Mathematical formulation of the relationship between photosynthesis and light for phytoplankton

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Abstract

Eight different mathematical formulations of the photosynthesis–light curve for phytoplankton (up to and including light saturation) were recast in terms of the same two parameters: the initial slope α, and the assimilation number $P_m{}^B$. Each equation was tested for its ability to describe empirical data from natural populations of marine phytoplankton: the results of 188 light-saturation experiments at three coastal locations in Nova Scotia over a 2-year period. The most consistently useful mathematical representation of the data was found to be the hyperbolic tangent function.

Three factors motivate the search for mathematical formulations of the relationship between photosynthesis and light for phytoplankton (the light-saturation curve). First, the simulation and prediction of changes in phytoplankton biomass by means of mechanistic models require a quantitative expression for photosynthesis. Second, if in situ productivity could be estimated with sufficient precision from more easily measured variables (irradiance, chlorophyll a, nutrients, temperature, etc.) we could collect productivity data with greater spatial and temporal resolution for the same amount of effort. Third, a mathematical formulation enables us to determine the physiological parameters of photosynthesis operationally by choosing those parameter values which produce the best fit between the equation and the experimental data.

Of the equations that have been proposed to describe the utilization of light by phytoplankton, a few are based on grossly oversimplified models of photosynthesis; the rest are completely empirical. This being the case, the only valid criterion for judging the relative merits of the different formulations is their ability to describe data with the minimum number of well chosen parameters. As discussed at some length in Platt et al. (1975), by "well

chosen" we mean parameters which are, as far as possible, mututally independent, and which have an informative physical interpretation, that is a significance transcending their role as operators in a particular mathematical expression.

Here we compare the merits of eight different representations of the photosynthesis–light relation judged according to this criterion of ability to describe experimental data. We treat only that part of the curve up to and including light saturation. We shall not consider the range of light levels above the threshold of photoinhibition, where the introduction of at least one additional, *independent* parameter would be required for a complete description (Platt et al. 1975).

The test data comprise measurements of ^{14}C uptake and irradiance from 188 experiments made at three coastal locations in Nova Scotia over a period of 2 years. We thank B. Irwin, P. Dickie, and D. Rudderham for technical help and K. L. Denman for constructive discussion. T. T. Bannister and J. Steele made helpful comments on the manuscript. We are indebted to S. Taguchi for permission to refer to his unpublished data.

Basis for comparing the equations

All mathematical expressions relating primary productivity per unit chlorophyll biomass, P^B (mg C[mg Chl a]$^{-1}$ h^{-1}), to irradiance, I (W m^{-2}), can be rewritten in terms of two common parameters: α (mg

Table 1. The different formulations of the light-saturation curve tested.

Equation number	Equation	Source*
1	$P^B = \begin{cases} \alpha I, & I \leq P_m^B/\alpha \\ P_m^B, & I > P_m^B/\alpha \end{cases}$	Blackman (1905)
2	$P^B = P_m^B \alpha I/(P_m^B + \alpha I)$	Baly (1935)
3	$P^B = P_m^B \alpha I/[(P_m^B)^2 + (\alpha I)^2]^{\frac{1}{2}}$	Smith (1936)
4	$P^B = \alpha I \exp(-\alpha I/P_m^B e)$	Steele (1962)
5	$P^B = \begin{cases} \alpha I \exp(-\alpha I/P_m^B e), & I \leq P_m^B e/\alpha \\ P_m^B, & I > P_m^B e/\alpha \end{cases}$	Steele (1962) modified†
6	$P^B = P_m^B[1 - \exp(-\alpha I/P_m^B)]$	Webb et al.(1974)
7	$P^B = \begin{cases} \alpha I - (\alpha I)^2/4P_m^B, & I \leq 2P_m^B/\alpha \\ P_m^B, & I > 2P_m^B/\alpha \end{cases}$	Platt et al.(1975) modified†
8	$P^B = P_m^B \tanh(\alpha I/P_m^B)$	original?

*The equations from various sources have been recast into common form in terms of the parameters α (initial slope of the light-saturation curve) and P_m^B (specific production rate at optimal light intensity). In each case, I is the available light intensity and P^B is the instantaneous production rate normalized to the chlorophyll biomass B.

†These modifications are consistent with our decision not to study the range of light intensities where photoinhibition occurs.

