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Aquatic primary production in relation to microalgal responses to changing light: a review

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ABSTRACT

Dynamic aspects of algal photosynthesis are set against the background of physical water motions which change the light experienced by the phytoplankton. These time-dependent photosynthetic responses are reviewed in relation to the proposition that phytoplankton primary production may be incorrectly estimated by the commonly used "static" incubation of light and dark bottles for periods significantly longer than the response-time of phytoplankton to changing light. This proposition is supported by the clear overlap between the timescales which characterize water motions and the timescales reported for the complex responses of algae to changing light. Empirical studies comparing static and dynamic incubations have been inconclusive, as have models incorporating some representation of the dynamic photosynthetic response to changing light. These results reflect weaknesses in the simple formulations used to describe photosynthesis in relation to irradiance, the simplicity of physical schemes used to generate changes in irradiance with time, and a lack of data (field and laboratory) on dynamic responses of microalgae to changing light. The quantitative significance of many physiological mechanisms is not known in relation to their effect on photosynthesis.

Introduction

The history of progress towards a combined understanding of the physical and biological processes affecting primary production by phytoplankton is documented by Legendre and Demers (1984) and Tett and Edwards (1984). This broad topic is also the focus of the review by Prézelin et al. (this volume). According to Legendre and Demers (1984), recognition of the different spatial and temporal scales of hydrodynamic and biological processes has been central to this progress. The comparison of timescales is also central to this review of phytoplankton responses to changing light because it is the overlap, or otherwise, of physiological and physical

timescales that conditions the effect, upon primary production, of the entrainment of algal cells in organized or turbulent flows.

If phytoplankton change their photosynthetic response with changed light (e.g. light and shade adaptation, photoinhibition) at a rate that is less than instantaneous but not vastly longer than the time taken for water movement to change the light experienced by an algal cell, then they may be regarded as having a "memory" of their recent light history. If this is so, then primary production estimates based on incubations significantly longer than the phytoplankton response-time cannot represent the actual circumstances of phytoplankton primary production. Further, it will be necessary to know the path of a cell within the mixed layer to determine its accumulated exposure to various light levels and to effectively model its photosynthetic response. Consequently, the duration of field primary production measurements, which is determined by the interaction between the method's sensitivity and the algal biomass, is crucial in that it may be necessary to resolve photosynthetic and respiratory rates at temporal scales no longer than those of effective phytoplankton response to a changed light field; for longer incubations, the result is always a function of the technique (Harris, 1986).

In this review, we have, of necessity, placed many restrictions on our view of the broader aspects of phytoplankton ecology. We focus on changes that occur within about a day and are mainly concerned with responses of the individual phytoplankter. Consequently we do not consider interspecific competition, loss factors such as zooplankton grazing, nor do we treat the effects of nutrients or temperature or daily physiological cycles in detail. The aims of the present account are 1) to provide a current view of the dynamic aspects of planktonic photosynthesis against the background of physical water motions that act to change the light climate experienced by the phytoplankton, 2) to document some experimental trials that have compared traditional primary production incubations with ones designed to simulate the effect of water motion and 3) to give a brief account of recent models that combine the time-varying photosynthetic response with some representation of the effects of water motion.

Timescales of physical processes in the upper layer of water bodies

Physical processes which affect the light experienced by phytoplankton are listed with their approximate timescales in Table 1. Processes longer than about 24 hours may be considered to operate on the phytoplankton community, affecting algal succession, and will not be considered in detail here. Although it is broadly correct to regard the timescales as either cyclical or irregular in their effect on light, some of the timescales given here refer to directional changes: specifically turbulent mixing and horizontal advection. Timescales of cyclical change refer to the time required to complete a cycle of movement. The time required to effect measurable change in the light experienced by a phytoplankton cell will, of course, be less than that given in Table 1 for the complete movement. In all cases, except for horizontal movements, the change will depend on the approximately exponential attenuation of light with depth.

Table 1. Dynamic change of light in the upper layers of water bodies

Cause	Approximate timescale	Source
Seasons	year (1)	
ice formation	year (1)	
Storm fronts	days (1–14)	
Diurnal pattern	hours (24)	
Clouds	seconds (30)–minutes (4)	Walsh and Legendre (1983)
Horizontal advection beneath ice; floating macrophytes; edge shadows	seconds–minutes seconds–minutes	
Surface waves (flicker effect)	seconds (0.1–10)	Walsh and Legendre (1983)
Tides (spring/neap)	days (13.7)	
Tides (semidiurnal)	hours (12.4)	
Internal waves (≤ 30 m displcmt)	minutes (3)–hours (16.7)	Denman and Gargett (1983)
breaking	hours (12)	Denman and Gargett (1983)
Langmuir circulation (< 10 m displcmt)	minutes (20–30)	Denman and Gargett (1983)
Turbulent mixing (10 m displcmt)	minutes (30)–days (11.6)	Denman and Gargett (1983)

It is convenient to arbitrarily group the processes in Table 1 according to those operating above or at the air/water interface and those operating beneath the surface. Both groups effect changes in the light quantity and quality experienced by phytoplankton and may considered to pose the same general problem to the algal cell (Marra, 1978a). Gallegos and Platt (1982) argue that the contribution of water movement to variance of the light quantity experienced by passively entrained phytoplankton is almost the same as that which can be attributed to the passage of scattered clouds. They contend that this contribution is greater than the variance caused by diurnal variation, at least for that part of the day in which most production incubations are conducted. According to Kirk (1983) the passage of scattered cloud can vary the light reaching a given point on the earth's surface (I_0) by 50–80% of full sunlight. Since circulation in a turbid water column may carry phytoplankton below the euphotic depth, water motion may impose a further variation of up to ~95% of I_0 for the wider range of aquatic environments, assuming ~5% reflectance at the air/water interface (Kirk, 1983). Variation in the spectral quality of the light sensed by algal cells is under greater control from water motion than from atmospheric processes (cf. Kirk, 1983).

Two subgroups of water movement processes may be recognized: organized flows such as Langmuir cells and internal waves, and disorganized or turbulent flows. Table 1 indicates that there is a continuous range of timescales from the "flicker effect" (Walsh and Legendre, 1983; 1988) of passing surface waves (seconds) to the much longer timescales that may be associated with particle movement by turbulent mixing (days). Of these subsurface processes, internal waves have the propensity for rapidly advecting phytoplankton over vertical distances of the order of 10 metres (Le Fèvre, 1986). The largest Langmuir cells are believed to scale with the depth of the mixed layer (Buranathanitt et al., 1982), i.e. of the order of 100 m for the ocean in summer and of the order of 10 m for a stratified lake. In their model of Langmuir circulation, Buranathanitt et al. (1982) indicate that the flow is assymmetric, with downwelling velocity being approximately twice that of upwelling. Passively entrained phytoplankton will, therefore, be moved more rapidly from high to low light than vice versa.

Timescales of phytoplankton responses to changing light

Tables 2 and 3 list algal photosynthetic responses to high (saturating) and low (subsaturating) photon flux density (PFD) respectively, with the range of published timescales. The tables follow approximately the same format, presenting the overall response and changes to P/I parameters first, followed by a more detailed account of the underlying physiological responses. Table 2 is specifically directed at photodamage and the responses that have been associated with it, rather than at adaptation to high PFD. These responses are not exclusive but appear to be distinguished fairly well on the basis of timescale: photodamage occurring most rapidly. Although Table 3 is cast in terms of responses to decreased PFD the listed changes are reversed in adaptation to increased PFD, though with different timescales in some cases. Given the relative nature of most of the responses (i.e. increased or decreased from

some starting point) changes in, for example, the P/I parameters or the chloroplast can be viewed as reciprocal and representative of the cells position on a gradient of potential adaptation. Timescales followed by question marks are those for which we did not find specific reference and we have offered approximations by analogy with similar or related processes. Figure 1 shows the parameters normally used to describe the P/I curve, while the numbered comments give the general physiological basis for different portions of the curve (after Raven, 1984; cf. Larkum and Barrett, 1983). Changes in dark respiration are also considered for the same range of photon flux (Raven, 1984). It should be remembered that in this review, with its primary focus on the microalgal phytoplankton of marine and fresh waters, we have to contend with "The charming, but alarming, diversity of aquatic plants ..." (Raven, 1984). The algae contain representatives of both of the fundamental types of cellular organization, prokaryote and eukaryote, and there is a much wider genetic (evolutionary) and structural diversity of the photosynthetic system than is the case in higher plants (Larkum and Barrett, 1983). It is well recognized, for instance, that the algae display marked divergence in the structure of their light harvesting pigment-protein complexes in comparison with the higher plants (Anderson and Barrett, 1986). This diversity is reflected in the light responses of different algal groups, for example, the dinoflagellates are reported to be more susceptible to damage by high PFD than are the green algae (Richardson et al., 1983) and these authors also conclude that there are important differences in the ability of different microalgal groups to grow at low PFD. We feel that the literature on dynamic (time-dependent) responses of algae to changed light is too sparse to permit us to differentiate between algal groups in any meaningful way, at present. Consequently, it must be recognized that some timescales given here derive from studies of single algal species and are unlikely to be universal within the very diverse group of organisms that comprise the phytoplankton.

Response to increased PFD – photodamage

Following Powles (1984), Kyle and Ohad (1986), and Critchley (1988) photoinhibition can be functionally described as a reversible reduction in photosynthetic capacity (P_{max}) incurred by exposure to photosynthetically available radiation (PAR; visible light of wavelength 400–700 nm), and involving no loss of chlorophyll. Continued exposure to a high photon flux density (PFD) results in progressive loss of chlorophyll by photooxidation and eventual disruption of the cell (Powles, 1984). Photoinhibition can be viewed as that part of the continuum of photodamage in which the cell's repair mechanisms can keep pace with the rate of damage caused by the absorption of visible light (Greer et al., 1986, cited in Critchley, 1988; Kyle and Ohad, 1986). This does not imply that the cell is incapable of recovery from some degree of photooxidation if it is subject to a lower PFD before losing the capacity to effect repairs. The term, photodamage, is used here to encompass both photoinhibition and photooxidation which are generally not distinguished in ecological field or laboratory studies.

