

Short-term variation of P_{\max} under natural irradiance conditions: a model and its implications*

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ABSTRACT: A model of the photosynthesis-irradiance (P-I) relation is presented in which P_{\max} , the maximum photosynthetic rate, is time variable and dependent on previous irradiance exposure. The model is applied to the description of photosynthesis time series measured in continuous cultures of 2 species of planktonic diatoms illuminated by sunlight in a window greenhouse. Irradiance history included the previous 10 h of light observations. Patterns of variation in irradiance histories were described by principal component analysis. Response functions of P_{\max} were formulated in terms of the derived components, and the model parameters were estimated using non-linear regression analysis. The model successfully represents the linear response characteristic of cloudy days, as well as the non-linear response of variably sunny days and the time-dependent decrease in photosynthesis at high irradiance on sunny days. Inspection of the relative magnitudes of response function coefficients reveal 2 primary time scales of light history effects. A short (< 2 h) scale probably reflects direct effects of high light on light harvesting and electron transport (e.g. photoinhibition) while a longer (> 5 to 6 h) scale may reflect physiological processes involved in protein and pigment turnover. The response functions of 2 species of planktonic diatom *Lauderia borealis* and *Chaetoceros gracilis* are similar. These time scales may be general features of phytoplankton response functions and should be considered in models of phytoplankton photosynthesis in a mixed layer.

INTRODUCTION

Short-term (minutes to hours) variation in phytoplankton physiology is a general problem in the measurement and prediction of primary productivity in surface mixed layers. Diel and shorter time scale variation has often been reported in the photosynthesis-irradiance (P-I) relation of phytoplankton communities (Sournia 1974, MacCaull & Platt 1977, Marra 1980, Harding et al. 1981). Vertical mixing combined with the gradient in downwelling irradiance can generate large irradiance variations with comparable frequency (Pollard 1977, Denman & Gargett 1983). Realistic models of mixed layer phytoplankton production will require knowledge of how irradiance conditions and phytoplankton physiology interact at short time scales (Platt & Gallegos 1980).

The literature on physiological mechanisms that may cause such short-term variation is large and diverse, and investigations have used both terrestrial and aquatic plants (see e.g. Harris 1980, Prezelin 1981, Falkowski 1984). However, few attempts have been made to identify which mechanisms are most important to photosynthetic response in natural sunlight (Gallegos et al. 1977, Marra & Heinemann 1982). We report here a quantitative analysis of short-term photosynthetic response which is a step towards understanding the role of short-term variation under natural conditions. The basis for the analysis is a mathematical model of the photosynthesis-irradiance (P-I) relation. This relation is fundamental to phytoplankton ecology and several models have been developed to represent it. These models may be classified according to whether they are empirical or rational (Platt et al. 1977) and whether they are steady-state or time dependent.

In most ecological applications, the models are empirical and steady-state. These models are hyperbolic with the form:

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$$P = f(\alpha, P_{\max}, I) + R \quad (1)$$

where P = net photosynthetic rate; f = a hyperbolic saturating function of I , irradiance; and with parameters P_{\max} (irradiance-saturated photosynthesis), α (initial slope of the P-I function), and R (the loss to respiration, regarded as a constant < 0 unaffected by irradiance or photosynthetic rate). Functions suitable for f may be obtained by expanding df/dI in a power series, truncating, and evaluating the parameters in the polynomial so obtained using appropriate boundary conditions on f (Chalker 1980). The function obtained by retaining up to quadratic terms in the power series is

$$f = P_{\max} \tanh(\alpha I/P_{\max}) \quad (2)$$

where \tanh = the hyperbolic tangent function (Gallegos & Platt 1981). Comparisons of this function to alternatives have shown that it gives the same or lower total sum squared residuals in representing data from incubator experiments at fixed light intensities (Jassby & Platt 1976, Lederman & Tett 1981, Malone & Neale 1981).

Though these models are structured from empirical, best-fit criteria, physiological interpretations of the parameters are possible. Light harvesting ability and quantum yield are represented by α . Capacity for photochemical activity and photosynthetic carbon reduction are represented by P_{\max} (Gallegos & Platt 1981). Hence models with the general form of Eq. (1) are termed 'semi-empirical' (Platt et al. 1977). A more rational and interpretable model would have parameters with discrete physiological identities. Rational steady state models have been attempted (Herron & Mauzerall 1972, Fasham & Platt 1983). In these models parameters are derived from such quantities as the concentration of photosystem II reaction centers (RCIIs), and promise to increase the physiological inferences that can be drawn from a single P-I experiment. However, even with increased physiological content these models are still steady state, photosynthetic processes are assumed to be at equilibrium, and the model does not account for short-term variation (Platt & Gallegos 1980).

Time-dependent, empirical, models form another class. Cross-spectral analysis has been employed to analyse time-series of photosynthesis and irradiance (Gallegos et al. 1977, Marra & Heinemann 1982). In these methods a linear response function relates photosynthesis and irradiance, a good assumption only in the light-limited portion of the P-I relation. Moreover, frequency domain methods require at least weak stationarity (i.e. the expected value and variance of an observation is a constant for all t) which is not true for photosynthesis or irradiance series. Nevertheless, this

method can be applied to the examination of general, qualitative characteristics of selected portions of the series (Gallegos et al. 1977, Marra & Heinemann 1982).

We propose here an alternative, time-dependent semi-empirical model that has the potential to display short-term variations. In this report we discuss the application of time-dependent, semi-empirical models to short-term observations of photosynthetic response (O_2 evolution) in continuous cultures of marine diatoms exposed to natural sunlight. The models are then used to address the question of what time scales of natural sunlight variation are most important to diatom photosynthesis. Some characteristics of the data and the results of initial data description of selected days using cross-spectral techniques are given in Marra & Heinemann (1982). Here we examine the general strategy used by the cultured species for photosynthesis under a wide variety of irradiance conditions and over a broader time scale than considered in that work.

