

A mechanistic model of the effects of light and temperature on algal primary productivity

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Abstract

In this work a model of algal primary productivity combining a mechanistic light function with a temperature Arrhenius function is presented.

Data on primary productivity obtained with algae acclimated to different environmental conditions was used to test the model. A simple method for model parameter estimation based on regression analysis is described. The parameter estimates can be improved by a non-linear least-squares method (e.g. the Gauss–Newton method) resulting in a significant fit to the observed data as tested by regression analysis.

According to the present model, the initial slope of the productivity/light curves is temperature dependent whilst the optimal light intensity is temperature independent. These model predictions were validated by the obtained experimental results.

Keywords: Algae; Light; Production, primary; Temperature

1. Introduction

During the last decades several mathematical formulations of algal primary productivity (P) as a function of light intensity (I) were developed (e.g. Steele, 1962; Vollenweider, 1965; Jassby and Platt, 1976; Platt et al., 1980; Iwakuma and Yasuno, 1983). Those formulations are mainly empirical giving a static representation of the dependence of the production rate on light intensity (Eilers and Peeters, 1988).

There are a few parameters that are common to almost all models or can be derived from them, namely the initial slope (S) of the P versus I curves (or quantum yield), the optimal light intensity (I_{opt}) and the maximal production rate (P_{max}).

The choice of a particular formulation may lead to different estimates of the P – I curve parameters (Frenette et al., 1993). A detailed description of some of the existing models can be found in Jassby and Platt (1976), Iwakuma and Yasuno (1983), Odum (1983) and Parsons et al. (1984).

Equations that combine the effects of several environmental variables such as light intensity, temperature and nutrient concentrations can also be found (e.g. Keller, 1989). In this case P_{max} is usually expressed as a function of an other parameter (e.g. temperature) and/or limiting factors multiplied by the light function (e.g. Cloern, 1977; Keller, 1989; Fasham et al., 1990).

Eilers and Peeters (1988) proposed a dynamic mechanistic formulation for the relationship be-

tween light intensity and the rate of photosynthesis. As stated by those authors a dynamic model can be more useful for testing the effects of different factors on model parameters and characteristics of the production curves. Eilers' model describes the photosynthetic processes and those connected with photoinhibition, producing $P-I$ curves similar to those obtained with the models of Vollenweider (1965) and Platt et al. (1980).

Eilers' model predicts that the initial slope of the $P-I$ curves is temperature independent whilst P_{\max} and I_{opt} change in the same proportion to temperature. This conflicts with recent physiological data (see e.g. Davison (1991) for a review). The initial photochemical reactions are temperature independent but the subsequent biochemical reactions are dependent on temperature. Because of this, the light harvesting efficiency or slope may also vary with temperature.

There seems to be general agreement on the temperature dependence of P_{\max} through an exponential relationship at temperatures below the temperature optimum (see Cloern, 1977 and Keller, 1989). The dependence of I_{opt} on temperature does not appear to be clearly established.

The experimental measurement of the $P-I$ curve parameters is complicated by the fact that they may change as algae adapt to varying environmental conditions. Light intensity, temperature and nutrient concentrations are known to influence the light harvesting efficiency of algae (Davison, 1991; Falkowski and LaRoche, 1991; Turpin, 1991). These changes may be relevant for multiple-day laboratory experiments.

A way to reduce the natural variability of the $P-I$ curve characteristics is to keep the individuals at constant conditions during a time period large enough for them to acclimate. The available data suggests that acclimation begins a few hours after the algae are exposed to a change in temperature and/or light (Algarra and Niell, 1990; Davison, 1991; Falkowski and LaRoche, 1991).

The objectives of this work are the following:

1. development of a production model incorporating the influence of temperature on photosynthesis;
2. development of a methodology allowing an easy estimation of the model parameters;
3. validation of the model by comparison of its predictions to experimental data obtained with the red algae *Gelidium sequipedale* pre-acclimated to different conditions.

