. \tag{4}$$

where P is the probability of encountering x number of photons during unit time t, and λ is the mean number of incident photons encountered per photosynthetic unit (PSU) during unit time t. The rate of photon encounter by a single chlorophyll molecule is σI, where σ is the molecular absorption coefficient of chlorophyll and I is the light intensity (Clayton, 1975). For N chlorophyll molecules per PSU, the rate of photon encounter per PSU (equivalent to the Poisson parameter λ) during unit time t is $N\sigma t I$. The time interval t is chosen to represent the photon-processing or turnover time of the PSU. The PSU is defined herein as the minimum number of chlorophyll molecules required for photosynthesis (≈ 2500) divided by the minimum photon requirement per molecule of O_2 evolved or CO_2 fixed (Emerson & Arnold, 1932; Knox, 1977; Radmer & Kok, 1977).

As a simple example, two events may be identified: either a PSU is hit by one (or more) photons during time t or it is not hit. The combined probabilities of these events must, by definition, equal 1. The probability that no photons are encountered during time t is:

$$P_0(\lambda) = e^{-\lambda} \tag{5}$$

The probability that one (or more) photons are encountered during the interval t is:

$$P(\lambda) \geqslant (\lambda) = \sum_{x=1}^{\infty} (\lambda) = 1 - e^{-\lambda} \tag{6}$$

The above equation assumes excess photons have no effect on photosynthetic performance. The first photon that the PSU unit encounters during time t is processed by the reaction center. No other photon can be processed during this interval, although other photons can be encountered by the light harvesting pigments of the PSU. The energy associated with these photons must be dissipated by a route other than photochemical conversion by that reaction center.

At low photon flux, the rate at which the PSU encounters photons places the greatest limits on photosynthetic rate, at higher photon flux (i.e. saturating light intensities) the rate of turnover of the reaction center sets limits for photosynthetic rate. In equation (6), the probability of saturation is based on the rate of photon encounter.

Photosynthetic rate P can then be considered equal to the probability of one (or more) photons being encountered times P_{max} $[(1 - e^{-\lambda})P_{max}]$. Equation (6) can be transformed to a direct relation of light intensity:

$$P/P_{max} = 1 - e^{-\beta I} \tag{7}$$

with β equivalent to $N\sigma t$.

For illustrative purposes, a possible value of N is 300 (Emerson & Arnold, 1932; Radmer & Kok, 1977), σ is 3×10^{-16} cm^2 (Clayton, 1975; Kohn, 1936), and t is approximately 0·0025 s photon^{-1}, or longer, depending on temperature (Emerson & Arnold, 1932; Radmer & Kok, 1977; Diner & Mauzerall, 1973). Thus β is estimated to be about 2×10^{-16} cm^2 s photon^{-1} per PSU.

Application of the model

If this model is realistic, then no strictly linear portion of the P vs. I curve is to be found. For the linear model, the range of light intensities over which linearity of photosynthesis is assumed strongly influences the value of PSE (cf. Table 7). A key feature of the Poisson model is that photons reaching photoreaction centers, or traps, that are closed (e.g. traps receiving more than one photon during the quantum turnover time) do not react. The assumption is that at low quantum flux, the transfer or spillover of quanta between PSU is

TABLE 8. Poisson correction for the difference in values between parameter estimates made by simultaneous and linear methods as a function of the ratio: $I_K (I_L)^{-1}$

$I_K (I_L)^{-1}$	Probability A^a ($\geqslant 1$ quanta)	Probability B^a ($\geqslant 2$ quanta)	$\left(\dfrac{A-B}{A}\right)^b$	$\left[\left(\dfrac{A}{A-B}\right)-1\right]^c$
10·00	0·095	0·0047	0·950	0·053
5·00	0·180^d	0·0175^e	0·910	0·099
3·30	0·260	0·0370	0·860	0·163
2·50	0·330	0·0620	0·800	0·260
2·00	0·390	0·0900	0·769	0·300
1·60	0·450	0·1200	0·730	0·370
1·40	0·500	0·156	0·680	0·470
1·25	0·550	0·191	0·650	0·530
1·10	0·593	0·227	0·610	0·640
1·00	0·632	0·264	0·590	0·700
0·50	0·860	0·590	0·310	2·220
0·33	0·950	0·800	0·160	5·300
0·25	0·980	0·908	0·071	12·000