MODEL DEVELOPMENT

General

In this model we consider a bivariate time series $\{P_t, I_t\}$, with t indexing a short (10 min) observation period. To construct the model we hypothesized that P_t obeyed Eq. (1) and (2) with the modification that the parameter P_{\max} is also time variable.

$$P_t = P_{\max_t} \tanh(\alpha I_t/P_{\max_t}) + R \quad (3)$$

Parameters α and R may also be time-variable, but, for reasons discussed below, P_{\max_t} is assumed to be the dominant cause of variability and in this initial application of the model we limit ourselves to 1 time-dependent parameter. We further hypothesized that P_{\max_t} is determined by the recent light history experienced by the cell,

$$P_{\max_t} = g(I_t, t - ND < \tau < t) \quad (4)$$

where g = a light history function; τ indexes those irradiances considered to be part of the light history; ND = the number of observations in 1 d, our definition of 'recent'. The definition of light history is motivated by the observation that abrupt changes in irradiance illuminating a culture affect photosynthesis over a 4 to 6 h period (Marra 1978b, 1980, Falkowski 1980, Rivkin et al. 1982), and that repeating daily patterns or 'rhythms' of P_{\max} are often reported in incubation data (e.g. MacCaul & Platt 1977).

Since the general form for the response function g (Eq. [4]) is unknown, we seek a function consistent with existing photosynthesis time-course studies, yet capable of representing a complex response. Photosyn-

thesis often follows first order kinetics in response to irradiance shifts. Such kinetics have been reported in studies of photoinhibition (Vincent et al. 1984) and light-shade adaptation (Falkowski 1980, Rivkin et al. 1982). In these examples parameter time-dependence is exponential with some mechanism-specific time scale (T) approaching an asymptote, usually light-dependent. In the simplest case of a fixed time scale and an asymptote (P_{∞}) that is linearly related to light intensity (i.e. $P_{\infty} = P_0 + \delta I$, with P_0 a dark-adapted initial value, and δ is a coefficient of linear variation of P_{∞} with light intensity, I) the equation

$$P(t) = P_0 + \delta I_{\text{new}}(1 - \exp[-t/T]) \quad (5)$$

describes the response of photosynthetic rate to an irradiance transition from 0 to I_{new} . A related equation can be used to express such a saturating exponential transition in the case of discrete time series. The variation in a P_{\max_t} time series is given by

$$P_{\max_t} = P_{\max_0} + \sum_{k=1}^{\text{ND}} \delta \exp(-k/T) I_{t-k}/T \quad (6)$$

with $I_t = 0$ for $t < 0$, $I_t = I_{\text{new}}$ for $t > 0$. This equation is in the form of a linear response function (Chatfield 1975), which relates P_{\max_t} (output) to I_t (input). The coefficients of the linear response function, h_k , relate the present level of the output series to past values of the input series (i.e. $h_k = \delta \exp[-k/T]/T$ in Eq. [6]). For photoinhibition δ is negative. Under sunlight, irradiance and photosynthetic response vary at several time scales. Nevertheless, the response function still has a general form of

$$P_{\max_t} = P_{\max_0} + \sum_{k=1}^{\text{ND}} h_k I_{t-k} \quad (7)$$

This linear equation can represent multiple response time scales, but a linear relation between the asymptote and irradiance is assumed, thus constraining the irradiance range of model application. While other choices of response function form are possible, we will only consider linear response functions as candidates for g (Eq. [4]). The limitations of such an approach will be discussed further below. Though the response function has a simple form, it is not parsimonious. Since $\text{ND} \cong 65$, there are many h_k that need to be estimated. This problem is discussed below.

Estimation of the response function

Our approach to finding the appropriate response function was to estimate the h_k 's directly from the observed $\{P_t, I_t\}$ series. A response function so determined will embody the P_{\max} dynamics that are the dominant sources of photosynthesis variance. Our esti-

mation technique consists of transforming the response function so that P_{\max_t} is dependent on the contribution of different principal components of irradiance (c_{it}) over the previous light period and using non-linear regressions to estimate the model coefficients. The remainder of this section is devoted to detailed discussion of statistical methods.

Standard techniques are designed to estimate the linear response function relating purely random input and output series (Box & Jenkins 1970), and cannot be applied to the present problem. Though 'prewhitening' techniques can be used to convert some series to random processes, the number of transformations required by highly autocorrelated, non-stationary series such as $\{I_t\}$ and $\{P_t\}$ increases the probability of spurious results (Chatfield 1975). More importantly the data series $\{P_t\}$ and $\{I_t\}$ are related by a linear response function imbedded within a hyperbolic function (Eq. [3]). Therefore, we are estimating parameters of a non-linear time-series model, a problem unsuited to the Box-Jenkins method.

An alternative to standard techniques is to approach the problem through non-linear regression. Trial values of the parameters are iteratively corrected until a minimum in sum squared residuals to predicted P_t is found (Conway et al. 1970). This approach has been previously successful in fitting semi-empirical steady state models (Eq. [1] & [2]) (Gallegos & Platt 1981, Malone & Neale 1981). Here we desire estimates not only of α and R , but also of h_k (Eq. [5]). This algorithm requires good trial values and low parameter correlations to converge (Conway et al. 1970).

The latter requirement is satisfied only after modification of the model. Estimates of h_k will be correlated, in general, because of high correlations between I_{t-k} (Conway et al. 1970). These correlations arise from definite patterns in the set of past irradiances $\{I_{t-k}\}$. Daily solar transit creates some of these patterns; cloudy or sunny conditions prevailing for several hours at a time can cause shorter term patterns.

Quantitative expression of these patterns can be obtained by analysis of the covariance matrix of past irradiances $\{I_{t-k}\}$. If light history consists primarily of varying contributions of fixed patterns, or components, of irradiance variation,

$$I_{t-k} = \sum_{i=1}^M c_{it} \varphi_i(k) + \varphi_0(k) \quad (8)$$

where $\varphi_i(k)$ = an irradiance component; $\varphi_0(k)$ = constants; c_{it} = component scores, which measure the contribution of the i^{th} component to light history at time t ; M = the number of components. The φ_i and c_{it} are computed by principal component analysis of the covariance matrix followed by computation of component scores (Morrison 1976). The computed $\varphi_i(k)$ are

ordered by their contribution to the total variance in the data, since no rotations are performed, and form an orthogonal set of functions (Morrison 1976). The technique is similar to determination of empirical orthogonal functions (EOFs) (Busch & Peterson 1971). However, standard EOF analysis considers observations at a fixed position within a time or space frame, not lagged variables.