2. Methodology

2.1. Structure of the model

Eilers and Peeters (1988) considered three possible states for the absorbing pigments ("photosynthetic factories" (PSF) sensu Crill, 1977): fundamental, excited and inhibited. The transitions from the fundamental to the excited state and from the excited to the inhibited state are proportional to I and to the rate constants k_1 and k_2 (Fig. 1). The recovery rate or probability of the excited PSF to the fundamental state (k_3 in Fig. 1) is assumed to be dependent on how fast energy is used in the dark temperature-dependent reactions. The recovery rate of the inhibited to the fundamental state (k_5 in Fig. 1) corresponds to repair from photoinhibition.

In the present model the existence of these three possible states for the light absorbing pigments (PSF) is also considered. The fluxes between the three states are biophysical and depend solely on light intensity and on the numerical values of the constants (k_2 to k_5) shown in

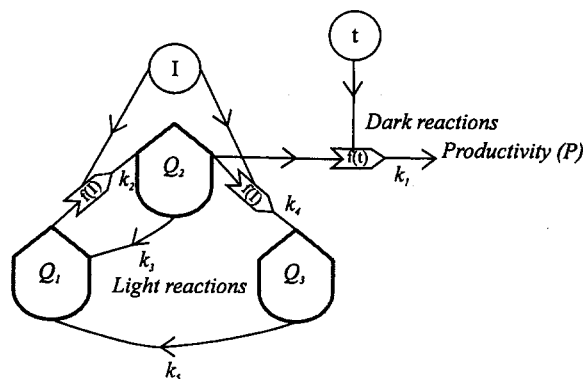


Fig. 1. States and transition rates between the three possible pigmentary states: fundamental, excited and inhibited (Q_1 , Q_2 and Q_3 , respectively) following the energy-circuit language (Odum, 1975); $f(I)$ represents the light effects and $f(t)$ is an Arrhenius function: $\exp(d - e/t)$ (see text for explanation).

Fig. 1. The constant k_3 is not assumed to be necessarily related to the dark reactions as in Eilers' model, because the recovery of the excited to the fundamental state may occur without the liberation of oxygen from the water (Megard et al., 1984) and consequent energy generation to the dark reactions. The transition of absorbed energy to the organic compounds that are synthesised in the dark reactions of photosynthesis is temperature dependent as all biochemical processes. This temperature dependence is represented by an Arrhenius function with coefficient's d and e (Fig. 1). This function can be improved to achieve a maximum above which temperature will inhibit photosynthesis (Odum, 1983). In the present work such modification was not implemented because the experimental data used to test the model did not cover a temperature range large enough to attain that maximum.

Therefore in the model presented in this paper there is a clear separation between the light and dark photosynthetic reactions. This is the main difference from Eilers' model where the recovery of the pigments from the excited state is directly connected to those reactions. In a recent paper Eilers and Peeters (1993) gave an interesting dynamic analysis of the previously described model (Eilers and Peeters, 1988), providing some important results that can help to clarify the influence of light intensity and incubation time in the analysis of productivity experiments. However, the influence of temperature is analysed in a way similar to their previous work (Eilers and Peeters, 1988).

In the derivation of differential equations that follows it will be clear how the differences between the Eiler's and the present model are reflected in the predicted behaviour of the P – I curve parameters.

Let Q_1 , Q_2 and Q_3 represent the quantities of PSF at the different states and P the photosynthetic gross productivity. From the possible transitions under steady state-conditions it follows:

$$\frac{\partial Q_1}{\partial t} = -k_2 Q_1 I + k_3 Q_2 + k_5 Q_3 = 0 \quad (1)$$

$$\frac{\partial Q_2}{\partial t} = k_2 Q_1 I - k_3 Q_2 - k_4 Q_2 I = 0 \quad (2)$$

$$\frac{\partial Q_3}{\partial t} = k_4 Q_2 I - k_5 Q_3 = 0 \quad (3)$$

$$Q_1 + Q_2 + Q_3 = k \quad (4)$$

These equations can be solved explicitly. Solving for Q_2 the result is:

