Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton

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ABSTRACT

A new empirical equation is introduced that describes the photosynthesis by phytoplankton as a single, continuous function of available light from the initial linear response through the photoinhibited range at the highest light levels liable to be encountered under any natural conditions. The properties of the curve are derived, and a procedure is given for fitting it to the results of light-saturation experiments for phytoplankton. The versatility of the equation is illustrated by data collected on natural phytoplankton assemblages from the eastern Canadian arctic and from the continental shelves of Nova Scotia and Peru. Photoinhibition indices derived from the fitted curve vary strongly with depth and with time of day: they may be useful in characterizing the physiological state of the phytoplankton.

1. Introduction

Our previous studies of the empirical form and mathematical representation of the relationship between photosynthesis and light in marine phytoplankton (Jassby and Platt, 1976; Platt and Jassby, 1976) have been restricted to the range of light intensities below the threshold of photoinhibition. For complete generality, it is desirable to extend the range of interest to include light intensities in the photoinhibited part of the light saturation curve.

In this paper we introduce an empirical equation that describes the photosynthesis by phytoplankton as a continuous function of available light from the initial linear response through the highest light levels liable to be encountered under any natural conditions. We illustrate the applicability of this new equation by fitting it to the results of light-saturation experiments carried out in the eastern Canadian Arctic and on the continental shelves of Nova Scotia and Peru.

2. Mathematical representation

Earlier work on the mathematical representation of the light-saturation curve is discussed in Jassby and Platt (1976) and Platt *et al.* (1977), where it is pointed out

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that below the threshold of photoinhibition the curve is described by a minimum of two parameters. A certain latitude exists in the choice of parameters; it is argued in Platt *et al.* (1977) that an appropriate selection is the initial slope α (mg C[mg Chl $a]^{-1}h^{-1}[W_m{}^{-2}]^{-1}$) and the specific production rate at optimal light intensity, often called the assimilation number, $P_m{}^B$(mg C[mg Chl $a]^{-1}h^{-1}$). With this choice of parameters, the dependent variable P^B is normalized to chlorophyll biomass and has the same units as $P_m{}^B$: the independent variable I has units Wm^{-2}.

In extending the range of description to include the photoinhibited part, there is some advantage in retaining the same parameters (Platt *et al.*, 1977), which have clear physiological interpretations (Platt and Jassby, 1976). But it will be essential to introduce a third, independent parameter to characterize the photoinhibition, since we have no reason to suppose that the mechanisms responsible for photoinhibition are other than independent of those controlling the initial slope. In the formulation of the light-saturation curve used by Steele (1962), the slopes on either side of the photosynthesis maximum were not independent, with the result that the goodness-of-fit was jeopardized at light intensities below the photosynthesis maximum (Jassby and Platt, 1976).

Another requirement is that the light-saturation curve be fit over the entire range of light intensities by the same, continuous function. It was suggested in Platt *et al.* (1977) that different functional forms might be applied to the uninhibited and inhibited portions of the curve. We have found this approach to be unacceptable in practice because of the subjectivity involved in deciding exactly which data points belonged to the photoinhibition regime. It is equivalent to introducing an additional (fourth) parameter, the light intensity at which photoinhibition begins, and fixing its value without reference to an objective criterion. In the experiments we examined, there was sufficient scatter in the data that this procedure could not be followed with any confidence.

The following equation has been found to satisfy the requirements outlined above:

$$P^B = P_s{}^B\,(1-e^{-a})\,e^{-b} \tag{1}$$

where $a = \alpha I/P_s{}^B$, $b = \beta I/P_s{}^B$. Here $P_s{}^B$ is a parameter whose relationship to $P_m{}^B$ will be deduced below, and β (same units as α) is the parameter chosen to characterize the photoinhibition.

We now derive some properties of equation (1). First, the derivative with respect to light,

$$\frac{\partial P}{\partial I} = (\alpha+\beta)\,e^{-(a+b)} - \beta e^{-b} \tag{2}$$

where, for convenience, we have suppressed the superscript B. Note that as $I \to 0$, $\frac{\partial P}{\partial I} \to \alpha$(constant), consistent with the identification of α as the slope of the initial, linear portion of the curve.

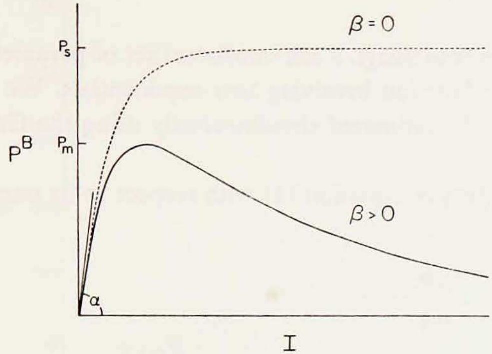

Figure 1. General form of the function described by equation (1).