It is generally accepted that photosystem II (PS II), the oxygen evolving photosystem, is more sensitive to photoinhibition than photosystem I (PS I) and is the first

affected site (Critchley, 1988). However, the biochemical mechanism of photoinhibition remains both poorly understood and controversial. Kyle and Ohad (1986) argue that photoinhibition occurs first through damage to the 32 kDa D1 (Q_B-binding) protein and therefore affects electron flow. However, Critchley (1988) considers that the weight of evidence now favours the PS II reaction centre (RC II) chlorophyll P 680 as the site of primary damage. Destabilization of the pigment-protein complex and disintegration of the apoprotein(s), which may include the D1 protein, follows from the primary damage to P 680 (Critchley, 1988). Resolution of the controversy as to the structure of the pigment-protein complex of RC II, specifically which of the proteins, D1/D2 (32/34 kDa) or the 47 kDa protein, bind the reaction centre chlorophylls (Critchley, 1988), will help to resolve this question. In contrast to Critchley, Andréasson and Vänngård (1988) do not acknowledge any controversy, stating that "... there is now definite proof that the reaction center of photosystem II is located in the D1 and D2 polypeptides in plants ...". The D1 protein has been reported to have a comparatively high turnover rate, linked to photoinhibition (Kyle and Ohad, 1986; Raven, 1989). Because this protein apparently has to be newly synthesized as part of the repair process (Critchley, 1988), it may offer an important insight into the cell's response to high PFD, particularly in concert with chemical inhibitors of protein synthesis Raven (1989). Photosystem I is also inhibited by excessive visible PFD and this manifests itself as inhibition of electron flow (Powles, 1984). In contrast to PS II inhibition, PS I inhibition requires the presence of oxygen and this may indicate that active oxygen species are important (Powles, 1984).

It is not satisfactory to consider only the photosynthetically available waveband in relation to photodamage. Using isolated spinach chloroplasts, Jones and Kok (1966, cited in Kirk, 1983) found that photodamage was greatest in the ultraviolet (UV) at 250–260 nm, occurring with a lesser quantum efficiency in the photosynthetically available 400–700 nm region. Kirk (1983) suggests that photodamage by UV light affects plastoquinone in the electron transport chain linking photosystems I and II. According to Lorenzen (1979) proteins and nucleic acids absorb and are damaged by UV-B radiation (290–320 nm). Lorenzen (1979) detected suppression of phytoplankton photosynthesis by UV-B light in the upper third of the euphotic zone in coastal waters and suggested that as much as half of the euphotic zone might be affected in clearer open-ocean waters. Kirk (1983) estimated that UV light may account for about 50% of photodamage to phytoplankton in oceanic waters but that it is unlikely to be important in coastal and inland waters where yellow substances (gilvin or gelbstoff) strongly absorb UV light. The effects of UV radiation on primary production in natural waters are poorly known partly for methodological reasons, in that most field measurements utilize glass bottles which absorb UV light (Falkowski, 1984). Similarly, in laboratory experiments artificial light sources which provide UV light at the levels characteristic of sunlight are rarely used and experimental chambers are generally made from UV-absorbing materials (Lorenzen, 1979).

In the context of estimating primary production, some important aspects of photodamage are that the depression of photosynthesis affects both light-saturated (P_{max}) and light-limited photosynthetic rates (Neale, 1987). This is shown by the

rapid (minutes) decrease in α reported by Cullen and Lewis (1988; Table 2). Photodamage depends on PFD, on other stresses being experienced by the cell, on time, and on the interaction of these factors. Because of the hysteresis involved in repair of photodamage, it is also a function of the time (hours) elapsed since the last exposure to high light (see Table 2). The longer-term history (days) of PFD exposure is also important in that low-light adapted algae are particularly sensitive to photodamage. Photodamage may be characterized from the P/I relationship by the threshold PFD at which photosynthetic capacity begins to decline (I_T) and the rate of the decline, usually expressed as an angle (β; Platt and Gallegos, 1980, and Fig. 1). Richardson et al. (1983) report I_T values (mainly for growth inhibition) in the range 50 to >300 µmol quanta $m^{-2} s^{-1}$, depending on the taxonomic group of the particular alga; other factors almost certainly contribute to this range as well. The magnitude of PFD to which the alga is exposed also affects β, with higher PFDs causing a greater rate of P_{max} depression (Neale, 1987). In some studies a plateau is observed in the P/I curve ($I_T > I_k$) while in others this is not evident ($I_T \approx I_k$) (Platt and Gallegos, 1980; Gallegos et al., 1983; Richardson et al., 1983). The range of I_T overlaps that of I_k, from 16 to 500 µmol quanta $m^{-2} s^{-1}$ (Kirk, 1983). The period of the exposure to high PFD conditions the extent to which P_{max} is reduced (i.e. the extent of photodamage) and the time required for recovery of the initial P_{max} (Belay, 1981; see Table 2). There is also a finite period before photodamage is manifest as P_{max} depression. Raven (1989) asserts that this lag period would be expected even in the absence of repair of photodamage because the number of functional reaction centres can fall to some extent before photosynthesis is affected and, possibly, through the operation of avoidance measures. Stresses such as nutrient deficiency (Kyle and Ohad, 1986; Neale, 1987) and thermal stress (Powles, 1984) exacerbate the effects of high PFD.

Sensitivity to photodamage

A decreasing sensitivity to increasing PFD has been reported for natural marine algal populations in the Arctic (Gallegos et al., 1983; Michel et al., 1988). This adaptation consisted of an increasing ability to tolerate high PFD without the decline in P_{max} indicative of photodamage. Gallegos et al. (1983) compared the photosynthetic response of phytoplankton from the surface layer and from a sub-pycnocline chlorophyll maximum using a series of two hour ^{14}C incubations. They found that the deep (shade-adapted) population was, initially, photodamaged at much lower PFD and at a greater rate than the surface population but that this sensitivity declined within 4–6 h to the extent that median I_T for the deep population was in the range of surface PFD. This apparent ability to recover from photodamage while still exposed to high PFD was also a feature of laboratory experiments on unialgal cultures, reported by Cullen and Lewis (1988). They found that the marine diatom (*Thalassiosira pseudonana*), grown under continuous light, responded to PFD increased from 20 to 2200 µmol quanta $m^{-2} s^{-1}$ with a temporary decline in P_{max} followed by a gradual recovery (Table 2). Michel et al. (1988) found that sea-ice algae ($\sim 74\%$ diatoms) decreased their sensitivity to photodamage, as indicated by

Table 2. Dynamic responses of phytoplankton to changing light – high PFD

Response		Extent/type of change	Approximate range of timescales	Source(s)
Photodamage: (inhibition/oxidation)	onset (decrease in P_{max})	63% ([1]: e-folding)	minutes (15)–hours (1–2)	Harris and Piccinin (1977); Takahashi et al. (1971); Marra (1978b); Cullen and Lewis (1988)
α	decrease	50%	minutes (~20)	Cullen and Lewis (1988)
Sensitivity to photodamage	recovery of P_{max}	100%	2 to 3 times exposure period	Belay (1981)
	increase I_T; decrease β	100% (Field popltn)	hours (4–6)–days (<2)	Gallegos et al. (1983); Michel et al. (1988)
Energy Dissipation:				
Fluorescence	quantitatively insignificant	continuous	<1 second	Powles (1984); Winter and Demmig (1987)
Photosynthesis (P)	electron flow (EF; non-cyclic)	continuous	<1 second	Powles (1984)
Energy expensive processes	increase (e.g. PS II EF; cyclic)	continuous	<1 second	Powles (1984); Raven (1984)
State transition	state II to state III	100%	minutes	Fork and Satoh (1986)
non-radiative decay (NRD)	heat	continuous	<1 second	Powles (1984)
	changing balance: P and NRD	detectable – 100%	seconds–hours (2–4)	Winter and Demmig (1987)
Light Absorption/Exposure:				
Chloroplast	volume change (shrinkage)	100%	minutes	Kiefer (1973)
	migration	100%	minutes–hours (2)	Kiefer (1973)
	re-orientation	detectable – 100%	minutes–hours (~4)	Nultsch et al. (1981)
Negative buoyancy		[2] exit NIZ	minutes (10)–years ($\gg$1)	Reynolds et al. (1987)
Motility		[2] exit NIZ	hours (~2)–days (7)	Spigel and Imberger (1987)
PSU Components:				
Photoprotection	increase carotenoids	detectable – 100%	minutes (15)–hours (<5)	Falkowski (1980); Algarra and Niell (1990)
Chemoprotection	increase enzyme conctrn – (e.g. superoxide dismutase)		as for pigment synthesis?	Powles (1984)
Respiration:				
Repair-associated	increase	detectable – 100%	minutes–hours?	cf. Photodamage and Fig. 1

[1] Calculated as reciprocal of the slope of $\ln(dP/dt)$ plotted against time

[2] Nominal Inhibition Zone: bounded by surface (PFD of 2500) and depth at which PFD = 200 μmol $m^{-2} s^{-1}$, for waters of K_d 1.53 and 0.08 m^{-1} equivalent to vertical displacement from 0 to 1.65 m and 0 to 31.6 m in lake and open ocean water, respectively (after Kirk, 1983; Neale, 1987)

β derived from 20 min ^{14}C incubations, within a two day sampling interval at a time when the estimated cell division time was four days. Although this adaptation may not have involved changes in population structure, it certainly included dark periods when the cells were not subject to the continuous stress of high PFD.

Energy dissipation

Confronted with a high PFD the most rapid responses within the cell are those of energy dissipation by nonradiative decay as heat (NRD) and the maintenance of photosynthetic electron transport. According to Powles (1984) energy dissipation as heat is thought to be an important process in coping with excess energy from high PFD. Although fluorescence also contributes to dissipation of energy on a similar timescale to that of NRD, it is very limited in its quantitative effect (Powles, 1984; Winter and Demmig, 1987). Winter and Demmig (1987), using the nonphotochemical component of fluorescence quenching as a measure of NRD, reported that NRD responded comparatively quickly (seconds – hours; Table 2) to changes in the balance between excitation energy and electron transport rate. That is, the proportion of energy being dissipated as heat through NRD can be expected to increase when photosynthetic electron transport is unable to dissipate the absorbed excitation energy (Winter and Demmig, 1987). Winter and Demmig (1987) recognized a rapid phase in the response of NRD to changed light (timescale 10 – 30 s for *Chlorella*) associated with the proton gradient in the thylakoid membrane, and a slower phase which they attributed largely to carotenoid (zeaxanthin) synthesis in the xanthophyll cycle but which may also have had a component associated with state transitions. This slower phase predominates under very high PFD (Winter and Demmig, 1987).