$$Q_2 = \frac{kk_2 k_5 I}{k_2 k_4 I^2 + k_5(k_2 + k_4)I + k_5 K_3} \quad (5)$$

The rate of photosynthetic production is proportional to the quantity Q_2 and to the temperature function:

$$P = k_1 Q_2 \exp(d - e/t) \\ = \frac{k_1 k k_2 k_5 I \exp(d - e/t)}{k_2 k_4 I^2 + k_5(k_2 + k_4)I + k_5 K_3} \quad (6)$$

To reduce the number of parameters the numerator and the denominator are divided by $k_1 k k_2 k_5$ and a , b and c introduced:

$$a = \frac{k_2 k_4}{k_1 k k_2 k_5} \quad (7)$$

$$b = \frac{k_5(k_2 + k_4)}{k_1 k k_2 k_5} \quad (8)$$

$$c = \frac{k_5 k_3}{k_1 k k_2 k_5} \quad (9)$$

The final result is:

$$P = \frac{I \exp(d - e/t)}{aI^2 + bI + c} \quad (10)$$

By differentiation of Eq. 10 in relation to I , the characteristics of the P – I curve can be calculated:

$$I_{\text{opt}} = \sqrt{\frac{c}{a}} \quad (11)$$

$$P_{\text{max}} = \frac{\exp(d - e/t)}{2\sqrt{ac} + b} \quad (12)$$

$$S = \frac{\exp(d - e/t)}{c} \quad (13)$$

The last equations demonstrate the non-dependence of I_{opt} on temperature and the exponential dependence of P_{max} and the slope on that parameter. The parameters a , b and c of the

light function can be expressed in terms of I_{opt} , P_{max} and S by the following reverse solutions:

$$a = \frac{\exp(d - e/t)}{SI_{\text{opt}}^2} \quad (14)$$

$$b = \frac{\exp(d - e/t)}{P_{\text{max}}} - \frac{2\exp(d - e/t)}{SI_{\text{opt}}} \quad (15)$$

$$c = \frac{\exp(d - e/t)}{S} \quad (16)$$

2.2. Experimental

Gelidium sesquipedale fronds were collected on the west coast of Portugal near Lisbon. After collection the algae were kept in the laboratory for a period of more than three weeks and acclimated to artificial “Winter” and “Summer” conditions. Water temperature, photoperiod and light intensity during daylight hours were kept stable during the acclimation pre-treatments. This pre-cautions were used in order to reduce the natural variability of the model parameters as a result of adaptation to varying environmental conditions (Cosby et al., 1984) and to evaluate its variability due to seasonal physiological adaptation.

Four pre-treatments were employed: two simulating winter conditions and two simulating summer conditions. Temperature was kept at 14.5°C in the first two pre-treatments and at 18.5°C in the last two, whilst photoperiod was respectively 11.5 and 14.5 h. Each pair of winter and summer pre-treatments differed only in the light intensity used, reproducing the average light intensity conditions at 9 and 13 m depth. In the winter pre-treatment these corresponded to 9 and 4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons respectively whilst in the summer pre-treatment corresponded to 16 and 11 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons respectively.

After the pre-treatment algal samples were placed in 1000-ml jars in an incubation chamber and submitted to various combinations of temperature and light intensity. Productivity was measured from oxygen differences. The temperatures used were 11, 14, 18, 22 and 26°C. At each of these temperatures, productivity was measured at the light intensities 0, 2, 4, 97, 206 and 270 μmol

$\text{m}^{-2} \text{s}^{-1}$, leading to five sets of productivity results versus light intensity from each pre-treatment. Three replicates and a control were used for each light/temperature combination. For further details on experimental procedures see Duarte (1990) and Duarte and Ferreira (1993).