Setting $\frac{\partial P}{\partial I} = 0$ specifies the point I_m at which photosynthesis is maximum,

$$I_m = \frac{P_s}{\alpha} \log_e \left(\frac{\alpha+\beta}{\beta}\right) . \quad (3)$$

Substituting this value of I in equation (1) gives the maximum productivity:

$$P(I_m) = P_m \equiv P_s \left(\frac{\alpha}{\alpha+\beta}\right) \left(\frac{\beta}{\alpha+\beta}\right)^{\beta/\alpha} . \quad (4)$$

In the limit as $\beta \rightarrow 0$, $P_m \rightarrow P_s$, that is P_m and P_s coincide if there is no inhibition. For $\beta > 0$, $P_s > P_m$ and we interpret P_s as the maximum, potential, light-saturated, photosynthetic rate under the prevailing conditions. In other words, P_s is the maximum photosynthetic output the sample could sustain if there were no photoinhibition (Fig. 1).

In fitting the results of experiments at light intensities below the threshold of photoinhibition (Jassby and Platt, 1976), we did not constrain the light-saturation curve to pass through the origin, but admitted the possibility of an intercept R^B on the ordinate, interpreted as the dark respiration rate. This quantity was found in practice to be a small number subject to a large error (Platt and Jassby, 1976). Fitting the new equation introduces an additional parameter and we can expect that R^B would be even less reliable than before. In this work, therefore, we have not included an R^B term in the fitting equation, which will then pass always through the origin.

To summarize this section, the light-saturation curve will be represented throughout the entire range of light levels normally available to natural phytoplankton assemblages by a single, continuous function of light having three parameters: α, characterizing the photochemical reactions of photosynthesis; P_s^B, characterizing the output of the dark reactions of photosynthesis; and β, characterizing the photoinhibition process.

3. Fitting the model

The fitting problem is to assign a self-consistent set of parameter values to a three-parameter non-linear function involving two exponentials. We have found that all three parameters may be estimated simultaneously using the Gauss-Newton method (Bard, 1974).

The partial derivatives of equation (1) with respect to its parameters are required for fitting. They are

$$\frac{\partial P}{\partial \alpha} = Ie^{-(a+b)} \quad (5)$$

$$\frac{\partial P}{\partial \beta} = I(e^{-(a+b)} - e^{-b}) \quad (6)$$

$$\frac{\partial P}{\partial P_s} = e^{-b}[(1+b)\,(1-e^{-a}) - a\,e^{-a}] \quad (7)$$

For the work reported here, initial or trial estimates of the parameters were made with the aid of a P vs I plot of the raw data as follows. The initial slope, α, was estimated by a linear regression of those data points judged to represent the linear part of the light-saturation curve. The initial estimate of P_s was chosen to be the highest observed value of P^B. The initial estimate of β was then obtained using the non-linear fitting routine, with α and P_s constrained at their initial values. With these values as initial estimates, we obtained the final parameter set, again using the non-linear fitting routine, but this time fitting all three parameters simultaneously; the fitting routine usually converged to the final parameter set within 20 iterations. We have since found that the first application of the fitting routine is unnecessary. With initial estimates for P_s and α chosen as above, the final parameter values are insensitive (to at least four significant figures) to the initial estimate of β, when all three parameters are estimated simultaneously.

Some consideration was given to the question of whether the data should be weighted before fitting. A suitable weighting function would be proportional to the inverses of the variances associated with each data point (e.g. Bevington, 1969). We have no way of estimating the relative variances of individual data points (which cannot be replicated) in the present work. However, the data reported by Therriault *et al.* (1978) allow us to estimate how the standard deviation of the estimate of P^B varies with increasing P^B (Fig. 2). The increase is roughly linear. When a weighting function with these characteristics was applied to our data, the fit was almost always less good than with unweighted data, and the fitting routine often failed to converge such that P_s and β increased apparently without bounds. We believe the explanation to be that with proportional weighting, those data points corresponding to the highest production rates are given the smallest weights such that the peak is poorly fixed,