^{a}From cumulative Poisson probability tables.
^{b}Equals $PSE_L (PSE_S)^{-1}$ assuming $P_{L.max} = P_{S.max}$.
^{c}Equals $(I_L - I_K)/I_K$ assuming $P_{L.max} = P_{S.max}$.
^{d}The fraction of light-saturated reaction centers, i.e. 18%.
^{e}In this instance, there is less than a 2% chance of $\geqslant 2$ quantum arriving at the reaction center per unit turnover time at quantum flux density I_L.

negligible but that it increases with increasing light intensity. The Poisson model predicts the probability of at least one photon arriving at the PSU trap as a function of increasing light intensity. At high light intensities, a corrected PSE is determined by calculating the probability that one or more photons arrive during t (turnover time of the PSU) minus the probability that two or more photons arrive, divided by the probability that one or more photons arrive (i.e. excess photons do not count). As ambient light intensity decreases, the probability of two encounters becomes exceedingly small (Table 8).

In the Poisson model, photosynthesis is always proportional to $1 - e^{-\beta I}$ despite the variety of time scales and plants in this study. With real data, as the scatter in P vs. I observations about a curve increases, it becomes more difficult to identify the shape of the experimental curve.

In the subjective linear method (designated by the subscript L), $PSE_L = P_L I_L^{-1}$, where P_L is the upper limit or maximal photosynthetic rate in the assumed linear region of the curve and I_L is the light intensity corresponding to P_L. According to the Poisson model (designated by the subscript S), using the exponential equation and simultaneously curve-fitting, $PSE_S = P_{Gmax} I_k^{-1}$. Depending on the choice of P_L and I_L, PSE_L will vary. The model describes how PSE_L depends on I_L in a simple but quantitative way that is determined by the ratio $I_k I_L^{-1}$. For example, when $I_k = I_L$ and $I_k I_L^{-1} = 1$, then (using the Poisson model as a specific frame of reference) $a_L = 0.59 a_S$ (cf. Table 7). If $I_k \gg I_L$ (i.e. $I_k \geqslant 8 I_L$) then $PSE_L = PSE_S$ (Table 7).

Some effects of light history on photosynthetic parameters

The model provides a simplified analysis of some effects of growth–light history or regime on photosynthesis parameters. When the light intensity of growth decreases, P_{max} and
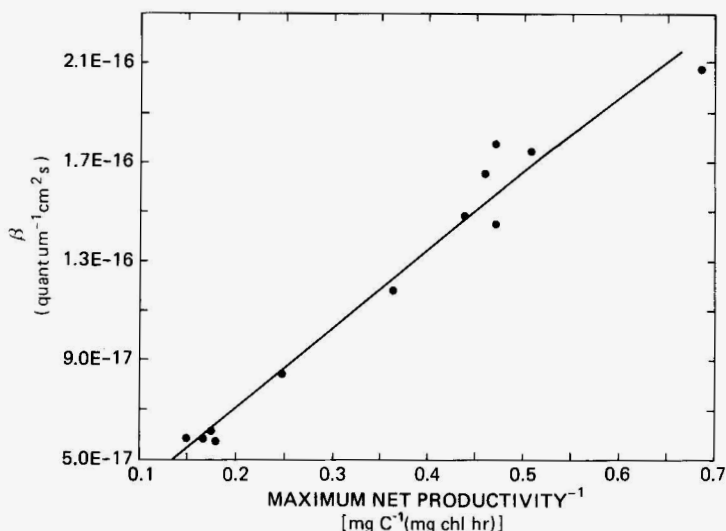
Figure 7. β and $(P_{max})^{-1}$ covary. Both increase as light intensity of growth decreases. Data are from Myers and Graham (1971) and unpublished data (see also Table 2). The number of moles of oxygen produced is assumed to equal the number of moles of carbon fixed.