2.3. Fitting the model to experimental data

Fitting was carried out separately on data obtained with algae pre-treated in each of the four different ways described previously. The fit of the model to experimental data is complicated by the fact that Eq. 10 is a two-dimensional function representing a surface rather than a line.

A two-step fitting methodology was followed in this work. In the first step preliminary estimates of a , b , c , d and e must be obtained. In the second step these estimates are optimised with a non-linear least squares procedure such as the Gauss–Newton or the Marquardt algorithm (Marquardt, 1963; Glass, 1967).

The first step can be divided in two stages. In the first, a second-order bivariate regression of P as a function of light and temperature is calculated using the usual formula:

$$P = a_0 + a_1I + a_2t + a_3I^2 + a_4t^2 + a_5It \quad (17)$$

By differentiation and maximisation of the regression equation in relation to I and t , I_{opt} and the optimum temperature t_{opt} can be estimated:

$$\frac{\partial P}{\partial I} = a_1 + 2a_3I + a_5t = 0 \quad (18)$$

$$\frac{\partial P}{\partial t} = a_2 + 2a_4t + a_5I = 0 \quad (19)$$

$$I_{\text{opt}} = -\frac{a_1 + a_5t}{2a_3} \quad (20)$$

$$t_{\text{opt}} = -\frac{a_2 + a_5I}{2a_4} \quad (21)$$

When the range of experimental data includes only the exponential part of the temperature dependence as in the present work, Eq. 21 will lead to a t_{opt} outside the experimental temperature range. In certain cases the obtained value may be biologically meaningless. If any of these problems

arises, a temperature as close as possible to the optimum value must be used to calculate I_{opt} with Eq. 20. The choice should be among the highest tested temperatures.

Solving the regression equation for I_{opt} and t_{opt} allows the calculation of P_{max} . The slope can be calculated as the value of the derivative when $I = 0$.

In the second stage, productivity values at the estimated I_{opt} and all measured temperatures are computed from the regression equation. A linear regression analysis is performed on the natural logarithms of the calculated P values as a function of $1/t$ to estimate the parameters d and e of the Arrhenius function. At I_{opt} light intensity, temperature will be responsible for most of the variance of the productivity data, under the assumption that there are no other limiting factors. The light function parameters a , b and c are then calculated with the reverse Eqs. 14, 15 and 16.

In the second step the partial derivatives of Eq. 10 with respect to each of the five parameters must be calculated and they are the following:

$$\frac{\partial P}{\partial a} = - \frac{I^3 \exp(d - e/t)}{(aI^2 + bI + c)^2} \quad (22)$$

$$\frac{\partial P}{\partial b} = - \frac{I^2 \exp(d - e/t)}{(aI^2 + bI + c)^2} \quad (23)$$

$$\frac{\partial P}{\partial c} = - \frac{I \exp(d - e/t)}{(aI^2 + bI + c)^2} \quad (24)$$

$$\frac{\partial P}{\partial d} = \frac{I \exp(d - e/t)}{aI^2 + bI + c} \quad (25)$$

$$\frac{\partial P}{\partial e} = - \frac{I \exp(d - e/t)}{(aI^2 + bI + c)t} \quad (26)$$

In the present work the Gauss–Newton and the Marquardt methods were used to optimise the parameter values by minimising the residual sum of squares (Glass, 1967). Normally the preliminary parameter estimates obtained as described above are generally accurate enough considering the experimental and analytical errors involved typically in productivity measurements.

Thus in some cases, the use of the non-linear least-squares techniques did not improve significantly the preliminary parameter estimates.

The predictive ability of the fitted model was tested by model II regression analysis (Laws and Archie, 1981; Sokal and Rohlf, 1981) between the measured and calculated values. The slope of the regression line, the y-intercept and the proportion of variance explained by the regression, were used as measures of the model goodness of fit.