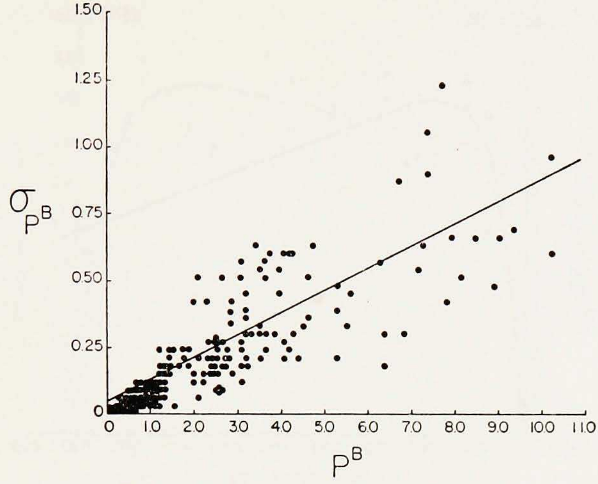

Figure 2. Relationship between standard deviation and mean of specific production rate for natural assemblages of coastal marine phytoplankton. Data from Therriault *et al.*, 1978.

leading to a bad overall fit. In any event, weighting the data was abandoned, and the results reported here are all based on unweighted fits.

4. Methods

Carbon fixation rates were measured using natural phytoplankton assemblages sampled usually from two depths corresponding to the nominal depths of penetration of arbitrary fractions of surface light (typically the 50% and 1% light levels) as roughly determined by Secchi disc.

All light-saturation experiments were made in duplicate for each depth, using an improved version of the linear incubator procedure described by Jassby and Platt (1976). Data from the duplicate incubators were pooled to construct one light-saturation curve, comprising some 50 observations, for each depth. To obtain the high irradiance levels required to study photoinhibition, a 2000 W Tungsten-halogen floodlight (Atlas[R] Model OHS 200) was used. Temperature inside the incubators was controlled by circulating sea water. An Eppley 40-junction pyranometer was used to measure total irradiance in each compartment of the incubator. The spectrum of light incident on each compartment was measured with a spectroradiometer (ISCO[R] Model SR) such that the total incident radiation could be expressed as photosynthetically active radiation (PAR) in watts m^{-2}. In later experiments PAR was measured directly using a quantameter (Li-Cor #170 fitted with #192S underwater sensor). The samples were usually incubated for four hours.

5. Results

Figure 3 shows two examples of light-saturation curves collected off the coast of Peru in November, 1977. Figure 3a describes a population of diatoms (*Chaeto-*

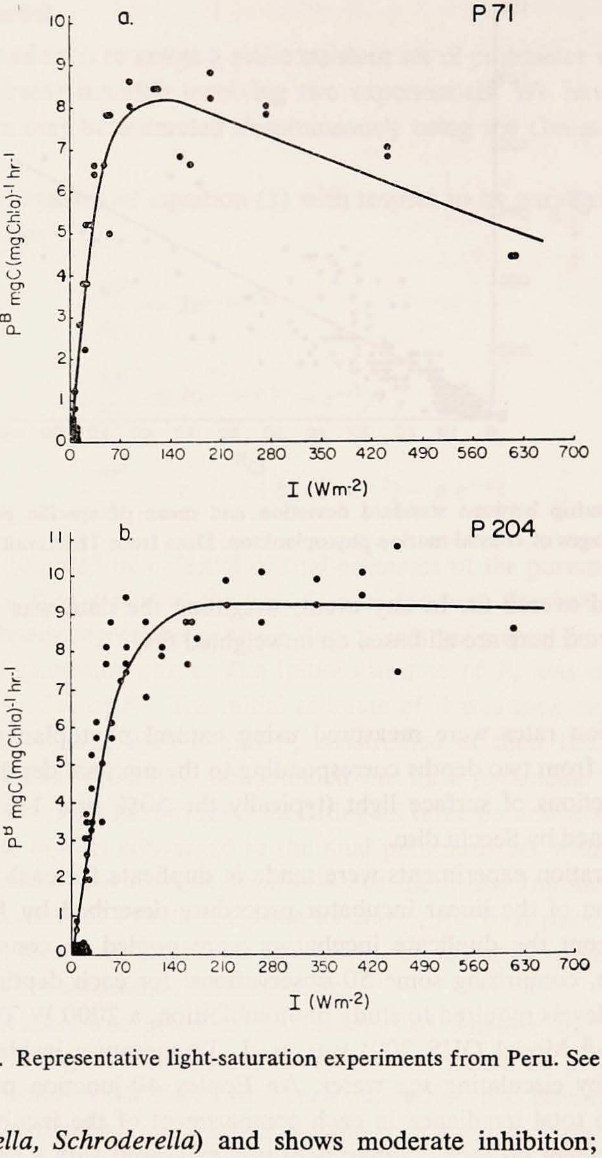

Figure 3. Representative light-saturation experiments from Peru. See Table 1.

ceros, Asterionella, Schroderella) and shows moderate inhibition; Figure 3b describes a bloom of the red-water organism *Mesodinium rubrum*.