$C[\text{mg Chl } a]^{-1} \text{ h}^{-1} \text{ W}^{-1} \text{ m}^{-2})$, the slope of the light-saturation curve at low light levels, i.e. in the linear range; and $P_m^B(\text{mg } C[\text{mg Chl } a]^{-1} \text{ h}^{-1})$, the specific photosynthetic rate at optimal illumination, i.e. the assimilation number. The influence of factors such as temperature, nutrients, and adaptation can be represented mathematically through their effect on the basic parameters, α and P_m^B. Furthermore, *only* these two parameters are required for a sufficient representation of the light-saturation curve up to light levels where photoinhibition begins (Platt et al. 1975). Models containing more than two parameters (Vollenweider 1965; Parker 1974) have therefore been excluded from consideration here.

Eight two-parameter formulations of the light-saturation curve are listed in Table 1. They have all been rewritten in terms of α and P_m^B. The list comprises several well known expressions from plant physiology as well as less widely used equations, including one that is used for the first time (as far as we are aware) in the context of photosynthesis. All eight equations are therefore cast in equivalent form and may legitimately be compared with respect to their success in fitting experimental data. Their general shapes are depicted in Fig. 1 for the same values of the parameters α and P_m^B.

The light-saturation curve usually refers to *gross* photosynthesis. Since our data are based on ^{14}C uptake, which corresponds
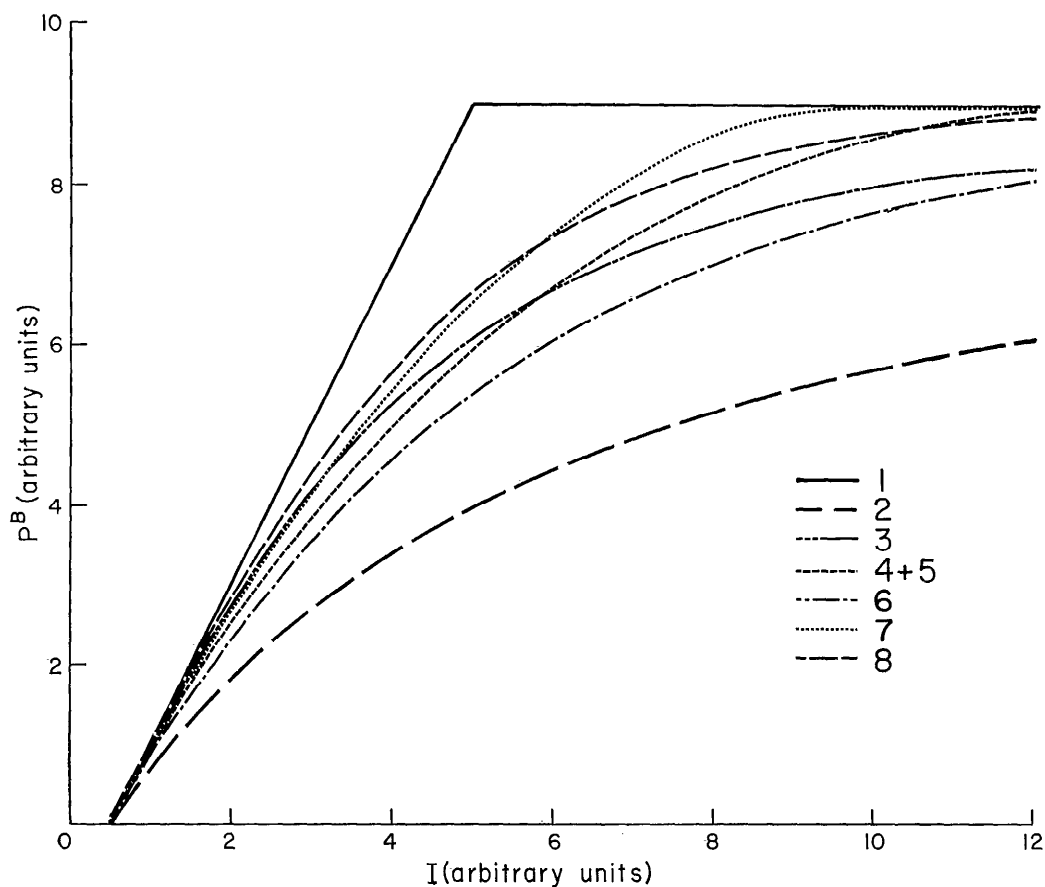
Fig. 1. The eight equations displayed for comparison. The same parameter values are used in each case: $P_m{}^B = 10;\ \alpha = 2;\ R^B = 1.$