2.4. Behaviour of the P – I curve parameters in relation to temperature

To test the model predictions on the behaviour of S and I_{opt} with changing temperature a second-order polynomial fit was carried out on each set of productivity results obtained at each of the five experimental temperatures (see above). S and I_{opt} were estimated in a similar way to that described above (Eqs. 17, 18, 19, 20 and 21) but having only light intensity as the independent variable:

$$P = a_1 I + a_2 I^2 \quad (27)$$

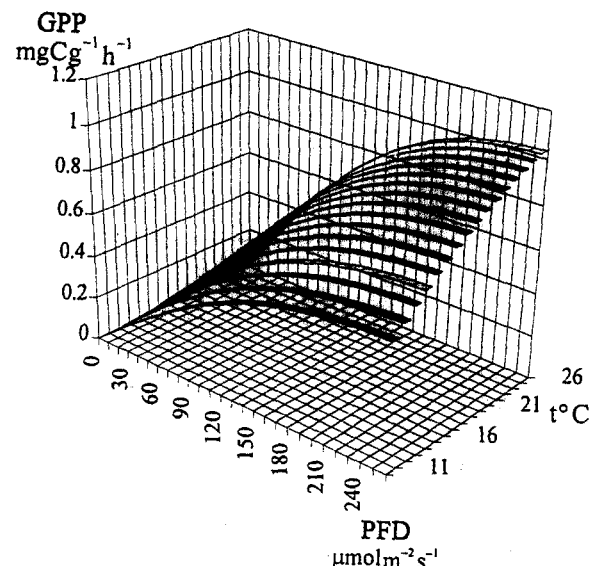


Fig. 2. Gross primary productivity (GPP) estimates by the model at various combinations of light (PFD, photon flux density) and temperature (t).

$$\frac{\partial P}{\partial I} = a_1 + 2a_2 I = 0 \quad (28)$$

$$I_{\text{opt}} = -\frac{a_1}{2a_2} \quad (29)$$

As before, the slope was calculated from the derivative when $I = 0$. Therefore, for each pre-treatment five values of S and I_{opt} were estimated.

The effects of temperature and acclimation on the variance of S and I_{opt} were tested by a two-way ANOVA model I without replication. Five levels were considered for temperature and four for acclimation (the four pre-treatments). A Tukey's test was used to confirm the absence of a significant interaction between the two factors at the 95% confidence level (Underwood, 1981). The use of the two-way ANOVA would not be correct in the presence of a significant interaction

between both factors due to the lack of replication (Sokal and Rohlf, 1981).

3. Results and discussion

Fig. 2 shows the general shape of the gross primary productivity curves obtained by fitting the model to the experimental data. There was no evidence of photoinhibition. The measured and calculated productivities are well within the range observed by the author during field experiments (Duarte and Ferreira, 1993).

Figs. 3a–d show the productivity results and estimates at three of the tested temperatures with algae pre-acclimated as explained above. It should be noted that fitting was carried on two dimensions (light and temperature), i.e. on a surface