PSE per unit chlorophyll-a ($PSE = P_{max} \beta$ or $P_{max} I_k^{-1}$) commonly decrease (Myers & Graham, 1971; Senger & Fleischhacker, 1978a; Perry et al., 1981). These parameters often are more a function of light history than of systematic classification. P_{max} and β often, but not always, covary in response to decreasing photon flux (cf. Figures 7 and 8, Platt et al., 1982). The obvious question is: what is the controlling mechanism common to both parameters? Three major variables in the statistical model are PSU size, which may increase with decreasing light intensity of growth (Myers & Graham, 1971; Alberte et al., 1976; Prezelin & Alberte, 1978; Withers et al., 1978; Perry et al., 1981), the turnover rate of photosynthesis, which may also be light history dependent (cf. Farquhar & Caemmerer, 1983; Bloom et al., 1983; Myers & Graham, 1971, 1975), and the molecular absorption coefficient or optical cross section of the light harvesting pigments (Morel & Bricaud, 1981; Welschmeyer & Lorenzen, 1981; Kiefer & Mitchell, 1983; Perry et al., 1981; Mishkind & Mauzerall, 1980).

A large PSU would be expected to saturate its trapping center at a lower photon flux than a PSU with a smaller number of light collecting chlorophyll molecules (e.g. the photon encounter rate is greater for PSUs with more antenna light harvesting chlorophylls) and the probability of capturing one or more photons at low light intensities would thus be greater for larger PSUs. Although spillover or transfer of excess photons to open traps can occur (Butler, 1980; Malkin et al., 1981; Malkin & Fork, 1981), spillover must decrease with decreasing photon flux. An increase in photon processing time per PSU for plants grown at low light intensities could result from a decrease in concentration of available acceptors for energized electrons (photosynthetic electron transport system) and/or from a decrease in requirement for reducing potential (decreased concentration of ribulose 1,5-bisphosphate carboxylase, etc.). Self shading within large PSUs may decrease mean molecular absorption efficiency per individual chlorophyll (Mishkind & Mauzerall, 1980; Perry et al., 1981). Hence, effects of low photon flux on photosynthesis are reflected in the model's parameters.
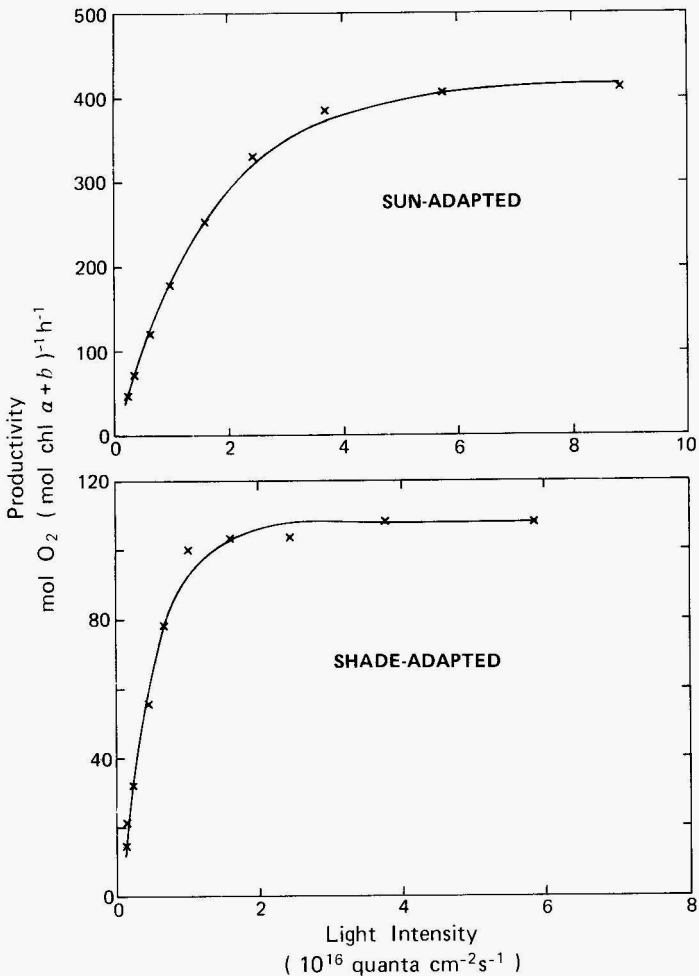
Figure 8. The exponential equation is applied to the photosynthetic rate as a function of light intensity for sun- and shade-adapted algae. Data are from Myers and Graham (1971) (see also Table 2).