The model is modified by recasting Eq. (7) in terms of the component scores:

$$P_{\max_t} = P_{\max_o} + \sum_{i=1}^M h_i c_{it} \quad (9)$$

where h_i weights the importance of light history component i to the response function. The component scores, c_{it} , are derived from independent, orthogonal functions, and are uncorrelated. Therefore, estimates of h_i will converge. The h_k of the irradiance response function can be obtained using

$$h_k = \sum_{i=1}^M h_i \varphi_i(k) \quad (10)$$

For the present data set, trial values of the parameters were obtained by a 2-step procedure. Estimates of α and R were obtained by inspection from plots of $\{P_t\}$ vs $\{I_t\}$ (Fig. 1). Eq. (3) was solved for P_{\max_t} after substituting P_t , I_t , and initial estimates of α and R , and

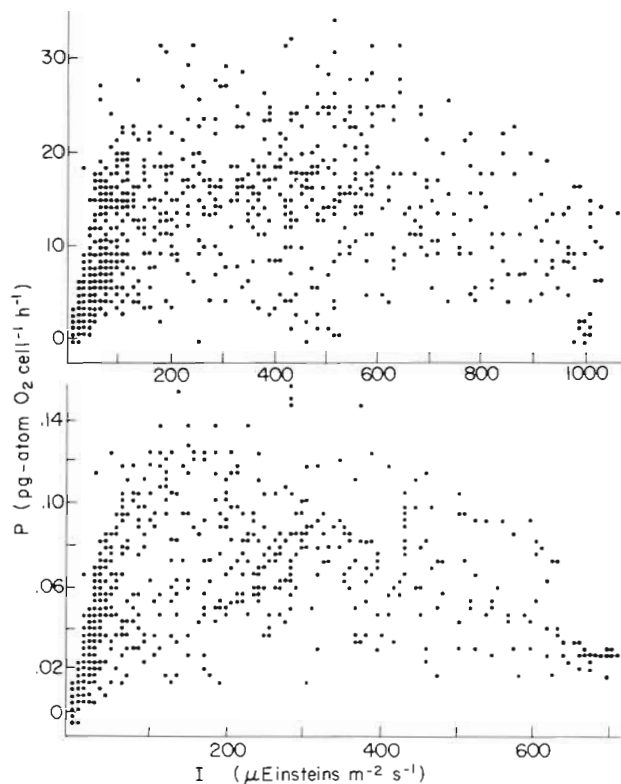


Fig. 1. Photosynthesis (P) plotted with incident irradiance (I) for all data from experiments GH IV (top) and GH V (bottom)

using Newton-Raphson iteration (Dorn & McCracken 1972). Multiple linear regression was then used to obtain initial estimates of h_i and P_{\max_o} (Eq. [9]).

The non-linear regressions were performed using the Marquardt procedure (Conway et al. 1970). For each experiment a sequence of regressions was performed, at each step including c_{it} with a larger index i , stepwise, until no further statistically significant increase was found in variance of P_t accounted for by the model (sequential F-test, Draper & Smith 1966). Convergence was considered to have been obtained when relative changes in all parameters between iterations was $< 10^{-5}$. Usually convergence was obtained in less than 10 iterations. F-test and confidence limits for parameter were computed by assuming close to elliptical contours of residual sums of squares in the parameter space neighborhood of the converged parameter set. Since a systematic bias remained in the residuals (see below), mean residual sums of squares overestimate SS (error) (Draper & Smith 1966). Though significance levels in these tests can only be approximate, bias in SS (error) suggest that they will be conservative. Confidence intervals for h_k , which are linear combinations of the estimated h_i , were computed using

$$\text{VAR}(h_k) = \mathbf{z}'\mathbf{S}\mathbf{z} \quad (11)$$

$$\mathbf{z}' = (z_1, z_2, \dots, z_m), z_i = h_i \varphi_i(k)$$

where \mathbf{S} is the estimated variance-covariance matrix of the h_i estimates (Snedecor & Cochran 1967). Note these are individual, not joint, confidence intervals. In addition confidence intervals are conditional on having the proper number of components included in the model.

Computations were performed using a LSI 11/23 minicomputer in the Division of Environmental Studies, University of California, Davis. All statistical calculations were performed using the BMDP statistical package, except the non-linear regressions which were computed using a FORTRAN 77 program written by J. C. Wilcox and modified by P. J. N.

EXPERIMENTAL METHODS

A full description of experimental methods is given in Marra & Heinemann (1982). Briefly, continuous cultures were maintained in a southfacing window greenhouse and received filtered solar irradiance simulating submarine conditions (spectral peak 550 nm, overall intensity 35 % of direct sunlight). In the experiments reported here, 2 species of marine diatom were used, *Lauderia borealis* (GH IV) and *Chaetoceros gracilis* (GH V). The cultures were nutrient enriched and growth on a 24 h basis was light-limited at the dilution rates (0.3 to 0.6 d^{-1}) used. Small deviations in culture density occurred because of light variation; instan-

taneous cell densities were determined from exponential interpolation between hourly cell counts. Photosynthesis (O_2 evolution cell^{-1}) was measured with the oxygen electrode previously described (Marra 1978a), and irradiance (μ Einsteins $\text{m}^{-2} \text{s}^{-1}$ PAR) was measured with a quantum sensor. Average photosynthesis and irradiance were simultaneously recorded over 5 min periods, 6 times h^{-1} . The complete record P_t , I_t of each experiment was analysed, a total of 2230 observations for GH IV and 1966 observations for GH V, about half of which are daytime observations. Only daytime observations of photosynthesis were used to estimate the parameters in Eq. (3) and (8). Night observations were used to obtain an average dark respiration.

RESULTS

Data series

Photosynthesis (P_t) is shown as a function of (I_t) in Fig. 1. The scatter is considerable, approaching an order of magnitude at any given irradiance. Note that the scatter in P_t is greatest when $I_t > 150 \mu\text{Einst m}^{-2} \text{s}^{-1}$, consistent with the hypothesis that a time variable P_{\max} can explain much of the observed variation.