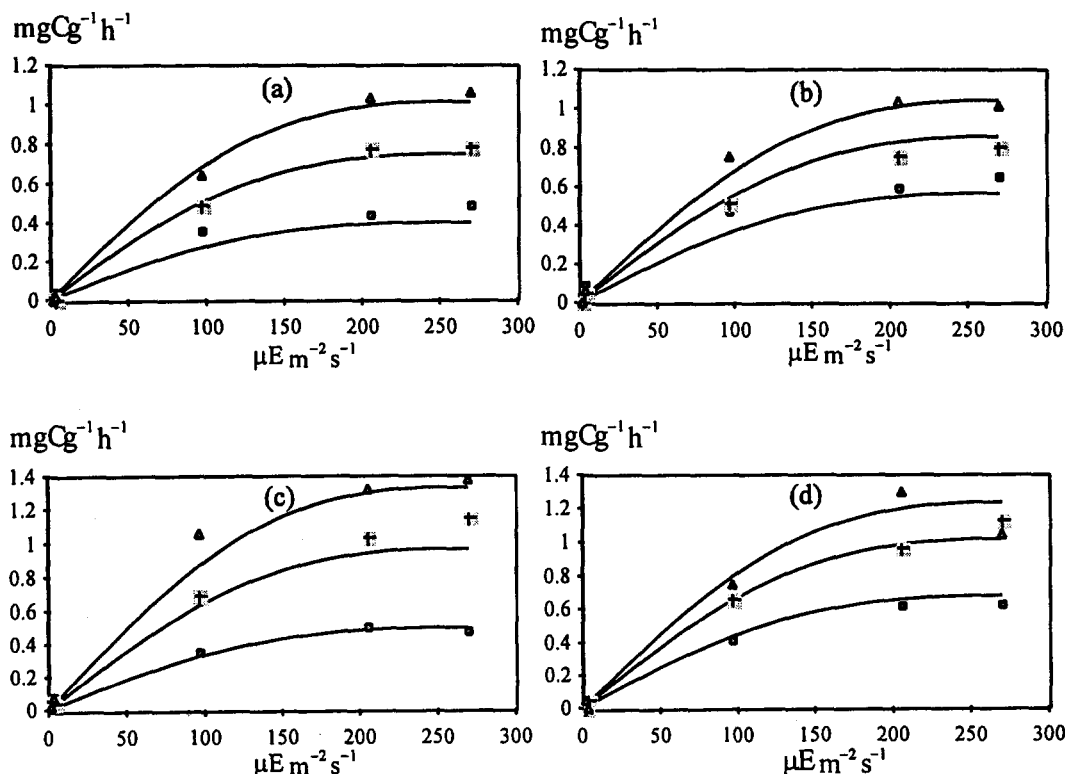


Fig. 3. GPP measured (average of three replicates) at three of the five tested temperatures (\blacksquare , 11°C; $+$, 18°C; and \blacktriangle , 26°C) and estimated (lines) by the model. (a) and (b): Measurements obtained with algae pre-acclimated to "winter" conditions and light intensity correspondent to 13 m and 9 m depth, respectively. (c) and (d): Measurements obtained with algae pre-acclimated to "summer" conditions and light intensity correspondent to 13 and 9 m depth, respectively (see text for explanation).

Table 1
Final model parameter estimates (see text for explanation)

Pre-treatment	Depth (m) simulated	Final parameter estimates				
		<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>
Winter conditions	13	0.00198	0.0009	125.8778	0.6966	17.9098
Winter conditions	9	0.00199	−0.0308	142.2606	0.5183	11.6373
Summer conditions	13	0.00124	0.8223	140.5868	1.5180	18.3652
Summer conditions	9	0.00198	−0.0199	131.4577	0.6716	11.5143

and not on each of the shown lines (see above). In Table 1 the final model parameter estimates used to calculate the productivity curves shown in Fig. 3 are shown.

Figs. 4a–d summarise the results of the linear regressions between the measured and predicted productivity values at all light/temperature combinations for algae acclimated in the four differ-