In summary, the simple exponential equation provides a quantitative description of *P vs. I* curves. Although more complex mathematical representations have been developed (Paillotin *et al.*, 1979; Butler, 1980; Farquhar & Caemmerer, 1983), this simple exponential equation appears to be more than adequate for describing *P vs. I* curves, such as in numerical modeling of estuaries. The error in assuming that productivity is proportional to $(1 - e^{-\beta I})$ is small when compared to uncertainties in other factors which affect phytoplankton productivity in estuaries, for example, vertical mixing dynamics (Marra, 1978), photoinhibition (Smith *et al.*, 1980), and light quality (Bannister, 1979; Bjorn, 1979).

For some purposes, estuarine phytoplankton and terrestrial plant productivity have been represented even more simply with two straight lines, i.e. P_{max} and PSE (Monteith, 1979; Fisher *et al.*, 1982; Wofsy, 1983). Such a representation of P_{max} is adequate, but a simple linear determination of PSE may be an underestimate.

The power of the simple exponential equation and underlying Poisson model is that it is a tested model which permits the determination of error terms and the use of all data

points. The use of a non-subjective method to determine photosynthetic parameters will improve our ability to evaluate and compare phytoplankton photosynthetic performance in diverse light environments.

Acknowledgements

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Appendix

Computation of exponential least-squares parameters

Derived parameters for the P *vs.* Z curve [equation (2) in text] were computed using an exponential least-squares method (Tektronix, 1977b). For a further discussion of efficient numerical methods for the computations, as well as the assumptions in applied statistics theory, see Carhahan *et al.* (1969), Dahlquist and Bjorck (1974), Draper and Smith (1966), Gelb (1974), Hald (1952), and Pollard (1977).

The estimated parameter errors are given by Jennrick and Ralston (1979). Statistical experiments using synthetic data indicate the derived parameters and their error estimates are not highly sensitive to the number of determinations, *N,* when the data points are close to the curve [equation (2) in text]. Error estimates
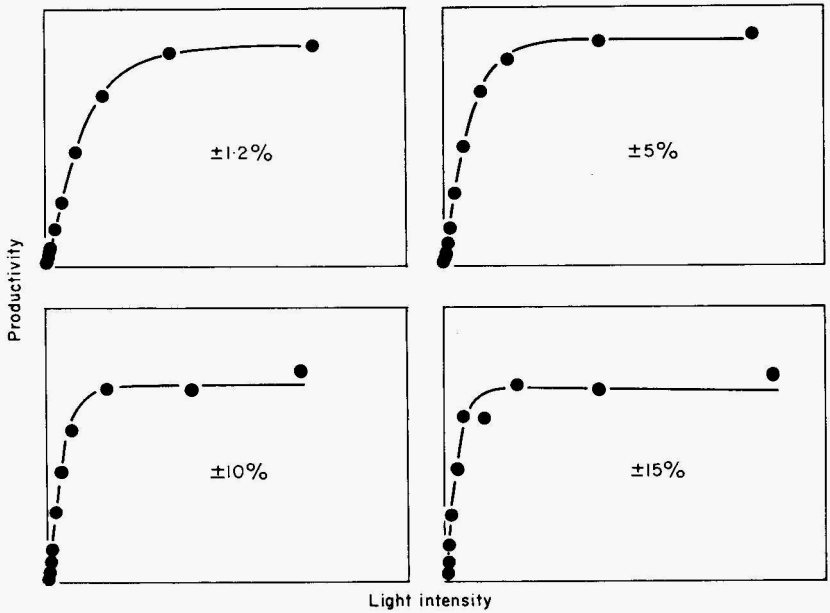
Figure A1. Examples of fit of Poisson equation (2), see text, to data with increasing error in the derived parameter β. Data from Irwin *et al.* (1975): $\pm 1 \cdot 2\%$ p. 157 data A; $\pm 5\%$ p. 63 data A; $\pm 10\%$ p. 48 data A; $\pm 15\%$ p. 179 data A.

increase with increasing scatter of observations about the curve [cf. Figure A1 illustrating error estimates in the parameter β using real observations]. Thus the parameter, β, which is an indicator of how sharply the curve breaks with increasing light intensity, becomes more difficult to identify when both the scatter of data points about the curve increases and the number of determinations along the curve, N, decreases.