Principal components computed for $\{I_{t-k}\}$ in each of the experiments are summarized in Table 1; typical components are shown in Fig. 2. Ten components represented 97 % of the total variance in $\{I_{t-k}\}$, with the first 3 components accounting for about 90 % of the variance. These components have a quasi-periodic form with the frequency of variation increasing with i (Fig. 2). However, the components are not sinusoidal, as they would be if light history variation was decom-

Table 1. Characteristics of principal components of variables in the response function, $\{I_{t,k}\}$. Computations for irradiance series from 17 Oct to 2 Nov (GH IV) and from 8 Nov to 21 Nov (GH V). For the i^{th} component, the cumulative per cent variance (% Var) and the number of zero crossings (Zeroes) is given

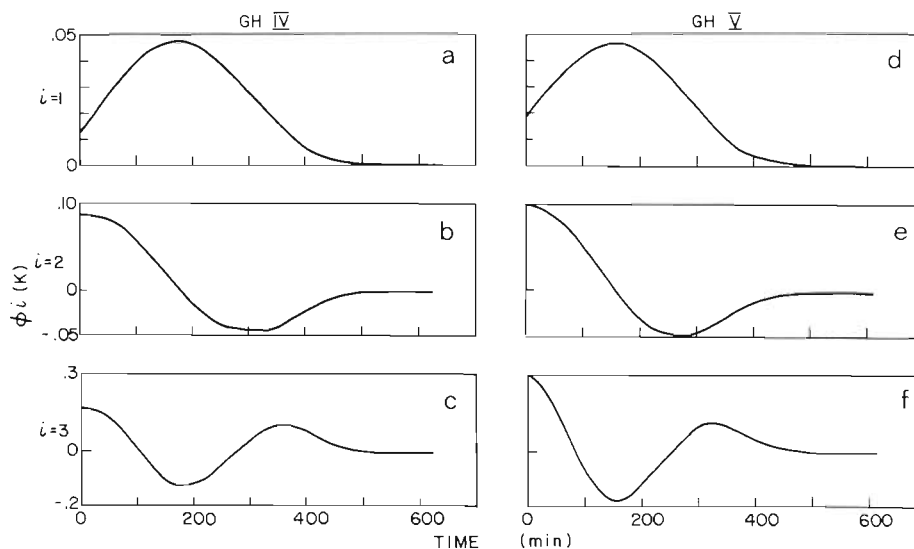
i	GH IV		GH V	
	% Var	Zeroes	% Var	Zeroes
1	58.1	0	64.8	0
2	83.3	1	89.4	1
3	88.6	2	93.5	2
4	91.4	3	94.4	3
5	93.0	3	95.4	4
6	94.0	5	95.9	5
7	94.8	7	96.3	6
8	95.5	7	96.6	7
9	96.2	8	96.9	11
10	96.8	9	97.1	11

posed into sine and cosine functions (Fourier analysis). This suggests the greater power of the principal components technique for representing a maximum amount of variation with a minimum number of components. A rough measure of the frequency of variation is the number of zero crossings, i.e. the number of times $\phi_i(k)$ changes sign as k varies from 1 to ND. The number of zero crossings increases monotonically with i (Table 1).

Model fitting

A large and significant increase in the variance explained by the model resulted from the inclusion of a time dependent P_{\max} . The coefficient of determination (R^2) of daytime data for *Lauderia borealis* was low (58.1 %) with a constant P_{\max} ; a good fit was obtained

Fig. 2. The first three principal components ($\phi_i[k]$, dimensionless) for irradiance observations during experiments GH IV (left column), and GH V (right column). Each component represents a pattern of irradiance variation occurring in the irradiance history series $\{I_{t-k}\}$. Component 1 (a, d) is a pattern spanning 480 min (8 h) with a peak 150 min (2.5 h) in the past. Component 2 (b, e) represents increasing irradiance over the last 250 min (ca 4 h). Component 3 is a pattern of alternating high and low light periods, each interval being approximately 120 min (2 h) long



only for the light limited ($I_t < \text{ca } 150 \mu\text{Einst m}^{-2} \text{s}^{-1}$) photosynthesis (ca 40 % of total variance). With a time dependent P_{max} , R^2 increased to 73.1 % (with $M = 3$). The corresponding increase was 65.5 % to 83.7 % for *Chaetoceros gracilis* (Table 2). R^2 increased as M increased; however, the increase in R^2 was not significant for $M > 3$ (Table 2). Nevertheless, regressions were performed for M up to 7 to ensure that R^2 had attained an approximate asymptote.

Increasing M resulted in only slight changes in estimates of parameters already in the equation. This is an indication of the stability of the estimation procedure and is primarily due to the orthogonal relation between the c_{it} 's. However, the non-linearity in the model does result in some correlation between the parameters (Marquardt 1963). Such correlation results in what small variation we found in parameter estimates as M increases.

Examples of model prediction vs observed photosynthesis are shown in Fig. 3. Photosynthesis was variable, but roughly symmetric around noon, on days of low light (Fig. 3A, D), had a mid-morning peak on sunny days (Fig. 3B, E), or an afternoon peak if dim morning conditions were followed by high irradiance in the afternoon (Fig. 3C). The model predicts the response pattern correctly in each of the 3 cases. The decrease in photosynthesis on sunny days continues until mid afternoon, at which point the model predicts a slight recovery. Usually, such a recovery was observed in culture oxygen evolution (Fig. 3E), however, in some instances recovery was not as strong as predicted (Fig. 3B).

A systematic bias (i.e. over- or underestimate) can be seen on some days, e.g. Fig. 3C. Mean residuals vary significantly from one day to the next (Fig. 4). However, variation in mean residual (Fig. 4) is unrelated to either the mean irradiance of that day or of the previ-

ous day (correlations have a $P > 0.10$). These variations in mean residual are probably due to variation introduced at the daily time scale by experimental methods, e.g. cell count determinations, and changes in dilution rate.