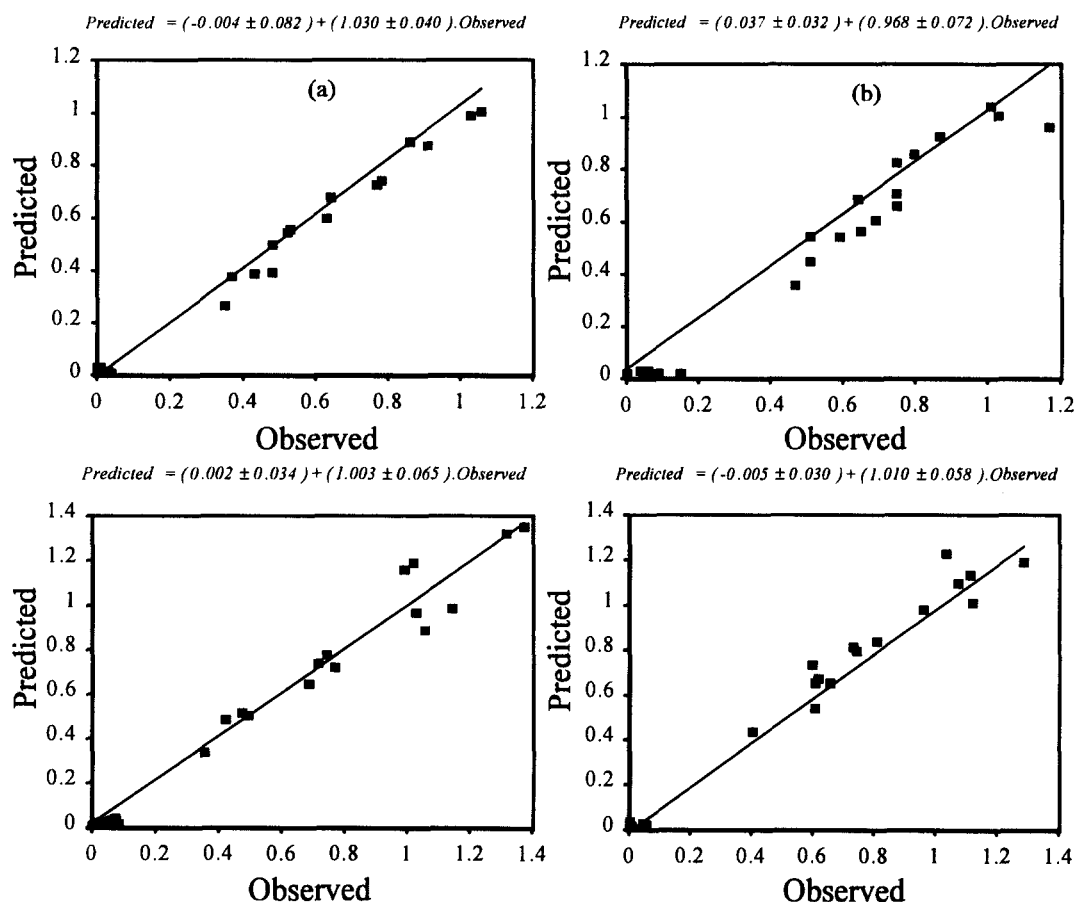


Fig. 4. Model II regression between observed versus estimated GPP (mg C g⁻¹ h⁻¹) for all combinations of light intensity and temperature. All regressions significant (ANOVA $p < 0.01$). (a) and (b): Results obtained with algae pre-acclimated to "winter" conditions and light intensity correspondent to 13 m and 9 m depth, respectively. (c) and (d): Results obtained with algae pre-acclimated to "summer" conditions and light intensity correspondent to 13 and 9 m depth, respectively (see text for explanation).

ent ways described above. None of the y-intercepts differ significantly from zero and none of the slopes differ significantly from 1 at the 95% confidence level. The ratio between explained to total variance is very close to 1 (always above 0.96). From these results it may be concluded that the quality of the fitting is good.

The results obtained with the two-way ANOVAs on the separate effects of acclimation and temperature on S and I_{opt} confirmed the null hypothesis about the absence of significant treatment effects in all cases except the temperature on the slope ($p < 0.05$). These results confirmed the model predictions on the temperature independence of I_{opt} and temperature dependence of S .

A linear regression analysis was carried out between $\ln(S)$ and temperature. The regression obtained is highly significant (Fig. 5) confirming the exponential relationship between S and temperature predicted by the model.

Recently, the model of Eilers and Peeters (1988) was used by Bendoricchio et al. (1993) for

modelling the photosynthetic efficiency of *Ulva rigida*. These authors fitted Eilers' model to different $P-I$ curves obtained at various temperatures by expressing the parameters a and b as an exponential decaying function of temperature.