State transitions

State transitions, which are more fully discussed below in relation to low-light adaptation, are a rapid mechanism by which the energy absorbed by PS I and PS II can be more evenly distributed, under conditions where the spectral quality of light favours absorbance by one of the photosystems. At least five light states have now been described (Fork and Satoh, 1986), each one representing a particular grouping of measured parameters e.g. the fluorescence emission spectrum at 77 °K, the kinetics of fluorescence, and Emerson enhancement (the ratio of yields of oxygen in the presence and absence of far-red background light).

In the context of photosynthetic response to high PFD, light state III, found for an intertidal red alga, is thought to help in avoiding photodamage (Fork and Satoh, 1986). In state III, there was found to be no increase in transfer of excitation energy between PS II and PS I but simply a re-arrangement of pigments about PS II such that less energy reached RC II (Fork and Satoh, 1986); this would presumably increase the energy being dissipated as heat in NRD (cf. Winter and Demmig, 1987). It has also been suggested that a cyclic electron flow around PS II may serve as a

means of dissipating excess light energy absorbed by the reaction centres and therefore help to limit photodamage (Fork and Satoh, 1986). This is an example of a rapid and energy expensive process (Table 2).

Light absorption/exposure

Changes in the chloroplast, in this case migration or volume change, both act to minimize its exposure to irradiance and have been suggested as mechanisms for avoidance of photodamage (Kirk, 1983; Powles, 1984). Both of these changes occur in minutes to hours (Table 2). Migration of the chloroplasts is well known in diatoms where, for instance, Kiefer (1973, cited in Kirk, 1983) found that for the marine planktonic diatom, *Lauderia borealis*, the ~50 chloroplasts of each cell were evenly distributed around the periphery of the cell in low light but were grouped at the valvar ends following exposure to high light. In filamentous algae, such as the green alga *Mougeotia* which has a single flattened chloroplast, the cell is able to change the orientation of the chloroplast to affect the amount of light to which the chloroplast is exposed (Kirk, 1983). Similarly, in benthic brown algae, it is reported that chloroplasts move towards parts of the cell not directly exposed to the light and orient themselves so that they present a minimum cross-section to the direct beam (Kirk, 1983). Nultsch and Pfau (1979, cited in Kirk, 1983), in a study of a benthic brown alga, found that chloroplasts moved to lie parallel to the least light-exposed cell walls within 1–2 h of exposure to high light. Kiefer (1973, cited in Kirk, 1983) found not only that the chloroplasts migrated to form self-shading groups at either end of the cell but that they shrank under high light. Shrinkage was noticeable within minutes of exposures to high light but the process continued for 30–60 min. Collectively, these mechanisms reduced the measured absorbance of the cells (at 440 nm) by about 40% (Kiefer, 1973, cited in Kirk, 1983). In a review of the cellular biochemistry of chloroplast movement, Haupt and Scheuerlein (1990) observed that, at least for the benthic alga *Dictyota dichotoma* (Nultsch et al., 1981), chloroplast reorientation proceeded much more slowly than the decline in P_{max} resulting from photodamage in high light, and that the recovery of P_{max} in low light was complete within the half-time of the chloroplast movement. Haupt and Scheuerlein (1990) concluded that there was little, if any, effect of chloroplast orientation on P_{max} under saturating PFD. However, they did admit that such movement, in response to high PFD, may serve to protect the chloroplasts from being damaged, although they maintained that there was no evidence for this.

Buoyancy and motility

The efficacy of buoyancy, positive or negative, and motility in changing the exposure of a cell to light obviously varies with the light attenuation in a particular water body. Further, there is a very broad range of movement speeds characteristic of different algal groups; this topic is reviewed by Heaney and Butterwick (1985). In Table 2, the range of timescales presented for motile or negatively buoyant algae is related to a change in PFD, rather than simply to a specific distance of movement

(see note 2, Table 2). A nominally inhibitory zone (NIZ) was defined as the depth range in which PFD > 200 μmol quanta $m^{-2} s^{-1}$ on the basis of the very approximate threshold for photodamage of natural phytoplankton populations given by Neale (1987). Using a subsurface PFD of 2500 μmol quanta $m^{-2} s^{-1}$ (after Kirk, 1983) the NIZ was determined for very clear oceanic waters and for comparatively turbid lake waters; medians of data (Kirk, 1983) for vertical attenuation coefficients (K_d) from three oceanic systems and 26 lakes were used. There is at least an order of magnitude difference in the vertical movement needed to exit the NIZ in these contrasting aquatic environments. Published values of sinking rates for various microalgae (Reynolds et al., 1987) yield timescales from minutes to many years for vertical movements equivalent to the depth of the NIZ (Table 2). The shorter of these timescales is that required for a large negatively buoyant cell or colony to sink from the surface to the base of the NIZ in lake water. Spigel and Imberger (1987) give a range of speeds for movement by flagellated microalgae. This range corresponds to timescales of hours to days (Table 2) for motile cells to traverse the NIZ of lake and oceanic waters, respectively.

In general, it is evident that motility and buoyancy can very significantly affect the light to which phytoplankton are exposed within the short timescales of particular interest here, especially in lakes which are usually characterized by considerably higher attenuation coefficients than are found in the oceans or in coastal marine waters. Two points are worthy of note: 1) cells below the surface could sink or move below the NIZ even more quickly than the minimum timescales given in Table 2, and 2) the effect of these movements is conditioned by water motions which dominate except under conditions of low kinetic energy and/or high stability in the water column.

PSU components

Carotenoid pigments are thought to dissipate excess excitation energy as heat (Powles, 1984). According to Larkum and Barrett (1983), the β-carotene, present in virtually all algae is the major photoprotectant associated with the reaction centres of both photosystems. Carotenoids are considered effective in quenching potentially damaging chemical species such as singlet oxygen (Powles, 1984). Synthesis of extra carotenoids may, therefore, help in avoidance of photodamage. Detectable changes in concentrations of these photoprotective pigments occur comparatively quickly (Falkowski, 1980), certainly there is evidence that significant change is possible within a few hours (Table 2). Algarra and Niell (1990) describe the complete transition associated with a daily cycle occurring within 5 h.

Critchley (1988), in her discussion of the mechanism of photoinhibition, states that if oxygen is mechanistically involved then the active species are likely to be the superoxide radical ($O_2^{\cdot -}$), or the more reactive hydroxyl radical ($OH^{\cdot}$) and singlet oxygen. Singlet oxygen may be formed through quenching of triplet-state chlorophyll (Powles, 1984). Hydrogen peroxide (H_2O_2) is another powerful oxidant which can be formed, in the Mehler reaction, when oxygen becomes the terminal electron acceptor for the photosynthetic electron transport chain (Beardall and Raven,

1990). The probable destructive effect of these chemicals is to oxidize the lipid components of membranes, particularly unsaturated fatty acids which can be directly oxidized by singlet oxygen (Halliwell, 1984, cited in Critchley, 1988). There are, however, specific enzymes which are able to remove these damaging oxidants. The presence of superoxide dismutase is known to increase the rate of $O_2^{\cdot}$-disproportionation, maintaining a low steady-state concentration (Badger, 1985); reduced ascorbate and glutathione may also contribute in this process. According to Powles (1984), superoxide dismutase has been shown to prevent photooxidative damage to plant tissue. In higher plants, ascorbate peroxidase rapidly detoxifies H_2O_2 and this enzyme has been detected in some miocroalgae (Beardall and Raven, 1990). Ascorbate, glutathione and α-tocopherol have all been ascribed some ability to dissipate either singlet oxygen or superoxide, and a flavenol has been shown to decrease photooxidative damage in chloroplasts (Powles, 1984).

Response to decreased PFD – adaptation to low light

Larkum and Barrett (1983) list the general characteristics of unicellular algal shade-adaptation for the major microalgal groups. They report a general tendency to increase light-harvesting pigments per cell: chlorophyll-a and -b for all algal groups, chlorophyll-c (diatoms), phycobiliproteins (Cyanobacteria; red algae), carotenoids (diatoms, Dinoflagellata). Also, for red algae there is a general increase in thylakoid membrane. A decrease in P_{max} (and I_k, but cf. Beardall and Morris, 1976) and cell volume is found for most algal groups. Richardson et al. (1983) also note the tendency towards lower specific respiration rates (carbon fixed per unit carbon) in algae grown at low PFD. Cunningham et al. (1989) used the red alga *Porphyridium cruentum* to investigate the changes resulting from growth at low PFD. These authors present electron micrographs of the decrease in cell volume and of the relative increase in thylakoid membrane per cell. In none of the references mentioned are timescales given for these changes but it can be assumed that they are related to growth and therefore to cell division timescales. Growth rates are broadly size related (Banse, 1976) but represent an integration of environmental factors such as growth-irradiance, temperature and nutrient supply. Langdon (1987) states that growth rates vary from 0.1 divisions day^{-1} (population doubling every 10 days) for large oceanic dinoflagellates to >3 to 4 divisions day^{-1} (population doubling every 6–8 h or less) for small diatoms and green algae. Marra (1978a) estimates a somewhat shorter minimum doubling time (1 h), while Culver and Smith (1989) report a longer doubling time for an arctic field population (33 days). The limits of this range span almost three orders of magnitude.