approximately with *net particulate* productivity (Eppley and Sloan 1965; Ryther and Menzel 1965), our curves of production versus light do not pass through the origin: ^{14}C uptake falls to zero while I is still positive. This is generally represented by assuming a constant, light-independent respiration loss R^B(mg C[mg Chl a]$^{-1}$ h^{-1}) and writing $P_{net}{}^B = P_{gross}{}^B - R^B$. We follow this convention, although it becomes increasingly untenable in the face of the accumulating evidence on photorespiration (Tolbert 1974). Our justification rests partly on pragmatism and partly on the principle of parsimony: the various formulations are, for the most part, empirical and the ultimate standard of validity is their ability to describe data.

Methods

Light-saturation experiments—Light-saturation measurements were made using populations taken from three coastal stations during the period July 1973 to March 1975: Bedford Basin (63°38'30"W, 44°41' 30"N), a small fjordlike inlet with a heavily populated watershed; St. Margaret's Bay (64°02'W, 44°35'N), a larger, more exposed bay in a relatively less populated area; and off Chebucto Head (63°30'W, 44°30'N), a promontory directly south of Halifax Harbor. Two depths were sampled on each sampling day (either 1 and 5 m, or 5 and 10 m). Each experiment was made in duplicate. In all, 188 duplicate experiments were made.

A linear incubator was used, illuminated at one end by a spotlight (Sylvania 150-W projector flood). Temperature was controlled by circulating seawater. The incubator was divided into compartments along its axis by means of transverse partitions consisting of a double layer of nylon mesh (Nitex, 153-μm mesh) sandwiched in Plexiglas. The incubators used at the beginning of the series of experiments had six compartments, but those used after March 1974 (when most of the data were taken) had ten. Duplicate incubators were used for each measurement. Total irradiance in each compartment was measured with a pyranometer (Eppley, black and white) and the photosynthetically active portion (PAR) with a spectroradiometer (ISCO, model SR). The irradiances varied from one experiment to the next as the lamps and the incubators changed, but in any one experiment the range of light levels covered was about 1–400 W m^{-2} of PAR.

Uptake of ^{14}C was measured according to standard procedures (e.g. Strickland and Parsons 1972) during the late morning; incubations lasted 4 h. Liquid scintillation counting, channels ratio method, was used to measure the activity of the filters. The scintillation fluid consisted of equal parts toluene and ethylene glycol monoethyl ether with 8.40 g liter^{-1} PPO and 0.106 g liter^{-1} POPOP. Chlorophyll concentration was measured in quadruplicate by the fluorometric method of Yentsch and Menzel (1963) as modified by Holm-Hansen et al. (1965), using a Turner model III instrument.

Fitting the models—For each experiment the results from the duplicate incubators were combined, giving a total of 12 to 20 paired measurements of P^B and I. From these, the occasional measurement showing photoinhibition was discarded for the purpose of our analysis.

In fitting the data to particular expressions for P^B, we did not find it rewarding to fit both parameters, α and $P_m{}^B$, simultaneously. Using nonlinear fitting procedures, e.g. the Marquardt algorithm (Conway et al. 1970), we frequently found that the

final parameter estimates for α were far outside the range of published values and grossly inconsistent with estimates of α made by subjective inspection of the data taken at low light levels. The reason seems to be that since the equations are only empirical, some of them do not follow very faithfully the details of the shape of the light-saturation curve. Under these circumstances a least-squares fit can lead to spurious results if both variables are subject to error.

We adopted therefore the following two-stage fitting procedure. First, noting that all of the eight formulations reduce to the same straight line for sufficiently small values of I, we found α and R^B by simple linear regression according to the equation

$$P^B = \alpha\, I - R^B.$$

This mathematical statement is equivalent to the assumption of constant quantum yield of photosynthesis at low light levels, with which our data were quite consistent.