The combination of modeled daytime variation and mean night respiration accounts for 84 % of the variance in net oxygen evolution per cell by *Lauderia borealis* (Table 3). A higher fraction of total variance (90 %) was accounted for in the *Chaetoceros gracilis* culture. The oxygen evolution measurements in the *L. borealis* culture contain more instrument noise than those in the *C. gracilis* culture, which would contribute to the observed differences in R^2 .

The absolute magnitude of the response function coefficient estimates differ between cultures but the relative variation of the coefficient vs lag is similar (Fig. 5). All h_k estimates either are negative or cannot be statistically resolved from zero: the greater past irradiances were, the more P_{max} decreased. Conversely as past irradiances proceeded from high to low (i.e. midday to late afternoon), P_{max} increased (i.e. recovered). The response functions shown in Fig. 5 were computed for $M = 3$. At higher M the functions have the same basic shape, with the addition of some smaller scale features. However, individual differences between response function coefficients for the $M = 3$ and $M = 4$ cases are not significant ($P > 0.05$). Since estimates of h_i vary little with increasing M , little change in the basic form of the h_k would be expected.

$P_{\text{max}0}$ is 22.33 and 0.104 pg-at $\text{O}_2 \text{ cell}^{-1}$ for *Lauderia borealis* and *Chaetoceros gracilis*, respectively. Approximate biomass specific rates are 7.4 and 4.3 g C (g Chl a) $^{-1} \text{h}^{-1}$, assuming a photosynthetic quotient of 1.2 and using biomass data from Marra & Heinemann (1982). $P_{\text{max}t}$ equals $P_{\text{max}0}$ at the beginning of the day (cf. Eq. [5]). $P_{\text{max}0}$ is an estimate of the maximum rate of

Table 2. Summary of non-linear regressions for *Lauderia borealis* (GH IV) and *Chaetoceros gracilis* (GH V) response functions. Component coefficients ($\times 10^{-2}$ for GH V) and coefficient of determination (R^2) are given for each total number of components in the equation; *** denotes a significant increase in variance accounted for by the model due to the last component added: F-test, $P < 0.001$

Experiment	n	M	R^2	Component			
				1	2	3	4
GH IV	1123	0	0.5811				
		1	0.7107***	-4.4			
		2	0.7279***	-4.2	-2.0		
		3	0.7311***	-4.6	-1.7	-0.83	
		4	0.7311	-4.6	-1.6	-0.89	0.12
GH V	973	0	0.6548				
		1	0.8314***	-2.3			
		2	0.8340***	-2.2	-0.33		
		3	0.8367***	-2.4	-0.18	-0.31	
		4	0.8368	-2.4	-0.19	-0.30	0.03

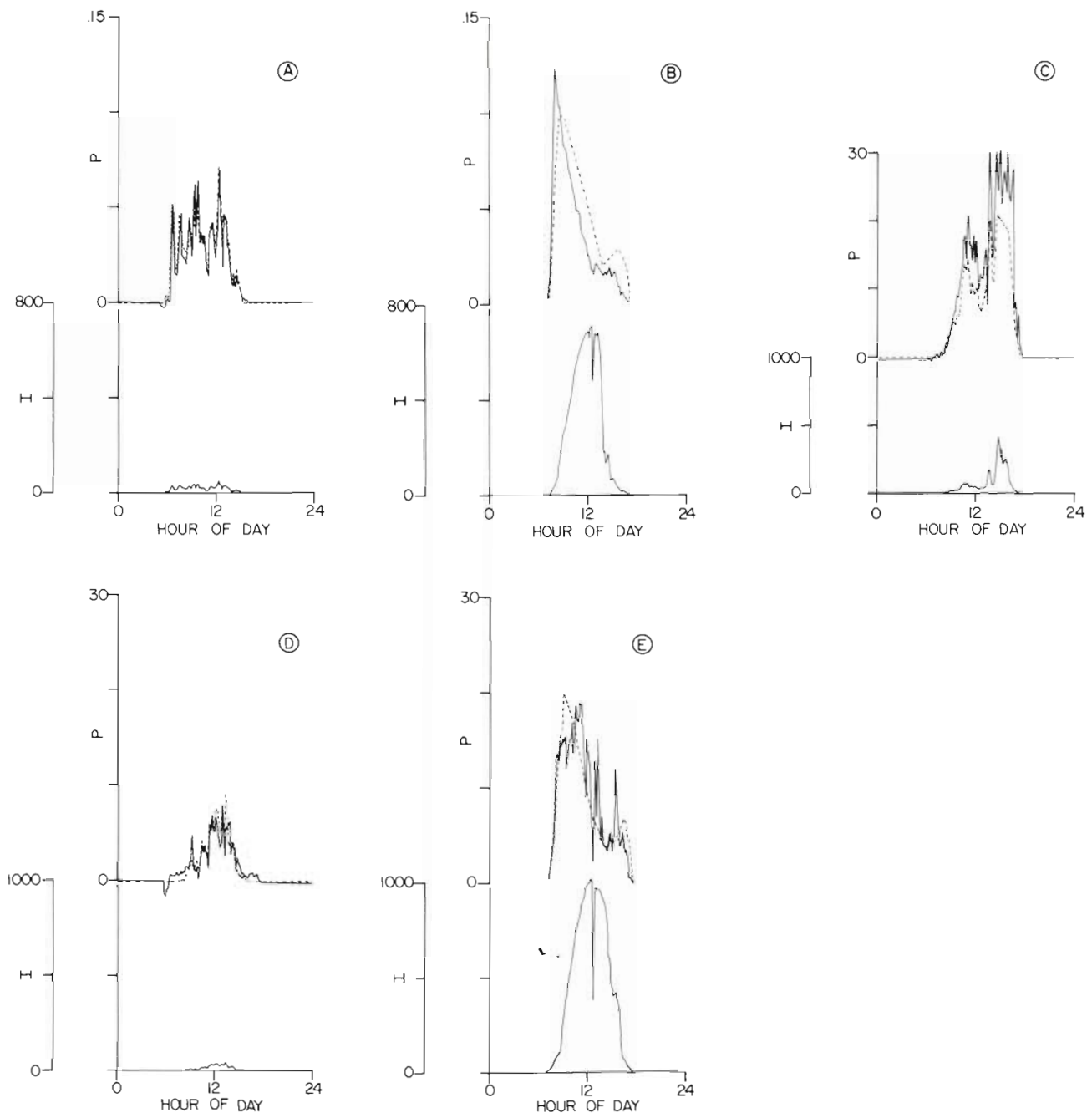


Fig. 3. Time course of observed photosynthesis (P , $\text{pg-at O}_2 \text{ cell}^{-1} \text{h}^{-1}$, solid line), photosynthesis predicted by the model (dashed line) and irradiance (I , $\mu\text{Einstein m}^{-2} \text{s}^{-1}$) for selected days. A, B from GH V; C, D, E from GH IV