P/I parameters

The *P/I* curve represents an empirical description of the combined effects of various biochemical processes on the rate of carbon fixation at different PFDs (Fig. 1). The traditional interpretation of the curve is that the approximately linear portion of the curve (limited by PFD) is determined by photochemistry and is independent of

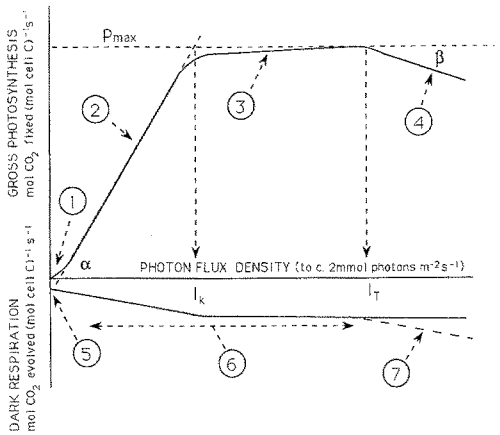

Figure 1. A schematic diagram of the photosynthesis/irradiance (P/I) relationship, showing the five parameters usually used to describe the curve. Changes in dark respiration are also shown (after Raven, 1984). Circled numbers refer to the following comments explaining the physiological interpretation of the curve (Raven, 1984):

① Sigmoid relationship determined by slippage and leakage reactions competing with low rates of energy transduction.

② Slope a function of mol pigment $(\text{mol C})^{-1}$; *in vivo* absorption coefficient of the pigments; excitation energy distribution between photoreactions; quantum yield of partial reactions of $NADP^+$ reduction and ATP synthesis; ATP and NADPH used $(CO_2 \text{ fixed})^{-1}$, and in other synthetic reactions.

③ Capacity determined by concentration and specific reaction rate of limiting catalysts; achieved rate determined by availability of CO_2, and temperature.

④ Photoinhibition determined by effectiveness of protective and repair mechanisms.

⑤ Intercept (dark respiration of dark-held cells) = specific maintenance requirement (mol C lost $(\text{mol cell C})^{-1}\,s^{-1}$).

⑥ Growth-related portion of respiration; depends on requirement for ATP, NADPH, C skeletons $(C)^{-1}$ from photosynthate assimilated into cell material, and extent to which ATP and NADPH from thylakoid reactions are used in biosynthesis as well as in photosynthesis.

⑦ Respiration related to repair of damage caused in photoinhibition?

temperature, while the asymptotic region (where PFD is saturating and/or damaging) is determined by enzyme-mediated biochemistry and is therefore affected by temperature. Various mathematical formulations have been developed to describe this saturation-curve (Jassby and Platt, 1976) and to include that part of the P/I curve in which P_{max} declines as a result of photodamage at high PFD (Platt and Gallegos, 1980). For gross photosynthesis, a minimum of four terms are required to describe the P/I curve including the effects of photodamage and the case where a plateau region occurs before photodamage affects P_{max}; these are α, P_{max}, I_T and β (Fig. 1, and Platt and Gallegos, 1980). The fifth term in Figure 1, I_k, was put forward by Talling (1957) to describe the transition from light-limited to light-saturated photosynthesis and to facilitate ecological comparisons between phytoplankton species.

There are a variety of difficulties which attend the determination, interpretation and comparison of P/I curves estimated for natural populations of algae, individual algal species and, even for a single species, over time. Among these difficulties are

1) choice of the biomass measure, frequently either chlorophyll concentration or cell numbers, used to normalize the photosynthetic measurement (Platt and Gallegos, 1980); also, the effect of normalizing P using P_{max} (Beardall and Morris, 1976), 2) choice of the most appropriate model for the particular curve (Jassby and Platt, 1976), 3) undersampling of P/I pairs, especially when the curve requires four parameters for its description (Platt and Gallegos, 1980), 4) the dependence of I_k on both α and P_{max} such that changes in I_k cannot be simply interpreted (Beardall and Morris, 1976) and 5) the difficulty of estimating confidence intervals for non-linear models, especially given the restricted number of replicate samples obtained in most experiments (Zimmerman et al., 1987). Statistical comparison of these parameters requires multiple sampling ($\sim$12 to 25 samples; Zimmerman et al., 1987), which remains rare although a short-term ^{14}C method (Lewis and Smith, 1983) has been used to estimate standard deviations for some P/I parameters in a recent field study (Brightman and Smith, 1989). Notwithstanding these difficulties, which compound the uncertainties associated with the commonly used methods of measuring primary production (Harris, 1980; Peterson, 1980), P/I curves remain fundamental to aquatic primary production studies (Yentsch, 1980; Zimmerman et al., 1987).

The α and P_{max} terms describe the shape of the P/I curve in the absence of photodamage and, although ideally independent, have been found to be correlated in natural phytoplankton populations (Platt and Gallegos, 1980). Changes in these two parameters have been interpreted in terms of whether PSU size or number changes in response to changed growth-illumination (Richardson et al., 1983). These PSU changes have also been viewed as adaptive strategies which may characterize the response of particular algal groups to different ecological niches (Falkowski and Owens, 1980). However, Richardson et al. (1983) delineated five types of P/I curve from published data and noted that it was difficult to account for this complexity simply on the basis of changes in PSU size or number.

Changes in P/I parameters have most often been considered in terms of the concept of light and shade adaptation and consequently much of the literature concerns growth-related changes occurring over days (Rivkin et al., 1982; Richardson et al., 1983). However, shorter-term responses have been examined (Cullen and Lewis, 1988) and found to be quite rapid in some instances. Cullen and Lewis (1988) reported very different timescales of response for α and P_{max}, depending on the direction of the light change imposed on cultures of the marine diatom *Thalassiosira psuedonana* (Tables 2 and 3). In the context of decreased PFD, Cullen and Lewis (1988) found that P_{max} declined rapidly, completing 50% of the measured change in less than an hour, while α increased comparatively slowly over a period of hours (Table 3). Under increased PFD, the photosynthetic efficiency (α) declined rapidly while the photosynthetic capacity (P_{max}) increased slowly, with a 50% completion time of $\sim$20 h (Cullen and Lewis, 1988).

Energy distribution between photosystems

In the aquatic environment any vertical movement is accompanied by some change in the spectral quality of the light as well as in light quantity. Changes in spectral quality can result in unbalanced excitation of PS I and PS II because there are

Table 3. Dynamic responses of phytoplankton to changing light – decreased PFD

Response		Extent/type of Change	Approximate range of timescales	Source(s)
Adaptation to low light	overall response	100%	hours–days (4; field)	Marra (1978b); Savidge (1988)
P_{max}	decrease	50%	minutes (~30)	Cullen and Lewis (1988)
α	increase	50%	hours (<8)	Cullen and Lewis (1988)
Growth rate	decrease	100%	hours (20)	Post et al. (1984)
Energy Distribution between PS I and PS II:				
State transition	reversible state I to state II	100%	seconds–minutes (a few)	Falkowski (1984); Fork and Satoh (1986); Kiefer (1973); Pick et al. (1987)
Light Absorption/Exposure:				
Chloroplast	migration	detectable–100%	minutes–hours (5–8)	Nultsch et al. (1981)
	re-orientation	100%	minutes (15)–hours (1)	Lechowski and Bialçzyck (1987); Haupt and Scheuerlein (1990)
Positive buoyancy		[1] Zeu to NIZ	hours (~1)–years (>1)	Heaney and Butterwick (1985)
Motility		[1] Zeu to NIZ	hours (~4)–days (~13)	Spigel and Imberger (1987)
PSU Components:				
Light harvesting pigments	increase concentration	detectable – 100%	hours (<3)–days (5–7)	Pick et al. 1987; Prezelin and Matlick (1980); Rivkin et al. (1982); Post et al. (1984)
Enzymes (Carboxylating)	decrease activity	100%	days? (as for pigments?)	Richardson et al. (1983)
Electron transport	decrease component conctrn	100%	days? (as for pigments?)	Richardson et al. (1983)
Respiration:				
EPIR	decrease in darkness	100%	hours (~2–>14)	Stone and Ganf (1981)
Maintenance	decrease	100%	days? (as for PSU compnts?)	Richardson et al. (1983)

[1] Depth bounded by 1% of subsurface PFD (25 μmol $m^{-2} s^{-1}$) and 200 μmol $m^{-2} s^{-1}$ in waters of K_d 1.53 and 0.08 m^{-1} equivalent to vertical displacement from 3 to 1.65 m in lakes and from 57.6 to 31.6 m in open ocean water (after Kirk, 1983; Neale, 1987)

differences in the pigment-protein complexes associated with each photosystem (Fork and Satoh, 1986). Photosynthetic electron flow requires the serial operation of the two photosystems and it is therefore necessary to balance the activity of the photosystems to achieve maximum efficiency (Larkum and Barrett, 1983). Within the spectral bands from 470–660 (red algae and Cyanobacteria) and 450 to 670 (green algae and higher plants) PS II absorbs more light than PS I, while PS I dominates above and below these bands (Fork and Satoh, 1986; Anderson and Barrett, 1986). Light states are related to this absorption dominance such that State I is promoted by relatively greater excitation of PS I while State II occurs when PS II is the dominant absorbing photosystem (Fork and Satoh, 1986). Further, in State I the quantum yield in low light is expected to increase for reactions associated with PS II (Oxygen evolving photosystem) while the quantum yield of reactions associated with PS I would decrease, and the reverse of this is true for State II (Fork and Satoh, 1986).