To make the regression we selected those data points that belonged to the linear portion of the light-saturation curve. This was a subjective decision, but it was found in practice that the decision could be made unequivocally, and when different people made the selection independently, they invariably came to the same conclusion.

In the second stage of fitting, the value of $P_m{}^B$ was found by a nonlinear least-squares fit to the model equation with α and R^B held fixed at the values determined in stage one by linear regression. The computation was performed by the grid-search method (Bevington 1969).

Criteria of fidelity for the models—Two indices were established to judge the success of the different representations in fitting the experimental data. They were calculated separately for each station location.

As a first attempt at an index of fidelity we calculated the mean squared deviation $\delta_i{}^2$ for each equation i:

$$\delta_i{}^2 \equiv \frac{1}{N} \sum_{j=1}^{N} \sum_{k=1}^{m_j} (\hat{P}_{ijk}{}^B - P_{jk}{}^B)^2,$$

where $P_{jk}{}^B$ is the measured production for

Table 2. Indices of goodness-of-fit to eight different formulations of the light-saturation curve using experimental data from three stations. For each station, δ_i^2 is the mean scatter about the line fitted by the ith equation, and N_i is the number of times the ith equation gave the best fit according to an unweighted least-squares criterion.

Equation Number i	Bedford Basin δ_i^2	N_i	St. Margaret's Bay δ_i^2	N_i	Chebucto Head δ_i^2	N_i
1	2.95	8	3.72	18	3.28	0
2	5.57	0	4.97	5	5.57	0
3	1.33	18	1.74	31	1.68	4
4	21.5	1	21.0	1	26.6	0
5	1.86	7	2.15	2	1.87	1
6	2.52	1	2.48	15	2.48	3
7	1.63	1	2.15	1	1.82	0
8	1.33	23	1.92	37	1.70	11
Total		59		110		19

the jth experiment at the kth light intensity and $\hat{P}_{ijk}{}^B$ is the value predicted by the ith equation for this data point, N is the total number of experiments made at that location, and m_j is the number of data points available for the jth experiment.

We also calculated for each experiment the quantity

$$\sum_{k=1}^{m_j} (\hat{P}_{ijk}{}^B - P_{jk}{}^B)^2,$$

and added up the number of times N_i for which this quantity was lowest when the ith equation was used or, in other words, the number of times the ith equation gave the best fit according to this criterion.

Results

The raw data are available as a technical report (Irwin et al. 1975).

Table 2 gives the values of δ_i^2 and N_i for each of the eight equations, calculated for the three stations. According to the index δ_i^2, Eq. 3 (Smith 1936) and 8 (hyperbolic tangent) were clearly superior to the rest at all three stations. The next best fit was given by the truncated parabola (Platt et al. 1975). The worst fits were given by Eq. 2 (rectangular hyperbola) and 4 (Steele 1962). The rank order of the equations with respect to the criterion δ_i^2 was identical for all three stations.

According to the index N_i, the hyperbolic tangent (Eq. 8) was the most successful formulation at each location. It gave the best fit in 38% of all the experiments. Smith's equation (Eq. 3) was the next most useful, but it fell substantially behind the hyperbolic tangent. Of the rest, the rectilinear representation (Eq. 1) gave the best fit in a surprisingly large proportion of cases. In any individual experiment, differences in the error variance between some of the curves may not have been significant. But the statistic N_i is based on the relative magnitude of the error variance in a large number of independent trials and should be a reliable guide to the best choice among the various empirical formulations of the light-saturation curve. We were not able to detect any effect of depth or season on the relative fit given by the different equations. A detailed analysis is the subject of another publication (Platt and Jassby 1976).

Discussion

The methodology described in this paper depends on the linearity of the light-saturation function for small light fluxes. Reports of nonlinearity, even at very low irradiances, appear from time to time in the literature. This nonlinearity has been ascribed to the interaction of mitochondrial respiration with photosynthetically produced ATP (Reid 1970). Nowhere in our data was there clear evidence of such a

phenomenon: for the time being, at least, it may be ignored in the ecological context.