photosynthesis possible by these cultured species in the given nutrient and temperature conditions. This parameter can be compared to the parameter P_s in the semi-empirical steady state model of Platt & Gallegos (1980). Predicted maximum rates of photosynthesis are usually less than P_{max0} because cells already have some 'light history' before I_t on a particular day reaches saturating levels.

DISCUSSION

Both the present technique and spectral analysis (Gallegos et al. 1977, Marra & Heinemann 1982) have been used to analyse short-term photosynthesis data. The underlying model for each method is different; thus we expect to extract different information. The scope of spectral analysis is limited to periods < 1 d,

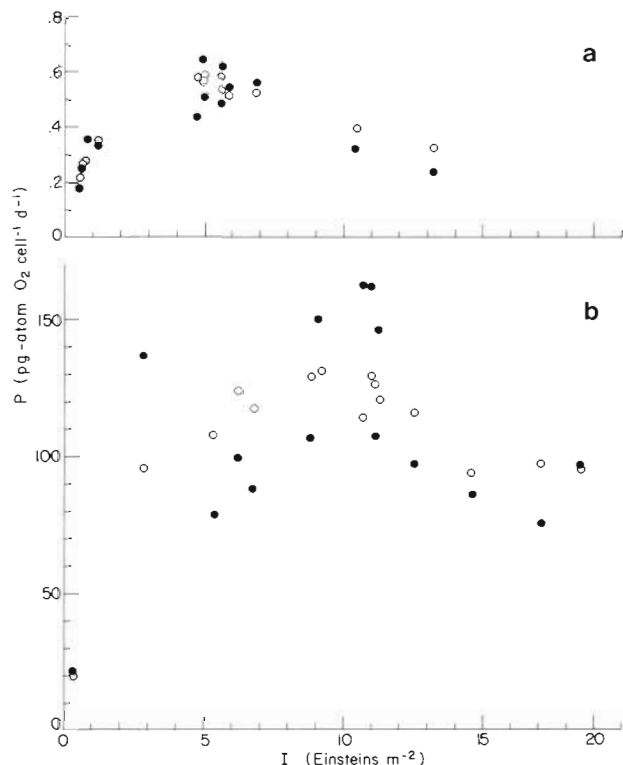


Fig. 4. Relation between daily photosynthesis (P) and total daily irradiance for GH IV (a) and GH V (b). (○) sum of observed oxygen evolution; (●) sum of model-estimated oxygen evolution. There is a significant day effect (proportional to the vertical distance between each pair of closed and open symbols) in the residual variance to the model (ANOVA, $P < 0.001$)

and can focus attention on interesting, though perhaps not common, features of the data. Response on cloudy or variable-irradiance days diverges least from the linear assumptions of the technique. Thus, we obtain information only on the light-limited to near-saturation portion of the curve.

The response function of P_{max} estimated here applies to the entire measurement period in the greenhouse cultures (ca 14 d). Because of the non-linear structure of the model, the technique is suited to the analysis of sunny days as well as variable and cloudy days. We obtain information on changes in light-saturated (vs light-limited) photosynthesis. Sunny days will dominate the response function estimate since they have a higher proportion of observations of light saturated photosynthesis. Irradiance was typically high (mean [SD] for GH IV: 233 [274]; GH V: 152 [184] $\mu\text{Einst m}^{-2} \text{s}^{-1}$) and 41 % of all daytime I_t were greater than $150 \mu\text{Einst m}^{-2} \text{s}^{-1}$ ($= P_{max0}/\alpha$). It is under such high irradiance conditions that fixed parameter P-I models are biased estimators of photosynthesis in the greenhouse cultures (Marra et al. 1985). Therefore, photosynthesis approximated saturating rates during much

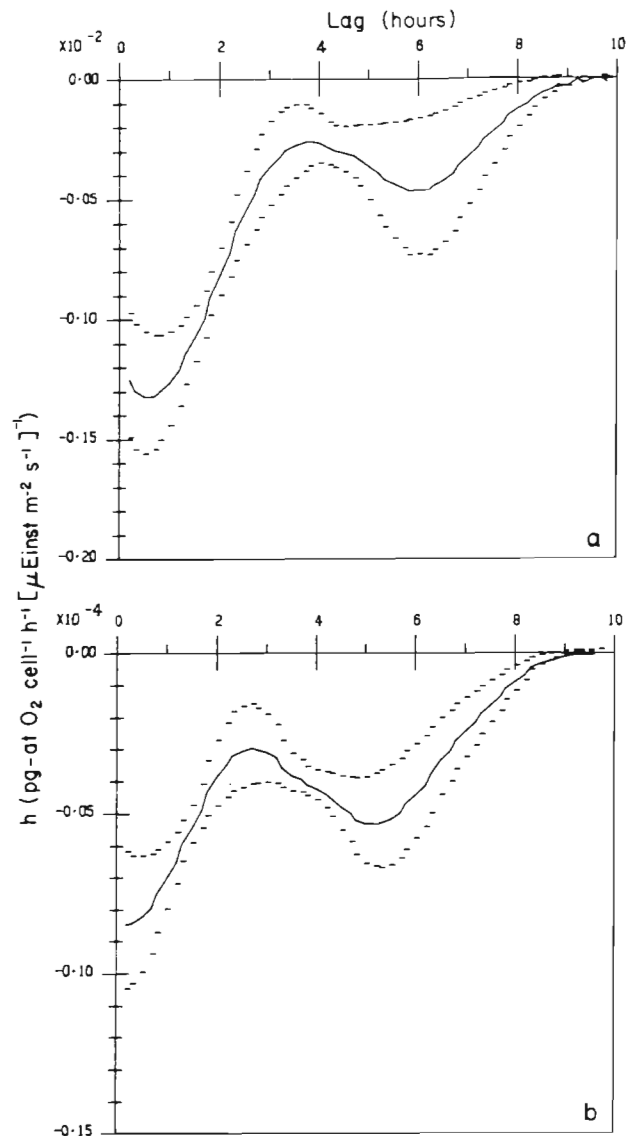


Fig. 5. Response function coefficients as a function of lag (solid line), for P_{max} , determined for 3 components in (a) GH IV and (b) GH V. Bars above and below line indicate approximate 95 % confidence intervals (see text)

of the measurement period and it is reasonable to concentrate on P_{max} in an overall analysis of the data.