Figure 4 shows two examples of light-saturation curves from the Nova Scotia Shelf, taken in June, 1978. They describe populations of flagellates, both dinoflagellates and naked flagellates, and show only moderate inhibition.

Figure 5 shows two curves (diatoms, mainly *Chaetoceros* spp) collected from the same station in Scott Inlet, Canadian Eastern Arctic in September, 1978. Figure 5a is from the 50% light level and shows little inhibition. Figure 5b is from the 1% light level and shows intense inhibition. We have observed consistently a similar

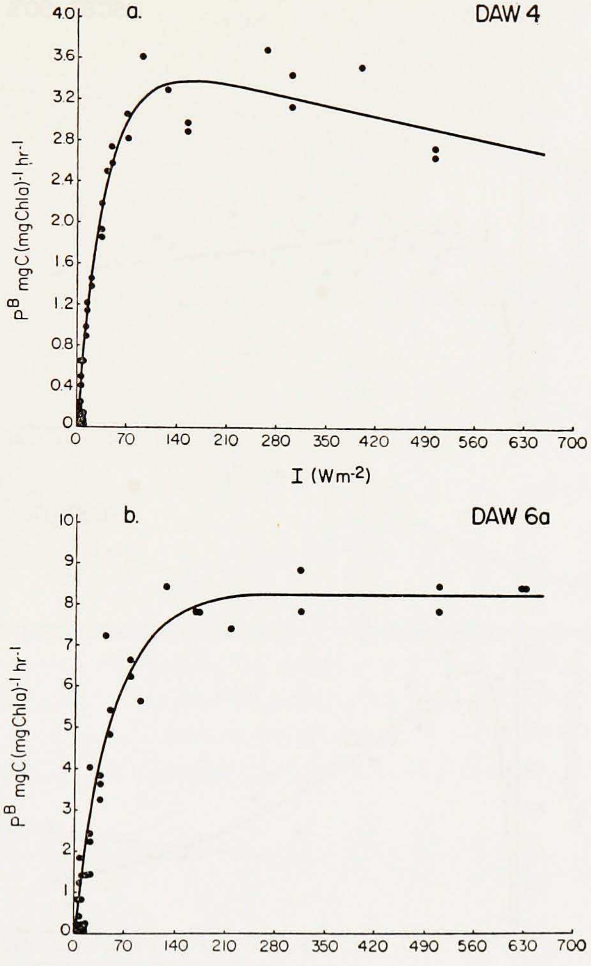

Figure 4. Representative light-saturation experiments from the Nova Scotia Shelf. See Table 1.

difference in strength of inhibition between near-surface and deep samples from some twenty stations made in the vicinity of Scott Inlet.

Figure 6 illustrates a diurnal sequence collected off Peru in November, 1977. Sampling depth was 10 m and the populations were dominated by diatoms. The trend in this series is for samples collected during the daylight hours to show much less photoinhibition than samples collected in the dark hours.

Ancilliary data relevant to Figures 3-6 are assembled in Table 1.