Of the two possible means of redistributing energy between photosystems, the active transfer of energy from PS II to PS I (spillover) is now thought less likely, at lest in green algae, than changes in the light absorption cross-section of the photosystems. Changing cross-section requires physical movement of the antennae pigments away from the reaction centre in a manner that prevents or reduces the transfer of energy. A reversible biochemical process which may facilitate this movement is the phosphorylation of the LHC II, which is well established for higher plants *in vitro* (Baker and Webber, 1987). This process is thought to be controlled by a light-regulated enzyme (kinase), mediated by the redox state of plastoquinone such that an over-excitation of PS II causes reduction of the plastoquinone pool and activates the kinase (Baker and Webber, 1987). Phosphorylating the LHC II causes its physical detachment from RC II and though light is still absorbed by the antennae pigments, the excitation energy is less effectively transferred to RC II. It has been suggested that phosphorylated LHC IIs migrate into the non-appressed region of the thylakoid (where thylakoids are not fused into stacks) and may transfer their energy directly to PS I (effectively spillover) but this remains controversial. Baker and Webber (1987) point out that even if the phosphorylation of LHC II simply distances it from RC II, without enhancing the migration of energy to PS I, there would still be a decrease in the energy effectively being absorbed by PS II relative to that being absorbed by PS I. According to Anderson and Barrett (1986), there is compelling evidence that the phosphorylation of LHC II is involved in thylakoid stacking (membrane appression). They point to the existence in LHC II of a 2 kDa fragment of protein exposed at the membrane surface which is required for restacking of the thylakoids. State transitions are temperature affected, something that is consistent with the role of LHC II phosphorylation and mobility within the thylakoid membranes because temperature affects the fluidity of the membranes (Fork and Satoh, 1986). Further evidence for a link between the ability to undergo state transitions and the physical properties of the membranes, specifically their change from liquid crystalline to gel phase, has been reported for thermophilic Cyanobacteria and from glutaraldehyde fixation experiments (Fork and Satoh, 1986).

The Chromophytes, which lack LHC II and appear unable to change the ratio of appressed to non-appressed thylakoids, cannot share the above mechanism for rapid

redistribution of energy between PS II and PS I (Anderson and Barrett, 1986). In the Cyanobacteria and red algae, where there is neither LHC II nor membrane appression, spillover remains plausible because of the greater physical proximity between the photosystems (Anderson and Barrett, 1986).

It is logical to assume that transitions between states I and II have their greatest benefits, in terms of photosynthetic efficiency, under conditions of low or very low light because these coincide with the greatest spectral bias in the aquatic environment. For this reason, the timescales of these transitions are included in Table 3, which indicates that State I to II transitions are achievable, reversibly, with timescales of seconds to minutes. State I to II transitions appear to be faster than the lesser known state II to III transitions (Table 2), which may simply reflect the greater body of knowledge of the former transition.

On longer timescales than those of state transitions, changing the stoichiometry of the two reaction centres (RC I and RC II) may represent another mechanism for regulating the energy distribution between PS I and PS II (Glazer and Melis, 1987); although the traditional interpretation of the Z-scheme of photosynthesis suggests a one to one stoichiometry. Glazer and Melis (1987) observe that the ratio of RC II to RC I varies considerably between different groups of photosynthetic organisms: Cyanobacteria commonly have quite low ratios (0.3–0.8) compared to higher plant chloroplasts (1.4–1.9). This may be explained by the functional analogy between the LHC II of higher plants and green algae, and the phycobilisome (PBS) of Cyanobacteria; the close association of PBS with PS II in Cyanobacteria compensates for the low RC II/RC I ratio (Glazer and Melis, 1987). More generally, Glazer and Melis argue that the thylakoid membrane adjusts the stoichiometry of the photosystems to promote a balanced absorption of light under the prevailing spectral conditions. The phosphorylations of LHC II may be part of a regulatory system in higher plants which identifies phosphorylated LHC IIs as surplus to requirements and removes them from the thylakoid membrane altogether (Glazer and Melis, 1987).

Light absorption/exposure

Under low light, changes in the chloroplast act to promote the maximum interception of light and are essentially the reverse of those changes occurring under high light. Single, flattened chloroplasts are reoriented to absorb as much light as possible while multiple chloroplasts migrate from relatively shaded positions to places where they are fully exposed to the available light. Such changes are adaptive, over relatively short timescales (minutes to hours; Table 3), to the move from high to low PFD. The reorientation of the ribbon like chloroplast of the green filamentous alga, *Mougeotia*, took less than 25 min in response to low light (Lechowski and Bialçzyk, 1987). Similarly, whereas shrinkage of the chloroplast reported by Kiefer (1973) can be considered a response to high light, equally, the reverse can be viewed as an adaptation to low light. Haupt and Scheuerlein (1990) note that, in contrast to the situation in high light, a low-light orientation of chloroplasts has been shown to increase photosynthesis under subsaturating PFD relative to photosynthesis measured for a high-light orientation at the same PFD.

In Table 3 the range of times for positively buoyant or motile cells to move vertically from the bottom of the euphotic zone (nominally 1 % of subsurface irradiance) into the NIZ (see note 2, Table 2) has been calculated for waters of contrasting clarity. It is evident that there is a wide range of timescales for this displacement, from hours to greater than one year. The shortest timescale (2 h) assumes the buoyant capacity of very large colonies of gas-vaculate Cyanobacteria. Motility, at its fastest, is also capable of producing this light change (vertical movement) within hours to days (Table 3). Heaney and Butterwick (1985) note that there is increasing evidence that the sinking rates of nonmotile algae are affected by physiological factors. Diatoms, particularly, show changes of sinking rate that correlate with physiological status, e.g. they usually sink more rapidly under conditions of stress, such as nutrient depletion. Ageing also affects diatom sinking rates, with senescent cells sinking 2–7 times faster than actively growing cells (Heaney and Butterwick, 1985). These changes of sinking rate occur "quite rapidly and are reversible" and may be related to density changes associated with cellular ionic composition or, possibly, to the effect of surface charge on the viscosity of the surrounding water (Heaney and Butterwick, 1985). Culver and Smith (1989) compare sinking rates measured for field populations of arctic marine algae with those determined for unialgal cultures of two diatoms (*Chaetocerus* spp) and report significant correlation between sinking rate and growth conditions in culture. Sinking rate increased with both growth-irradiance and growth-rate, opposite to the trends suggested above. However, although field studies indicated in similar tendency for sinking rate to increase with growth rate, they found a negative correlation between irradiance and sinking rates for mixed, field populations (Culver and Smith, 1989). Despite what may be indicative of methodological complexity in field studies, these authors data support the idea that diatom sinking rates are affected by microalgal physiology and are therefore related to environmental conditions.

PSU components

As stated earlier, it is generally found that the light-harvesting pigments increase as part of low light adaptation. Detectable changes have been reported to occur within a few hours (Prezelin and Matlick, 1980) while changes of 100 % can take days and are therefore probably related to cell division and population growth. A study of daily changes in pigment composition of the green alga *Pyramimonas parkeae* (Prasinophyceae) showed that chlorophyll-synthesis proceeded during the day at rates of c. 0.2 pg cell^{-1} hr^{-1}. This rate of chlorophyll-synthesis, at a time when cell numbers changed very little, corresponds to a pigment increase per unit volume of culture of $\sim$40 % of the initial chlorophyll concentration. During the night, reduction in chlorophyll content was as high as 0.5 pg cell^{-1} hr^{-1} when this alga was dividing, i.e. in relation to changing cell numbers (Kohata and Watanabe, 1989). It should be noted, however, that nutrient-replete cells grown in culture tend to have greater concentrations of chlorophyll per cell than are found in natural populations and are presumably in the best physiological state (unstressed) to respond rapidly.

Decreasing the activity of carboxylating enzymes and the component concentrations of the electron transport chain under conditions of decreased PFD (low light)

are considered by Richardson et al. (1983) in the context of cellular energetics. Such changes represent strategies to reduce the capital costs to cells grown in conditions of low light, when these components may be considered surplus to requirements. According to Richardson et al. (1983), it is unclear whether this is a universal response of microalgae, but it has been noted in some studies. Michel et al. (1988) observed that a natural populations of Arctic, sea-ice microalgae increased the activity of their carboxylating enzymes as light increased in spring; these changes were completed in a single generation ($\sim$4 days). Although in the opposite context, i.e. of increased PFD, this indicates that enzyme activity could be adjusted in response to changed light. According to Richardson et al. (1983), again in their energetic analysis, it is possible that some microalgae may be able to further reduce their energetic costs at low PFD by decreasing the turnover rates of certain components. They cite chlorophyll, which is observed to have high turnover rates in some microalgae, as an example.

Respiration

The difficulty of determining respiration affects both of the commonly used methods for estimating primary production. Even if respiration is assumed to be a constant and fairly small percentage of P_{max} (commonly about 10 %) it has a significant effect on depth integrated estimates of primary production because of its assumed constancy over the full euphotic depth and, therefore, its effect on estimates of the depth below which net photosynthesis is no longer possible (i.e. the compensation depth of the population; Harris, 1980). Respiration is also significant as a link between photosynthesis and population growth in phytoplankton (Stone and Ganf, 1981; Falkowski et al., 1985; Tilzer, 1987). In the oxygen light and dark bottle method, gross primary production is estimated from respiratory uptake of O_2 measured in darkness by adding the absolute value of this uptake to the net O_2 evolved in the light. The situation is less clear with the ^{14}C method because respiration is not measured directly from dark uptake of $^{14}CO_2$ (Harris, 1980). Recent methodology favours short incubations to limit the excretion and reassimilation of labelled carbon and thereby to approach a direct measure of respiration in the dark bottles, but see Weger et al. (1989). The controversy as to whether net or gross photosynthesis is estimated using ^{14}C light and dark bottles has continued for many years and this history has been reviewed by Peterson (1980).

The assumption that respiration measured in darkness correctly estimates that occurring in the light hinges on whether photorespiration occurs in microalgae and on the significance of the enhanced respiration that can be measured immediately after illuminated cells are transferred to darkness (Enhanced Post-illumination Respiration; EPIR). The various known respiratory pathways in microalgae have recently been reviewed and illustrated by Beardall and Raven (1990). Very briefly, light-dependent respiratory processes, which are not measured in darkened production bottles, are the oxygenation of ribulose-1,5-P2 (RuP2) with the metabolism of the phosphoglycollate so produced (photorespiration), and the Mehler reaction

(Beardall and Raven, 1990; cf. Badger, 1985). The Mehler reaction only represents a net consumption of oxygen if the end product, hydrogen peroxide (H_2O_2), accumulates in the cell. This is not generally the case unless the enzymes which act to detoxify this potentially destructive oxidant are unable to cope with the rate of its production (Beardall and Raven, 1990) and this may occur under conditions of prolonged exposure to high PFD (Powles, 1984). Under certain conditions photorespiration may account for 50% of fixed CO_2 in C_3 higher plants (Tolbert, 1974, cited by Peterson, 1980). A variety of marine and freshwater microalgae, including Cyanobacteria, have the biochemical machinery to photorespire. However, it now appears that accumulation of CO_2 (or bicarbonate) by a carbon concentrating mechanism (CCM) reduces the oxygenase activity of RUBP-c/o, suppressing photorespiration under most natural conditions and conferring on microalgal photosynthesis a superficial resemblance to that of C_4 higher plants (Beardall, 1989; Spalding, 1989). Although this supports the idea that respiration occurring in illuminated cells has the same biochemistry as respiration occurring in darkness and eases this concern about the validity of dark bottle incubations, it leaves the question of whether dark respiratory processes are linked to photosynthesis and therefore responsive to light.