In our analysis, the response function was estimated through the relation of P_{max} to different light history patterns, or components. A light history, for the greenhouse analysis, is an ordered set of ca 65 10-min averages of irradiance $\{I_{t-k}\}$, ranging from 10 min (I_{t-1}) to ca 11 h (I_{t-65}) in the past. A total of 65 sets can be defined for each day: at daybreak all irradiances in the set are 0; at midday I_{t-36} to I_{t-1} will contain the previous morning's irradiance; at sunset I_{t-65} to I_{t-1} will be the whole time course of irradiance for that day. Though each of these sets is a unique pattern, common features can be found. The expected value of each

Table 3. ANOVA of oxygen evolution ($\mu\text{g-at O}_2 \text{ cell}^{-1}$) by *Lauderia borealis* GH IV) and *Chaetoceros gracilis* (GH V) in greenhouse experiments. Separate analyses are presented for daytime data only (DAYS) and complete data (DAYS + NIGHTS). Sources of variation include the time-dependent semi-empirical model with 3 light history components (regression), and mean night period oxygen consumption (mean night). Coefficient of determination (R^2) of total variance is presented for each analysis. All treatment MS have $P < 0.001$

Experiment	Data type	Mean	Source of variation	DF	Variance ^a	Mean square	R^2
GH IV	DAYS	8.94	Regression	6	5.26	0.88	0.73
			Residual	1117	1.94	0.0017	
			Total DAY	1123	7.20		
	NIGHTS	-0.17	Total NIGHT	1107	0.0067		
	DAYS + NIGHTS	4.42	Regression + mean NIGHT	7	9.88	1.41	0.84
		Residual	2223	1.95	0.0009		
		Total DAY + NIGHT	2230	11.83			
GH V	DAYS	0.0398	Regression	6	1.03	0.17	0.84
			Residual	967	.20	0.0002	
			Total DAY	973	1.23		
	NIGHTS	-0.05	Total NIGHT	993	0.0001		
	DAYS + NIGHTS	0.0190	Regression + mean NIGHT	7	1.80	0.26	0.90
		Residual	1959	0.20	0.0001		
		Total DAY + NIGHT	1966	2.00			

^a For GH IV only, variance is expressed as $10^4 (\mu\text{g-at O}_2 \text{ cell}^{-1})^2$

member of the light history set $\{\bar{I}_{t-k}\}$ decreases with increasing k . Before midday $I_{t-k} > \bar{I}_{t-k}$ for low k (e.g. $k < 20$), and $I_{t-k} < \bar{I}_{t-k}$ at high k , a deviation pattern similar to the shape of Component 2 (Fig. 2). In the afternoon, intermediate range I_{t-k} ($20 < k < 40$) exceed \bar{I}_{t-k} , resembling the pattern of Component 1. Intermittent cloudiness may impose deviations of alternating bright and dim conditions similar to Fig. 3. In practice each light history will consist of a mixture of several components, the importance of which is measured by a component score (c_{it}). Component scores are linear functions of the light history irradiances; the coefficients of the linear function are determined in the principal components analysis (Eq. [10]). As light history changes through the day, so do the component scores (Fig. 6), typically with Component 2 being positive in the morning and Component 1 being positive in the afternoon. Note also that a component score can be negative (Fig. 6). The relation between P_{\max} and component scores was estimated by non-linear regression. Since each component score is a linear function of light history, an equation for component scores can easily be transformed into a linear function for light history irradiances (Eq. [10]). Using this transformation we obtained an estimated linear response function of P_{\max} on $\{I_{t-k}\}$ (Fig. 6).

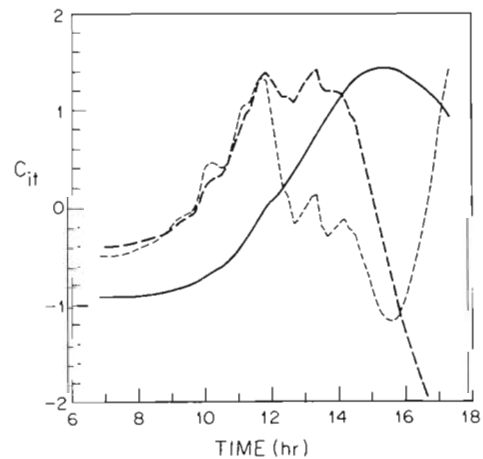


Fig. 6. Daily time course of component scores (c_{it} , nondimensional) for the first 3 components ($i = 1$ to 3) of the irradiance history set on a selected day (291) in GH IV. Solid line: Component 1; heavier dashed line: Component 2; lighter dashed line: Component 3

It is clear from the estimated response functions that for these diatoms extended (> 1 h) exposure to high irradiance ($I_t > 150 \mu\text{Einst m}^{-2} \text{ s}^{-1}$) results in decrease in photosynthesis. The predicted reduction in light-saturated photosynthesis at a fixed irradiance is comparable to that reported by Marra (1980) for 'step-

function' (0 to a fixed irradiance) time course experiments. For example, Marra (1980) reports a 37.3 % reduction in oxygen evolution per cell of *Lauderia borealis* after 1 h exposure to a fixed irradiance of $870 \mu\text{Einst m}^{-2} \text{s}^{-1}$. The present response function estimates a 35.8 % reduction for the same exposure intensity and duration, the mean time during the day that $I_t \geq 870 \mu\text{Einst m}^{-2} \text{s}^{-1}$ during GH IV. With a longer duration exposure the model predicts a greater amount of depression than observed in the fixed-irradiance time course. This inflexibility in the model response arises from the assumption of linear variation of the P_{max} asymptote (Eq. [5]). The response function also agrees with fixed irradiance experiments reported in Marra (1980) in that photosynthesis decreased or remained more or less constant in all cases except *L. borealis* at $70 \mu\text{Einst m}^{-2} \text{s}^{-1}$ where there was a slight increase over the light period. If such low light increases are occurring in GH IV they add little to the total variation in photosynthesis. The residual variance when $I_t < 75 \mu\text{Einst m}^{-2} \text{s}^{-1}$ is less than 3 % of the total variance in P_t .