6. Discussion

a. Magnitude and variation of the parameters. We have illustrated with examples

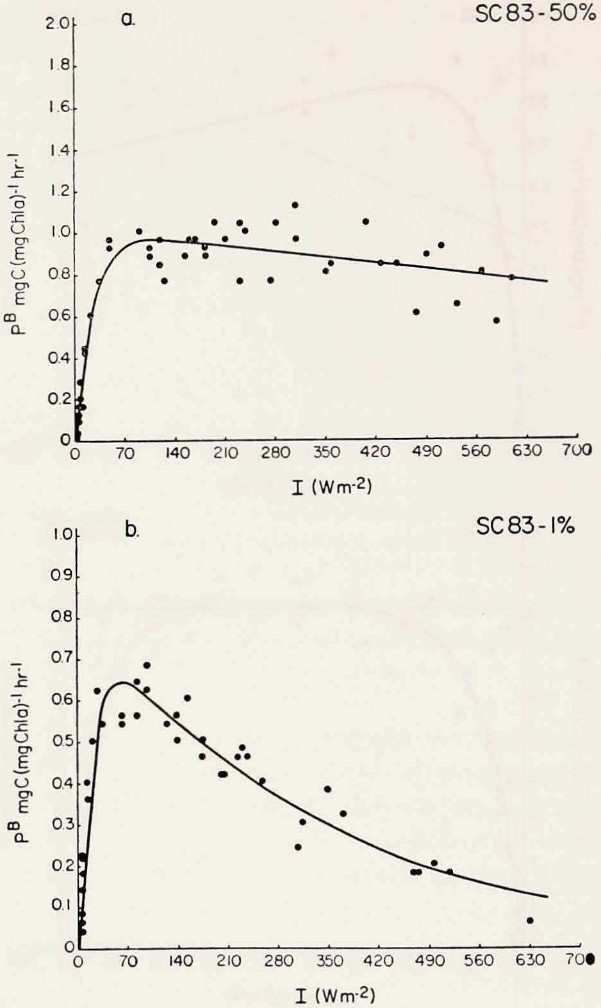

Figure 5. Representative light-saturation experiments from Scott Inlet, Canadian Arctic. Samples from 50% and 1% light levels at same station. See Table 1.

the versatility of the new equation in its application to light-saturation curves for phytoplankton populations sampled from a variety of oceanographic situations. Table 2 shows the light-saturation parameters extracted from these experiments. The derived quantities are (Fig. 7) I_k, the conventional index of light adaptation (e.g. Talling, 1957), defined by the identity $I_k \equiv P_m{}^B/\alpha$; I_s, an analogous parameter to I_k, defined by $I_s \equiv P_s{}^B/\alpha$, that we have introduced to non-dimensionalize equation (1) (see below).

A relatively higher value of β is indicative in general of stronger photoinhibition, but it is important to realize that the effect is scaled by the value of P_s. A more con-

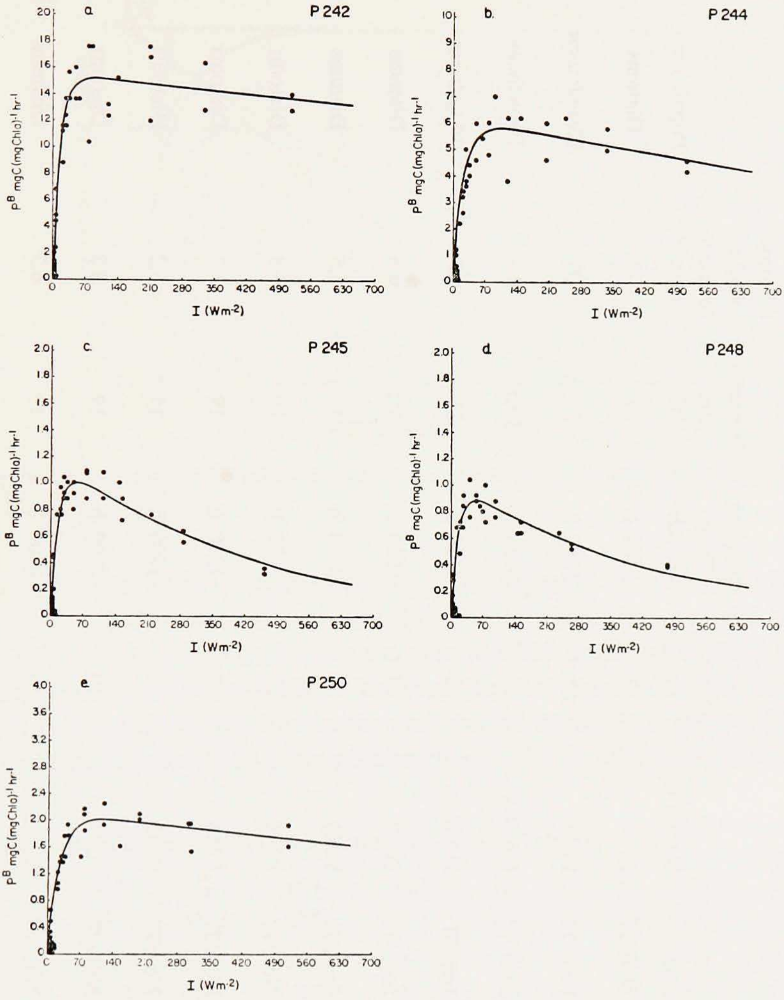

Figure 6. Diurnal series of light-saturation experiments made off Peru. See Table 1.

sistent index of comparison then is the quantity $I_b \equiv P_s{}^B/\beta$ which has the dimensions of a light flux (units Wm^{-2}) and is the intensity at which $P^B = 0.37\ P_s(I{>}I_m)$. A small value of I_b is indicative of strong photoinhibition. In the case that no photoinhibition is observed over the range of light intensities to which the cells are exposed, such that β is identically zero, the index I_b is undefined. Such a case was observed on the Scotian Shelf at station DAW-6a. Excluding this case (where I_b would be infinitely large), the range of values of I_b in Table 2 is from 370 to 4200 Wm^{-2}. The smallest of these was measured in the Arctic at station SC83 (36 m): on the same station the 5 m sample showed an I_b of 2100, i.e., a difference of more than a factor of five between surface and deep samples (Fig. 5). A comparable

Table 1. Data relevant to experiments illustrated in Figures 3-6.