Dark respiration consumes oxygen in the production of ATP and NADPH (reductant) from stored carbohydrate to support biosynthesis and cell growth (Beardall and Raven, 1990). Three biochemical processes are involved: glycolysis, the tricarboxylic acid (TCA) cycle plus oxidative phosphorylation, and the oxidative pentose phosphate (OPP) pathway (Beardall and Raven, 1990). Indirect evidence for the light responsiveness of dark respiration has come from studies using oxygen electrodes to determine changes in net production under varying light. A hysteresis has been observed in the photosynthetic oxygen evolution rate measured when microalgae are exposed to increasing and then decreasing light (Harris, 1973; Harris and Lott, 1973; Falkowski and Owens, 1978). Under these conditions, the rate of oxygen production was markedly less for the equivalent PFDs in the decreasing series. This "hysteresis effect" has been variously ascribed to state transitions (Falkowski and Owens, 1978), an artefact of their experimental procedure, and photorespiration (Harris and Lott, 1973) based on oxygen sensitivity of EPIR. Falkowski (1984) has since suggested that this hysteresis reflects the difference in the timescales which characterize the photosynthetic and respiratory responses to changing light. Recently, the TCA cycle plus oxidative phosphorylation (termed mitochondrial respiration in eucaryotic microalgae) has been shown by Weger et al. (1989), using mass spectrometry of stable isotopes, to be light responsive in the marine diatom *Thalassiosira weisflogii*.

In a study of EPIR, Stone and Ganf (1981) used four freshwater microalgae, two species of green algae and two Cyanobacterial species, to determine the effects of PFD and the duration of light exposure on respiration. Initial respiration (R_i) was determined after two hours dark-adaptation of cells growing exponentially under a PFD of 100 μmol quanta $m^{-2}s^{-1}$ and a 14:10 hr light/dark regime. EPIR was determined, after light exposures of varying PFD and duration, assuming that the rate of respiration measured immediately after a transfer to darkness ($EPIR_0$; i.e. EPIR at $t = 0$) approximates the level of respiration of the illuminated cells just prior

to the light/dark transfer. After 10 min light exposures their data showed $EPIR_0$ increasing with photosynthetic rate for subsaturating PFDs, although not in direct proportion, then levelling off at saturating PFDs except for Microcystis. $EPIR_0$ was from 68% to 275% greater than R_i following 10 min exposure to high PFD (550 μmol quanta $m^{-2} s^{-1}$). When long term exposures to high PFD were used, the increase of $EPIR_0$ from R_i consisted of a rapid rise for 10 to 20 min followed by a slower increase over four to eight hours depending on the algal species; $EPIR_0$ was from ~400% to ~600% greater than R_i after 7.5 h light exposures.

The subsequent decline of EPIR in darkness ($EPIR_t$; where t = time) was also determined. Following a 10 min exposure to high PFD, $EPIR_t$ declined to 40–60% of $EPIR_0$ in 30–45 min of darkness. Here, Stone and Ganf (1981) observed that the two Cyanobacteria tended to show a slower decline of $EPIR_t$ in this initial, rapid phase. However, in 2–2.5 h all species had recovered their initial respiration rate (R_i) to within 10%. A similarly biphasic decline of $EPIR_t$ was observed after 7.5–8.5 h exposures to high PFD but in all cases $EPIR_t$ was still $> R_i$ after 14 h. The distinction between Stone and Ganf's (1981) 10 min and ~8 h light exposures may reflect the effects of photodamage and is consistent with the idea, based on energetic considerations, that respiration should increase with exposure to high PFD in response to the requirement for repair of photodamage (Raven, 1984; Fig. 1). It may also be reasoned that the $EPIR_t$ after 14 h represents a newly adapted state reflecting a higher maintenance respiration in cells with greater capacity to grow at high PFD, i.e. with more energy devoted to maintaining cellular repair mechanisms. Understandably, this hysteresis between the increase and decrease of dark respiration meant that a series of light and dark exposures of equal (10 min) duration resulted in a cumulative increase in $EPIR_0$ (Stone and Ganf, 1981).

Static and dynamic estimation of primary production

It is evident from Tables 2 and 3 and the preceding discussion that algal response to changing light rests on a complex of factors which act over a range of timescales from nearly instantaneous to periods of days for individual species of phytoplankton. This indicates that the algal response to either high or low PFD can proceed significantly within the range of timescales characteristic of water motion (Table 1). According to our original propositions, therefore, it is true that light/dark bottle incubations conducted over periods of 2–8 h (Harris, 1980) do not reflect the actual circumstances of aquatic primary production because there is likely to be interaction between the physical processes of water motion and the biological responses to the changing light field that results from these motions. What remains to be determined is the effect of this interaction on depth-integrated estimates of phytoplankton production: is it significant and under what circumstances?

There have been two general approaches to these questions, 1) Empirical studies comparing static and moving algae (in bottles, glass tubing, shipboard incubators), and 2) Modelling, based on empirical data, to generate time dependent models of production which usually incorporate the effects of photodamage or light/shade adaptation with some dependence on light history.

Field studies

Consideration of the time dependence of photodamage and latterly of the photosynthetic "hysteresis effect" has led to various studies which have compared the "static" incubation (Gallegos and Platt, 1982) of light and dark bottles with production estimated using bottles moved within the water column (dynamic incubation). The findings of some of these studies are summarized in Table 4. Most of the experiments were conducted using field populations and were designed to mimic organized flows such as Langmuir circulation. Exceptions to this are Gallegos and Platt (1982), who also simulated disorganized water motions, and Grobbelaar (1989) who used unialgal cultures in a laboratory-based study. The motivation for these studies has primarily been the hypothesis that the photodamage observed in static incubations is a methodological artefact. By this argument photodamage may be the result of holding algal cells at high PFDs for longer than would occur in nature where water motion, motility, or buoyant movement by the algae may limit such exposure (Harris and Piccinin, 1977; Gallegos et al., 1978; Harris, 1978, 1980; Marra, 1978 a, b; Gallegos and Platt, 1982). Less attention has, so far, been accorded to the slower and less spectacular increase in P (i.e. increase in α) displayed by some algae in subsaturating light.

It is clear from Table 4 that the result of these studies are equivocal, with only a few finding the enhanced production that a simple erasure of photodamage would predict. There are various differences between studies that may account for the disparate results. Jewson and Wood (1975) used very rapid circulation times, moving natural populations of phytoplankton through 50 to 100% of the euphotic depth in less than one minute. These authors also noted that there may be some inherent difference between circulated and static incubations because the circulated algae would remain in suspension while those held stationary could accumulate by settling or floating (Jewson and Wood, 1975), causing local depletion of nutrients or gases and thereby limiting their production. Marra (1978b) reported that depth-integrated production was only enhanced when the surface irradiance was sufficient to cause photodamage in the near-surface static incubation bottles. However, he found that only $\sim$11% of the maximum enhancement could be explained by diminished photodamage; estimated by extrapolating the P_{max} from its observed depth to the water surface. Yoder and Bishop (1985), in reporting that circulation had little effect on integral production, observed no photodamage in any of their static incubations. Gallegos and Platt (1982) found enhancement mainly for algae taken from below the mixed layer, that is algae which were probably low-light adapted and therefore sensitive to photodamage. Both Randall and Day (1987) and Grobbelaar (1989) observed that circulating populations yielded lower estimates of net production than static incubations in turbid waters where the ratio of euphotic to mixed depth (z_{eu}/z_{mix}) was low.

Gallegos and Platt (1985) have attempted to define the conditions under which static light/dark bottle incubations would be expected to differ (positively or negatively) from production estimated using circulated bottles (dynamic incubations). They define a space according to two dimensionless variables, one which scales the incubation time to the time required for the phytoplankton to move vertically by one

Table 4. Comparisons of static and moving incubations

Difference as % of Static Incubation	Method O, Oxygen C, ^{14}Carbon (incubation time)	Sampled depth	Rate of movement cm s^{-1}	Conclusion	Source
−20 to +10	O/C (?) glass loop		2 to 3	NO EFFECT	Jewson and Wood (1975)
+19 to +87	C (4 hr) moving bottles	surface	0.1 to 0.2	ENHANCED	Marra (1978b)
−3 to +76	C (2 hr) analog incubator	surface and deep	0.78 to 1.4 [1] 4.8 to 80.3	ENHANCED for deep samples	Gallegos and Platt (1982)
−45 to +290 (most ±30)	C (3.5 hr) moving bottles	surface	0.17 to 0.83	NO EFFECT largely	Yoder and Bishop (1985)
+10 to +127	C (4 to 5 hr) moving bottles	surface	0.56	ENHANCED	Joiris and Bertels (1985)
−84 to +42	O (4 hr) moving bottles	surface	0.09 to 0.22	DECREASED for turbid water	Randall and Day (1987)
−35 to +28	C (0.5 hr) moving bottles	culture	0.9 to 11	DECREASED for low Zeu: Zm ratio	Grobbelaar (1989)

[1] $cm^2 s^{-1}$

optical attenuation length and the other which represents an index of photodamage. Plotting the results of four experiments summarized in Table 4 (Jewson and Wood, 1975; Marra, 1978b; Gallegos and Platt, 1982; Yoder and Bishop, 1985), Gallegos and Platt (1985) delineate three regions, two of which depend on the index of photodamage alone and an intermediate region where the interaction of both variables is significant. For low susceptibility to photodamage, where mixing is sufficient to prevent any vertical gradient of light responsive attributes of the microalgal population (cf. Lewis et al., 1984), static and dynamic incubations should yield similar results. For high susceptibility to photodamage, e.g. where mixing is strong enough to entrain shade-adapted algae into the upper mixed layer (cf. Lewis et al., 1984), dynamic incubation will show enhanced estimates of production compared to static incubation. Between these extremes of susceptibility to photodamage interpretation of differences between static and dynamic incubations is difficult and requires specific knowledge of physical structure in the upper layer. An example from this intermediate region, which may result in dynamic incubations giving relatively higher estimates of production, may occur when weak mixing permits a vertical gradient of light-responsive attributes of the microalgal population to develop (cf. Lewis et al., 1984). It is noteworthy that this analysis does not delineate any region in which the production estimated by dynamic incubation is less than that from static incubation, as was found by Randall and Day (1987) and Grobbelaar (1989) for turbid waters (low z_{eu}/z_{mix}) atypical of marine conditions but quite common in some estuaries and lakes and possibly in highly productive artificial mass cultures of microalgae. Lewis et al. (1984) used somewhat different dimensionless variables to define mixing conditions in which gradients of light-responsive attributes may form in the algal population of the upper layer. Their analysis was directed at the possible use of these attributes (e.g. variable fluorescence) to infer the extent of vertical mixing in the oceanic mixed layer (cf. Falkowski, 1980) and also as an aid in scaling experimental microcosms to further investigate the interaction between photosynthesis and mixing.