Despite this general agreement between previous fixed-irradiance experiments and the response predicted from a time-variable P_{max} model, the response function is more complex than might be suggested from the results of Marra (1980), i.e. a simple exponential response (Eq. [6]). The response function coefficients have a primary minimum at up to 1 to 2 h and a secondary minimum at 5 or 6 h (Fig. 5). These results should be considered in the context of the resolving power of the estimation procedure at different time scales. First, the component system (the functions $\varphi_i(k)$) will not resolve step function responses. All components are smoothly varying (Fig. 2). The shortest response time that can be represented by the system is about 1 h (Table 1). Second, the component set cannot resolve response to more than the past 8 h of irradiance. Because of daylength, light histories were usually less than 8 h long; longer light histories contribute little to the variance and hence the pattern components $\varphi_i(k)$. Thus, the peak at 1 h may include physiological processes with response scales shorter than 1 h which are not resolved by the technique. Likewise, processes contributing to a response at a scale of 6 h may continue to be important at periods > 6 to 8 h, but again are not identified by the model.

These response scales have been shown to be important for 2 different species of planktonic diatom. Since these different species exhibited similar responses it is likely that other diatoms, and perhaps other planktonic species, would also have the same general form of response. Semi-empirical time-series models as applied here make identification of response time scales possible. These time scales are a guide to what types of

physiological responses are most important to primary production under natural sunlight. Though no mechanistic information is provided by the time series *per se*, we can use the time-scales constraint to select from previously reported physiological mechanisms occurring at fast (< 2 h) or slow (> 5 to 6 h) time scales which cause decreasing photosynthesis.

Though decreases in photosynthesis at high light intensities are often reported as photoinhibition (Harris 1978) the form of the response function indicates a more complex response mechanism. Short-time-scale responses with rapid rates are typical of biophysical mechanisms of photoinhibition for which light has some direct effect on the PSU structure or electron transport (Powles 1984). Long-term responses are more typical of changes in the activities of enzymes, possibly through end product inhibition of the Calvin cycle carboxylating enzyme, ribulose biphosphate carboxylase (RUBPcase, Bassham et al. 1978, Jensen et al. 1978), or changes requiring synthesis and/or turnover of cellular constituents (Riper et al. 1979), such as light-shade adaptation or recovery from photoinhibition. Such changes can cause photosynthetic depression but are not causes of photoinhibition in a strict sense.

An important implication of the 2-time-scale structure of the response function is that depression and recovery kinetics will differ. The model predicts a rapid decrease of P_{max} in high light due to the response function component at short time-lags. Recovery will be slower in a succeeding low-light period; both the short time-lag and, later, the long time-lag effects will contribute to a reduced P_{max} . Not only does the P-I relation differ in increasing vs decreasing irradiance (an effect previously termed 'hysteresis' of photosynthesis, Harris & Lott 1973, Platt & Gallegos 1980), but also recovery dynamics make an important contribution to the overall effect of high light on photosynthesis.

These culture experiments were run under high average irradiance and the observed photosynthetic depression contrasts with reports on shade-adapted communities. Photoinhibition in the latter can be severe (75 % reduction in a 10 min exposure) and is related to the large PSU sizes of shade-adapted phytoplankton, especially diatoms (Perry et al. 1981). When these phytoplankton are exposed to high irradiances, photosystem II reaction centers are inactivated to protect the photosystem from high energy loads (Critchley & Smillie 1981). However, after continued exposure to high mean irradiance, this extreme sensitivity to photoinhibition can be lost in a matter of hours (Gallegos et al. 1983). In the present cultures, response characteristics did not change significantly over the experimental period. Because of a high but variable

light regime, these diatom species adopt a strategy which is a compromise between maximum light utilization and minimum sensitivity to photoinhibition, characteristics of pure shade- and sun-adapted communities, respectively. Further specification of response mechanisms will require, at the least, some parallel measurement of O_2 evolution and supplementary physiological assays such as fluorescence parameters and enzyme activity. Accepting in the interim that the estimated response function has a general physiological basis, we proceed to outline briefly the application of this model to the study of phytoplankton photosynthesis in surface mixed layers.

Vertical mixing introduces both random and deterministic short-term variations in the irradiance field (Denman & Gargett 1983). The effects of these variations have been simulated either experimentally (Jewson & Wood 1975, Marra 1978a, b, Gallegos & Platt 1981) or numerically (Platt & Gallegos 1980, Falkowski & Wirick 1981). These models offer insight into possible effects of vertical mixing, however general conclusions have yet to emerge. Each modeling approach has its own limitations: realistic vertical mixing regimes are difficult to simulate in the former approach, realistic biological responses are difficult to include in the latter class of models. The response function approach offers a model of biological variation that displays a full range of time scale behavior. In theory the response function can be used to predict photosynthetic response to an arbitrary time series of irradiance variation; this will be a useful exercise when once the general characteristics of phytoplankton response functions are better established. Nevertheless, the response functions estimated here suggest features that should be considered in constructing time-dependent models of phytoplankton production regardless of approach: (1) variation of P_{max} is a primary source of time-dependence; (2) P_{max} variation, no matter what the exact physiological mechanism, can be related to light history; (3) allowance should be made for multiple time scales of response, in particular, responses to shifts from low to high irradiance will probably be quicker than to shifts from high to low irradiance.

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