Figure	Location	Position	Date	Station #	Depth m	Sampling Time (Local)	Temperature °C	Chlorophyll *a* biomass mg m⁻³	Populations
3a	Coast of Peru	8°39′S 78°48′W	5 Nov/77	P71	2	1500 h	17	13	Diatoms
3b	Coast of Peru	8°50′S 79°11′W	16 Nov/77	P204	Surface	1230 h	20	97	*Mesodinium*
4a	Scotian Shelf	42°25′N 63°25′W	4 Jun/78	DAW-4	10	0630 h	10.5	0.4	Flagellates
4b	Scotian Shelf	42°25′N 63°25′W	6 Jun/78	DAW-6a	10	1130 h	11	0.3	Flagellates
5a	Arctic	74°46′N 78°2′W	11 Sept/78	SC83	5	0930 h	+0.5	0.6	Diatoms
5b	Arctic	74°46′N 78°2′W	11 Sept/78	SC83	36	0930 h	−0.5	4.5	Diatoms
6a	Coast of Peru	9°21′S 78°51′W	20 Nov/77	P242	10	0600 h	19	0.8	Diatoms
6b	Coast of Peru	9°21′S 78°51′W	20 Nov/77	P244	10	1200 h	19	3.7	Diatoms
6c	Coast of Peru	9°21′S 78°51′W	20 Nov/77	P245	10	1800 h	19	8.2	Diatoms
6d	Coast of Peru	9°21′S 78°51′W	21 Nov/77	P248	10	2400 h	19	3.3	Diatoms
6e	Coast of Peru	9°21′S 78°51′W	21 Nov/77	P250	10	0600 h	19	6.3	Diatoms

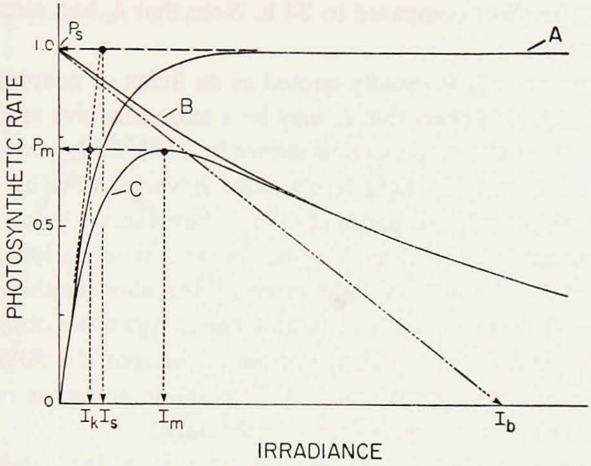

Figure 7. Showing the geometric relationships of the photosynthetic parameters and derived parameters.

range of variation in I_b was observed during a 24 h period at a station off Peru (Fig. 6), with the lowest values occurring during the dark hours and the highest during the light hours (at this station the sun rose at 0527 h and set at 1800 h).

It is tempting to make a connection between the low values of I_b in the deep water at the arctic station and those in the dark period at the Peru station. If these are indeed manifestations of the same phenomenon, then the adaptation time of the

Table 2. Light saturation parameters for experiments listed in Table 1.

Station	P_s^B (*)	α (**)	$10^3 \cdot \beta$ (**)	P_m^B (*)	I_m (†)	I_k (†)	I_s (†)	I_b (†)
P71	10.1	0.25	11.0	8.4	130	33	40	930
P204	9.60	0.20	0.61	9.40	280	47	48	1600
DAW-4	3.80	0.091	1.9	3.4	160	38	42	2000
DAW-6a	8.33	0.16	0	8.3	— (††)	51	52	— (††)
SC83(5m)	1.05	0.041	0.50	0.98	110	24	26	2100
SC83(36m)	0.81	0.038	2.2	0.64	61	17	21	370
P242	15.6	0.95	3.7	15.2	92	16	17	4200
P244	6.37	0.24	3.6	5.9	110	25	26	1800
P245	1.20	0.082	2.7	1.04	50	13	12	380
P248	1.04	0.064	2.3	0.90	55	14	16	450
P250	2.14	0.086	0.84	2.02	120	24	25	2600

* mg C(mg Chl a)$^{-1}$h^{-1}

** mg C(mg Chl a)$^{-1}$h^{-1}(Wm^{-2})$^{-1}$

† Wm^{-2}

†† I_m and I_b are undefined for $\beta = 0$

parameter I_b must be short compared to 24 h. Note that I_b had already fallen to its lowest value by sunset.