It is apparent from this account that although static incubations may poorly represent the reality of a phytoplankter's existence, dynamic incubations must be combined with measurement of the physical structure of the water column and interpreted with care.

Modelling

There are a wide variety of numerical models of photosynthesis in plants, ranging from those attempting a mechanistic approach based on cell biochemistry (Farquhar and von Caemmerer, 1982) to the largely empirical models, reviewed by Platt and Gallegos (1980), in common use for estimating primary production. Over the past fifteen years or so models that incorporate dynamic responses of higher plant photosynthesis have been published (Thornley, 1976), as have some models specifically describing time-dependent responses of phytoplankton to changing light. We will briefly review some of these (see also Patterson, this volume). These models, like earlier models, are based on the empirically determined P/I curve which has only a

very general relationship to the complex physiological processes that determine its shape (Fig. 1).

Fałkowski and Wirick (1981) use a time-dependent model incorporating both light and shade adaptation (long term) and Monte Carlo random walk processes to simulate vertical mixing. The model does not include the effects of photodamage. The instantaneous photosynthetic rate is based on P/I curves and adjustments of the photosynthetic rate are made according to chlorophyll:carbon ratios, by varying the photosynthetic efficiency (α) or photosynthetic capacity (P_{max}). Only comparatively long term (several hours) adjustments to the parameters of the P/I curve are incorporated in this model.

Liou and van Eybergen (1982) present a model with a somewhat more physiological basis. This assumes a stochastic distribution of light reaction centres into one of three states (inactive/dark, active/light, inhibited). However, in the active state this model also relies on a function closely analogous to a P/I curve to estimate production. The model incorporates the effects of both photodamage and the slower adaptation (hours), but assumes that photodamage occurs instantaneously.

Denman and Marra (1986) model light adaptation using a function which effectively alters P_{max} according to the inhibiting strength of the irradiance and exposure time to that irradiance. The model essentially scales the algal response, between P/I curves representative of fully light adapted and fully shade adapted cells, according to the recent light history of the phytoplankton population. This model has no specific term for photodamage but is able to represent the effects of photodamage seen in Marra's (1978b) data. In contrast, DYPHORA (Pahl-Wostl and Imboden, 1990) uses a specific time-dependent term to describe photodamage and also incorporates a hysteresis in the photosynthetic response such that photosynthesis has a time delay (induction period, cf. Harris and Piccinin, 1977) under increasing light but responds immediately to decreasing light. Both models recreate most aspects of the single data set from which they were derived: that of Marra (1978b). Both of these models are also capable of reproducing some behaviour independent of this single data set, specifically the afternoon depression of photosynthesis known from algal cultures (Neale and Marra, 1985), larger systems such as high rate oxidation ponds (Schanz and Dubinsky, 1988) and from some *in situ* production incubations in lakes (Harris, 1980).

Although these latter models address the medium- (Denman and Marra, 1986) and also short- (<10 min; Pahl-Wostl and Imboden, 1990) term photosynthetic responses, neither model accounts for the slow increase in P_{max} at low PFD seen in Marra's (1978b) data and neither one models short term changes in α that are independent of P_{max}. Further, neither model specifically addresses the dynamic response of algal respiration (indicated by EPIR), despite their ability to generate a hysteresis of photosynthesis under seqentially increasing and then decreasing light.

For those authors who have addressed the question of integrated primary production under conditions where phytoplankton adapt their photosynthetic response to changed irradiance there are, as for the field studies, equivocal results. Farmer and Takahashi (1982) concluded that photodamage could significantly affect the daily average of gross photosynthesis integrated over the mixed layer and also the compensation depth (depth at which gross photosynthesis and respiration are balanced;

net photosynthesis = 0). Similarly, Denman and Marra's (1986) model reproduced the depressed P_{max} measured in unialgal cultures subject to high PFD for a prolonged period. Liou and van Eybergen (1982) considered that quite long-term adaptation (10–14 h) could be significant, especially when relatively deep mixing allowed algal cells to adapt to low light in between exposures to damaging PFD. In contrast, Falkowski and Wirick (1981) suggested that variations in light regimes due to turbulence would have negligible influence on the integrated water column primary production in the mixed layer.

Denman and Marra (1986) pointed out that adaptation of microalgae to light changes caused by their position on internal waves was of potentially greater importance than adaptation to displacement by turbulence. Several papers have since considered this possibility. Fahnenstiel et al. (1988) modelled the effect of internal waves on the subthermocline phytoplankton population in Lake Michigan by combining field measurements of production with numerical estimates of the light variation caused by internal waves. They found no significant difference between production estimated for static and oscillating microalgae when the amplitudes of the internal waves were typical of those measured in the lake. Only when wave amplitudes exceeded five metres was there any significant enhancement of production in the oscillating population; this effect was largest at the greatest depth (50 m). These authors did, however, make the general observation that oscillating communities always receive more light than a community held at the mean depth of that oscillation. Lande and Yentsch (1988) expressed this effect in relation to a deepening of the compensation depth and concluded from their model that primary production in the lower euphotic zone of eutrophic marine waters may have been significantly underestimated, though less so if the whole water column production was considered. Similarly, Holloway and Denman (1989) calculated that internal waves deepened the compensation depth in the open ocean but noted a depth dependence such that, above a certain depth, mean production would be depressed by internal wave motion.

Most of these models have used very simple schemes of water motion, usually symmetric representation of Langmuir circulation or diffusive approximations of turbulent flow. However, Woods and Onken (1982) present a more sophisticated "Lagrangian-ensemble" model of the water movement and associated light change. This model follows the movement of single phytoplankters in the mixed layer, calculating statistics for the whole population on the basis of the many individual paths. However, Lande and Lewis (1989) conclude that the simpler bulk-property models are as accurate, at least for the defined physical circumstances they modelled.

The photosynthetic response models fail to account for potentially important aspects of phytoplankton adaptation to changed PFD, e.g. the dynamic change of respiration. It is generally also true that these models are based on very few experimental data: two of them on a single data set for one species of marine diatom (cf. also Patterson, this volume). There is a clear need to expand the range of species for which dynamic responses to changed PFD are measured in the laboratory and in the field, and especially to include some freshwater microalgae.

Conclusions

Commonly used methods of measuring primary production do not resolve the very rapid responses of microalgae to changing light. The overlap of these timescales with those of turbulent and organized motions in the mixed layer of lakes and the ocean indicates the likelihood of significant interaction between these factors affecting estimates of primary production. The inconclusive results from both field and modelling approaches to this observation reflect weaknesses in the simple formulations used to describe photosynthesis in relation to irradiance, the simplicity of physical schemes used to generate changes in irradiance with time, and a lack of data (field and laboratory) on dynamic responses of microalgae to changing light. It is also undoubtedly the case that the quantitative significance of many physiological mechanisms (Table 2 and 3) is not known in relation to their effect on photosynthesis; this needs to be addressed both in the laboratory and in the field.

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REFERENCES

Algarra, P. and F. X. Niell, 1990. Short-term pigment responses of *Corallina elongata* Ellis et Solander to light intensity. Aquatic Botany 36:127–138.

Anderson, J. M. and J. Barrett, 1986. Light-harvesting pigment-protein complexes of algae. In: Encyclopedia of Plant Physiology, new series. L. A. Staehelin and C. J. Arntzen (eds), Springer-Verlag, Berlin: Photosynthesis III. Photosynthetic Membranes and Light Harvesting Systems, pp. 269–285.

Andréasson, L-E. and T. Vänngård, 1988. Electron transport in photosystems I and II. Ann. Rev. Plant Physiol. Plant Mol. Biol. 39:379–411.

Badger, M. R., 1985. Photosynthetic oxygen exchange. Ann. Rev. Plant Physiol. 36:27–53.

Baker, N. R. and A. N. Webber, 1987. Interactions between photosystems. Adv. Bot. Res. 13:1–66.

Banse, K., 1976. Rates of grwoth, respiration and photosynthesis of unicellular algae as related to cell size – a review. J. Phycol. 12:135–140.

Beardall, J., 1989. Photosynthesis and photorespiration in marine phytoplankton. Aquatic Botany 34:105–130.

Beardall, J. and I. Morris, 1976. The concept of light intensity adaptation in marine phytoplankton: some experiments with *Phaeodactylum tricornutum*. Mar. Biol. 37:377–387.

Beardall, J. and J. A. Raven, 1990. Pathways and mechanisms of respiration in microalgae. marine Microbial Food Webs 4:7–30.

Belay, A., 1981. An experimental investigation of inhibition of phytoplankton photosynthesis at lake surfaces. New Phytol. 89:61–74.

Brightman, R. I. and W. O. Smith Jr, 1989. Photosynthesis-irradiance relationships of antarctic phytoplankton during austral winter. Mar. Ecol. Prog. Ser. 53:143–151.