According to the model described in this work the temperature functions obtained by those authors could not be explained by changes in the parameters a and b itself but to the parameters S and P_{max} on which they depend. Neglecting the temperature functions from the model presented here, Eqs. 14 and 15 can be rewritten as in Eilers and Peeters (1988):

$$a = \frac{1}{SI_{\text{opt}}^2} \quad (30)$$

$$b = \frac{1}{P_{\text{max}}} - \frac{2}{SI_{\text{opt}}} \quad (31)$$

Using these equations and assuming that S and P_{max} will behave as predicted in this work, a and b will decay exponentially with temperature.

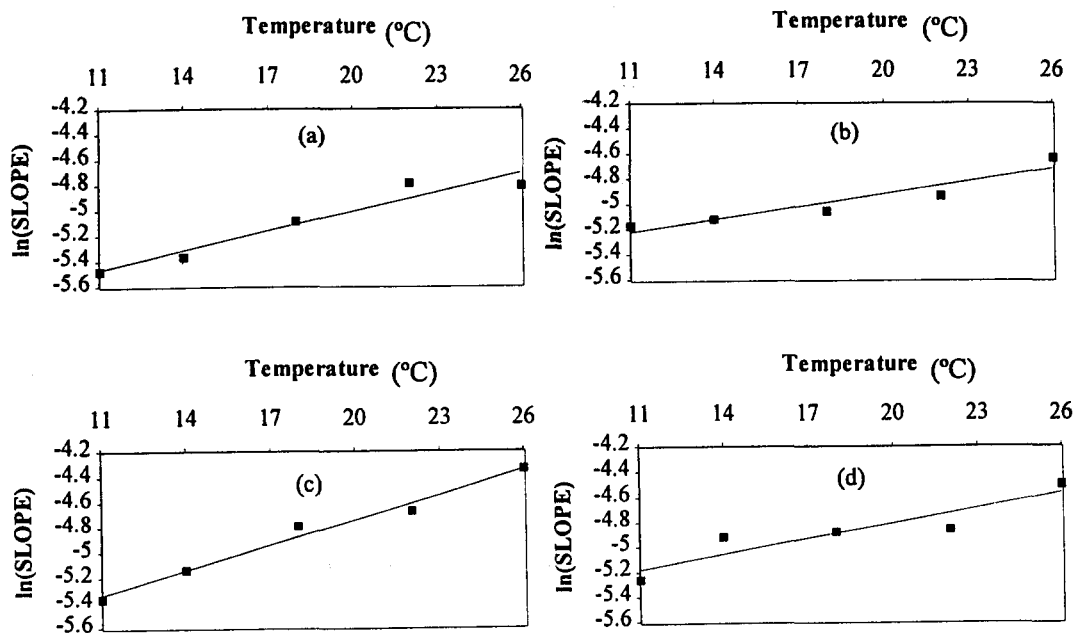


Fig. 5. Model I regressions between temperature ($^{\circ}\text{C}$) versus the natural logarithm of the initial slope. All regressions significant (ANOVA $p < 0.01$). (a) and (b): Results obtained with algae pre-acclimated to "winter" conditions and light intensity correspondent to 13 m and 9 m depth, respectively. (c) and (d): Results obtained with algae pre-acclimated to "summer" conditions and light intensity correspondent to 13 and 9 m depth, respectively (see text for explanation).

This could explain the trends observed by Bendoricchio et al. (1993). On the other hand, if Eqs. 14 and 15 are used, since S and P_{\max} change exponentially with temperature, the ratios between the temperature functions and these parameters are constant, reason why a and b will not change with incubation temperature. This is a very important difference between the model presented here where a and b are assumed to account only for biophysical reactions and Eilers' model in which a and b also account for temperature-dependent biochemical reactions.

From the results described above the present model appears to provide a good description of the behaviour of the P – I curve parameters according to what is known from the physiology of photosynthesis. The usefulness of the model has been demonstrated by the quality of the fittings obtained with experimental data. The two-step fitting procedure described above proved very effective in overcoming the natural difficulties in fitting a two-dimensional function with five parameters (Eq. 10) to experimental data.

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