Another basic assumption of the method is that the respiration R^B is independent of light level. A simple correction for the effect of light on respiration is often formulated as

$$R_{\text{light}}{}^B = rP_{\text{gross}}{}^B + R^B,$$

in which it is supposed that a constant fraction r of the recent photosynthate is respired in addition to some basal level R^B (Tooming 1970). With this correction, all eight equations tested can be recast, in entirely equivalent forms, in terms of the new parameters $\alpha' = (1-r)\alpha$ and $P_m{}^{B'} = (1-r)P_m{}^B$. So if a linear correction is an adequate approximation for the effect of light on respiration, the interconversion of gross and net photosynthesis is still justified, but with a reinterpretation of the parameters. Of course, the basal or mitochondrial respiration R^B is not totally unaffected by light; futhermore it is clear that the new parameters α' and $P_m{}^{B'}$ will be modified by the photorespiratory activity r: two further factors are therefore recognized which contribute to the variability of the physiological parameters.

The methods laid out here could be used to find the optimal formulation of the relationship between photosynthesis and light beyond the threshold of photoinhibition. This problem is more complex however since an additional, independent experimental variable would have to be introduced, namely, the time for which the cells are exposed to higher-than-optimal light fluxes. It has been known for some time that the damaging effect of light at these high irradiances can lead to short term changes in net production rate at a fixed level of I (Steemann Nielsen 1949). Most of the data available on photoinhibition do not permit the effect of exposure time to be deduced, and there is a need for systematic investigation along these lines. A suitable mathematical representation of the light-inhibition range could then be made in terms of time-dependent parameters (time-scale $\lesssim$ minutes).

The two equations which gave the poorest description of the experimental data are among the most widely used in all phytoplankton ecology. One of these is the rectangular hyperbola (Eq. 2). Because of the frequent application of this function, in analogy with Michaelis-Menten enzyme kinetics, to describe nutrient uptake by phytoplankton, the temptation has been strong to extend its use to describe other phenomena, including photosynthesis. Our results indicate that such temptations are to be resisted. The other popular equation which proved to be inadequate is 4 (Steele 1962). The reason is that photoinhibition is built into the equation in such a way that the photosynthetic response below the inhibition threshold is not independent of the response above the threshold. The result is that, if the α used represents the true initial slope, the equation exhibits inhibition for irradiances which are too low. If Steele's equation is modified to exclude the possibility of inhibition (Eq. 5) a far superior fit is obtained (Table 2), but this contradicts the original intent of the model (Steele 1962).

The results presented here indicate that of the equations tested, from zero light up to the onset of photoinhibition, the light-saturation curve for natural populations of coastal phytoplankton is best described by a hyperbolic tangent function. For most purposes, this expression suffers from no disadvantage, compared to the others, of difficulty in either mathematical analysis or numerical computation, and we recommend its use as an operational model for the elucidation of physiological parameters in photosynthesis–light experiments and for theoretical investigations in phytoplankton ecology. In the latter context, however, we should point out that for integration over depth (*see* Platt et al. 1975), an analytic solution cannot be obtained with the hyperbolic tangent for $\alpha I_0'/P_m{}^B \geq \pi/2$ (where I_0' is the photosynthetically active radiation available just below the sea surface). This condition is too restrictive for the range of I_0' encountered in the field, and we are

Table 3. Values of δ_i^2 and N_i (*see text*) calculated from light–saturation experiments on seven species of marine diatom* in pure culture (S. Taguchi unpublished). The cells were grown in seawater enrichment "f/2-t" at a temperature of 5–8°C and an irradiance of about 10 W m⁻². Light-saturation measurements were made at various points in the log phase of growth, a total of 16 experiments.

i	δ_i^2	N_i
1	1.95	1
2	3.89	3
3	1.88	3
4	3.33	0
5	2.11	0
6	2.59	0
7	1.72	4
8	1.63	5
Total		16

*Phaeodactylum tricornutum Bohlin, Fragilaria sp., Skeletonema costatum (Greville) Cleve, Chaetoceros septentrionale Oestrup, Thalassiosira nordenskioldii Cleve, Ditylum brightwelli Grunow, Coscinodiscus centralis Ehrenberg.

obliged to use numerical integration. In those cases where it is considered essential to have an analytic solution for the integral over depth, we recommend the use of Smith's equation.

Finally, we would also like to mention that a recent investigation in this laboratory of the nature of the light-saturation curve for seven different species of marine phytoplankton in culture (S. Taguchi unpublished) has also led to the conclusion that the hyperbolic tangent function affords the best description of the experimental data (Table 3).

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