The derived parameter I_k is usually quoted as an index of adaptation to low light levels (Talling, 1957). It appears that I_b may be a more sensitive index of adaptation than I_k. For example at the arctic station shown in Table 2, I_b varied by a factor of 5.7 between the 50% and 1% light levels while I_k varied only by a factor of 1.4. We have observed this kind of response at many other stations in the Arctic.

The formulation we have used to describe our results, equation (1), permits objective estimates of I_m, the optimal light intensity for photosynthesis, equation (3), excluding the case $\beta = 0$ for which I_m is undefined. Again we observe (Table 2) a similar variation over 24 h at the Peru station as between the 50% and 1% light levels at the arctic station: approximately half as much energy is required to saturate photosynthesis of populations collected in the dark.

It is well known that photoinhibition is a time-dependent phenomenon (Kok, 1956; Takahashi *et al.*, 1971; Harris and Lott, 1973; Harris and Piccinin, 1977). In the analysis we have done so far, we have ignored this time-dependence, relying on the consistency of methodology from experiment to experiment and the constancy of incubation time. In this way we hope that the light-saturation parameters, determined under standard procedures, will have a useful interpretation in the physiological ecology of phytoplankton. In one experiment however (Canadian Arctic, Stn Sc 45, Sept. 1978), we have compared the light-saturation parameters as determined from 4 h incubations with those determined from 8 h incubations. We found minimal differences in $I_m(86\ Wm^{-2})$, $I_k(24\ Wm^{-2})$ and $\alpha(0.042$ mg C(mg Chl $a)^{-1}h^{-1}(Wm^{-2})^{-1})$. On the other hand P_s^B was reduced from 1.49 mg C $m^{-3}h^{-1}$ at 4 h to 1.13 at 8 h and β was reduced from 0.0038 mg C(mg Chl $a)^{-1}h^{-1}$ $(Wm^{-2})^{-1}$ to 0.0018. Since the changes in P_s^B and β were both in the same sense, the change in I_b was less than the change in either: it increased from 400 Wm^{-2} at 4 h to 630 at 8 h. More work has to be done on the effect of exposure time in these experiments.

b. Scaling the equation. In comparing different light-saturation curves, the eye is sometimes a misleading judge of degree of inhibition since one, two or all three of the photosynthetic parameters α, P_s^B and β might differ between the curves. It is therefore convenient to recast the equation in dimensionless form by scaling the variables P and I. Using asterisks to denote dimensionless variables, let us write the scaling equations as

$$P_* \equiv P/P_s \tag{8}$$

and

$$I_* = I/I_s \tag{9}$$

where $I_s \equiv P_s^B/\alpha$. With these choices of scale, equation (1) takes the very simple dimensionless form

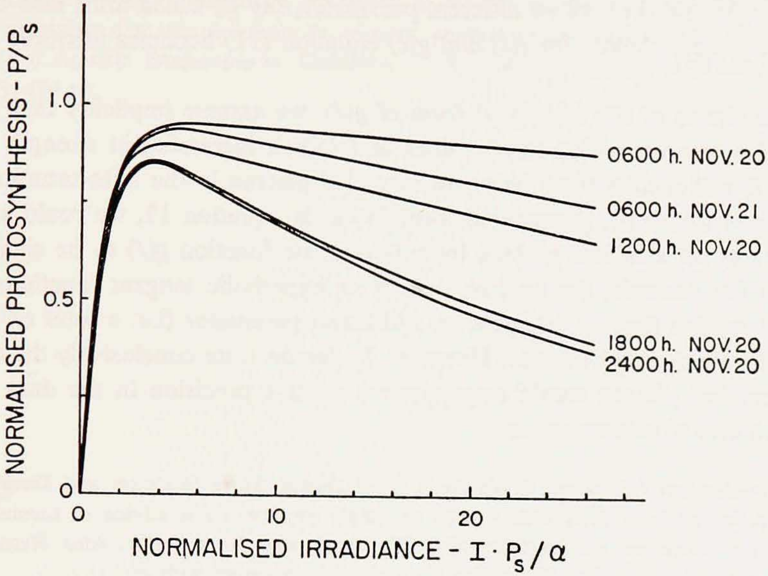

Figure 8. Data of Figure 7 replotted in scaled form.

$$P_{\bullet}(I_{\bullet}) = [1-\exp(-I_{\bullet})] \exp(-\beta I_{\bullet}/\alpha) \tag{10}$$

An example of the application of this equation is given in Figure 8 where each curve of the diurnal series of Figure 6 is replotted in the same set of axes.

c. Justification of the model. The most plausible explanation of the observed form of the light-saturation curve for phytoplankton (Fig. 1) is that over at least part of the range I, two opposed physiological processes are taking place simultaneously: one photoenhanced, the other photoinhibited (see Vollenweider, 1965). If this were not so, every light-saturation curve would either be sharply peaked or have an extended plateau. Let us assume that there is some physiological maximum production rate P_s for the population and that whatever process is responsible for photoinhibition results in a reduction of the photoenhanced production by an amount dependent on I. Let us call the photoenhanced function $f(I)$ and the factor by which it is reduced through photoinhibition $g(I)$. Then we can write for the observed production P

$$P = P_s f(I) \cdot (1-g(I)) \ . \tag{11}$$

The function $f(I)$ may be any increasing function asymptotic to unity at large values of I and linear (slope α) as I approaches zero. A functional form that is particularly tractable is $f(I) = 1-e^{-\alpha I/P_S}$. To ensure that equation (11) does not yield estimates of $P < 0$, the function $y(I)$ should have an upper bound of unity. It should also be zero at $I = 0$. It is then convenient and tractable to take the same functional form for $g(I)$ as for $f(I)$, but with a different parameter, say β, which must also be scaled to P_s. With these choices for $f(I)$ and $g(I)$ equation (11) becomes identical to equation (1).

By our choice of the functional form of $g(I)$, we assume implicitly that photoinhibition is a process acting at all values of I (albeit increasing in strength with increasing I) rather than there being an extended plateau in the light-saturated range of the curve. Using the generalized formulation in equation 11, we could admit the possibility of an extended plateau by choosing the function $g(I)$ to be sigmoidal in shape, as for example, the inverse tangent or hyperbolic tangent functions. To do so would require that we estimate an additional parameter (i.e. a total of four), to control the width of the plateau. However, to demonstrate conclusively the existence of an extended plateau would require more relative precision in the data than we have been able to achieve so far.

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REFERENCES

Bard, Y. 1974. Nonlinear parameter estimation. New York, Academic Press, 332 pp.

Bevington, P. R. 1969. Data reduction and error analysis for the physical sciences. New York, McGraw Hill, 336 pp.

Harris, G. P. and J. N. A. Lott. 1973. Light intensity and photosynthetic rates in phytoplankton. J. Fish. Res. Bd. Canada, *30,* 1771–1778.

Harris, G. P. and B. B. Piccinin. 1977. Photosynthesis by natural phytoplankton populations. Arch. Hydrobiol., *80,* 405–457.

Jassby, A. D. and T. Platt. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr., *21,* 540–547.

Kok, B. 1956. On the inhibition of photosynthesis by intense light. Biochim. Biophys. Acta, *21,* 234–244.

Platt, T. and A. D. Jassby. 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J. Phycol., *12,* 421–430.

Platt, T., K. L. Denman and A. D. Jassby. 1977. Modeling the productivity of phytoplankton, *in* The Sea: Ideas and Observations on Progress in the Study of the Seas. Vol. VI. Goldberg, E. D. (Ed.), New York, John Wiley, 1048 pp.

Steele, J. H. 1962. Environmental control of photosynthesis in the sea. Limnol. Oceanogr., *7,* 137–150.

Takahashi, M., S. Shimura, Y. Yamaguchi and Y. Fujita. 1971. Photoinhibition of phytoplankton photosynthesis as a function of exposure time. J. Oceanogr. Soc. Japan *27,* 43–50.

Talling, J. F. 1957. The phytoplankton population as a compound photosynthetic system. New Phytol., *56,* 133–149.

Therriault, J.-C., D. J. Lawrence and T. Platt. 1978. Spatial variability of phytoplankton turnover in relation to physical processes in a coastal embayment. Limnol. Oceanogr., *23,* 900–911.

Vollenweider, R. A. 1965. Calculation models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurement, *in* Primary Productivity in Aquatic Environments. Goldman, C. R. (Ed.), University of California Press, Berkeley, 464 pp.

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