Buranathanitt, T., D. J. Cockrell and P. H. John, 1982. Some effects of Langmuir circulation on the quality of water resource systems. Ecol. Modelling 15:49–74.

Critchley, C., 1988. The molecular mechanism of photoinhibition – facts and fiction. Aust. J. Plant Physiol. 15:27–41.

Cullen, J. J. and M. R. Lewis, 1988. The kinetics of algal photoadaptation in the context of vertical mixing. J. Plankton Res. 10:1039–1063.
Culver, M. E. and W. O. Smith Jr, 1989. Effects of environmental variation on sinking rates of marine phytoplankton. J. Phycol. 25:262–270.
Cunningham Jr, F. X., R. J. Dennenberg, L. Mustardy, P. A. Jursinic and E. Gantt, 1989. Stoichiometry of photosystem I, photosystem II, and phycobilisomes in the red alga *Porphyridium cruentum* as a function of growth irradiance. Plant Physiol. 91:1179–1187.
Denman, K. L. and A. E. Gargett, 1983. Time and space scales of vertical mixing in the upper ocean. Limnol. Oceanogr. 28:801–815.
Denman, K. L. and J. Marra, 1986. Modelling the time-dependent photoadaptation of phytoplankton to fluctuating light. Elsevier Oceanogr. Ser. 42:341–360.
Fahnenstiel, G. L., D. Scavia, G. A. Lang, J. H. Saylor, G. S. Miller and D. J. Schwab, 1988. Impact of inertial period internal waves on fixed-depth primary production estimates. J. Plankton Res. 10:77–87.
Farmer, D. M. and M. Takahashi, 1982. Effects of vertical mixing on photosynthetic responses. Jap. J. Limnol. 43:173–181.
Farquhar, G. D. and S. von Caemmerer, 1982. modelling of photosynthetic response to environmental conditions. In: Encyclopedia of Plant Physiology, new series. O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler (eds), Springer-Verlag, Berlin: Physiological Plant Ecology II. Water Relations and Carbon Assimilation, pp. 549–587.
Falkowski, P. G., 1980. Light-shade adaptation in marine phytoplankton. In: P. G. Falkowski (ed.), Plenum, New York: Primary productivity in the sea, pp. 99–119.
Falkowski, P. G., 1984. Physiological responses of phytoplankton to natural light regimes. J. Plankton Res. 6:295–307.
Falkowski, P. G. and T. G. Owens, 1978. Effects of light intensity on photosynthesis and dark respiration in six species of marine phytoplankton. Mar. Biol. 45:289–295.
Falkowski, P. G. and T. G. Owens, 1980. Light-shade adaptation: two strategies in marine phytoplankton. Plant Physiol. 66:592–595.
Falkowski, P. G. and C. D. Wirick, 1981. A simulation model of the effects of vertical mixing on primary productivity. Mar. Biol. 65:69–75.
Falkowski, P. G., Z. Dubinsky and K. Wyman, 1985. Growth-irradiance relationships in phytoplankton. Limnol. Oceanogr. 30:311–321.
Fork, D. C. and K. Satoh, 1986. The control by state transitions of the distribution of excitation energy in photosynthesis. Ann. Rev. Plant Physiol. 37:335–361.
Gallegos, C. L. and T. Platt, 1982. Phytoplankton production and water motion in surface mixed layers. Deep Sea Res. 29:65–76.
Gallegos, C. L. and T. Platt, 1985. Vertical advection of phytoplankton and productivity estimates: a dimensional analysis. Mar. Ecol. Prog. Ser. 26:125–134.
Gallegos, C. L., T. Platt, W. G. Harrison and B. Irwin, 1983. Photosynthetic parameters of arctic marine phytoplankton: vertical variations and time scales of adaptation. Limnol. Oceanogr. 28:698–708.
Glazer, A. N. and A. Melis, 1987. Photochemical reaction centers: structure, organization, and function. Ann. Rev. Plant Physiol. 38:11–45.
Greer, D. H., J. A. Berry and O. Björkman, 1986. Photoinhibition of photosynthesis in intact bean leaves: role of light and temperature, and requirement for chloroplast-protein synthesis during recovery. Planta (Berl.) 168:253–260.
Grobbelaar, J. U., 1989. Do light/dark cycles of medium frequency enhance phytoplankton productivity? J. Appl. Phycol. 1:333–340.
Halliwell, B., 1984. Oxygen-derived species and herbicide action. What's New Plant Physiol. 15:21–24.
Harris, G. P., 1973. Diel and annual cycles of net plankton photosynthesis in Lake Ontario. J. Fish. Res. Board Can. 30:1779–1787.
Harris, G. P., 1978. Photosynthesis, productivity and growth: the physiological ecology of phytoplankton. Arch. Hydrobiol. Beih. Ergebn. Limnol. 10:1–171.
Harris, G. P., 1980. The measurement of photosynthesis in natural populations of phytoplankton. In: I. Morris (ed.), Blackwell Scientific Publications, Oxford: The physiological ecology of phytoplankton, pp. 129–187.

Harris, G. P., 1986. Phytoplankton ecology: structure, function and fluctuation. Chapman and Hall Ltd.
Harris, G. P. and J. N. A. Lott, 1973. Light intensity and photosynthetic rates in phytoplankton. J. Fish. Res. Board Can. 30:1771–1778.
Harris, G. P. and B. B. Piccinin, 1977. Photosynthesis by natural phytoplankton populations. Arch. Hydrobiol. 80:405–457.
Haupt, W. and R. Scheuerlein, 1990. Chloroplast movement. Plant, Cell Env. 13:595–614.
Heaney, S. I. and C. Butterwick, 1985. Comparative mechanisms of algal movement in relation to phytoplankton production. In: M. A. Rankin (ed.), Contributions in Mar. Sci. Suppl. 27: Migration – mechanisms and adaptive significance, 21 pp.
Holloway, G. and K. Denman, 1989. Influence of internal waves on primary production. J. Plankton Res. 11:409–413.
Jassby, A. D. and T. Platt, 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. 21:540–547.
Jewson, D. H. and R. B. Wood, 1975. Some effects on integral photosynthesis of artificial circulation of phytoplankton through light gradients. Verh. Internat. Verein. Limnol. 19:1037–1044.
Joiris, C. and A. Bertels, 1985. Incubation under fluctuating light conditions provides values much closer to real in situ primary production. Bull. Mar. Sci. 37:620–625.
Jones, L. W. and B. Kok, 1966. Photoinhibition of chloroplast reactions. Plant Physiol. 41:1037–1043.
Kiefer, D. A., 1973. Chlorophyll a fluorescence in marine centric diatoms: responses of chloroplasts to light and nutrient stress. Mar. Biol. 23:39–46.
Kirk, J. T. O., 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University press, Cambridge, 401 pp.
Kohata, K. and M. Watanabe, 1989. Diel changes in the composition of photosynthetic pigments and cellular carbon and nitrogen in *Pyramimonas parkeae* (Prasinophyceae). J. Phycol. 25:377–385.
Kyle, D. J. and I. Ohad, 1986. The mechanism of photoinhibition in higher plants and green algae. In: Encyclopedia of Plant Physiology, new series. L. A. Staehelin and C. J. Arntzen (eds), Springer-Verlag, Berlin: Photosynthesis III. Photosynthetic Membranes and Light Harvesting Systems, pp 468–476.
Lande, R. and M. R. Lewis, 1989. Models of photoadaptation and photosynthesis by algal cells in a turbulent mixed layer. Deep-Sea res. 36:1161–1175.
Lande, R. and C. S. Yentsch, 1988. Internal waves, primary production and the compensation depth of marine phytoplankton. J. Plankton Res. 10:565–571.
Langdon, C., 1987. On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. Pt I. A comparative study of μ-I relationship of three phytoplankton species: *Skeletonema costatum, Olisthodiscus luteus* and *Gonyaulax tamarensis*. J. Plankton Res. 9:459–482.
Larkum, A. W. D. and J. Barrett, 1983. Light-harvesting processes in algae. Adv. Bot. Res. 10:1–219.
Lechowski, Z. and J. Bialçzyk, 1987. Interaction between green and far-red light on the low fluence rate chloroplast orientation in Mougeotia. Plant Physiol. 85:581–584.
Le Fèvre, J., 1986. Aspects of the biology of frontal systems. Adv. Mar. Biol. 23:163–281.
Legendre, L. and S. Demers, 1984. Towards a dynamic biological oceanography and limnology. Can. J. Fish. Aquat. Sci. 41:2–19.
Lewis, M. R. and J. C. Smith, 1983. A small volume, short-incubation-time method for measurement of photosynthesis as a function of incident irradiance. Mar. Ecol. Prog. Ser. 13:99–102.
Lewis, M. R., J. J. Cullen and T. Platt, 1984. Relationships between vertical mixing and photoadaptation of phytoplankton: similarity criteria. Mar. Ecol. Prog. Ser. 15:141–149.
Liou, J. K. and G. C. van Eybergen, 1982. Light adaptation and -inhibition: processes important in modelling the growth of algae in drinking water basins. Water Res. 16:765–773.
Lorenzen, C. J., 1979. Ultraviolet radiation and phytoplankton photosynthesis. Limnol. Oceanogr. 24:1117–1120.
Marra, J., 1978a. Effect of short term variations in light intensities on photosynthesis of a marine phytoplankter: a laboratory simulation study. Mar. Biol. 46:191–202.

Marra, J., 1978 b. Phytoplankton photosynthetic response to vertical movement in a mixed layer. Mar. Biol. 46:203–208.
Michel, C., L. Legendre, S. Demers and J-C. Therriault, 1988. Photoadaptation of sea-ice microalgae in springtime: photosynthesis and carboxylating enzymes. Mar. Ecol. Prog. Ser. 50:177–185.
Neale, P. J., 1987. Algal photoinhibition and photosynthesis in the aquatic environment. In: D. J. Kyle, C. B. Osmond and C. J. Arntzen (eds), Topics in photosynthesis 9, Elsevier, Amsterdam: Photoinhibition, pp. 39–65.
Neale, P. J. and J. Marra, 1985. Short term variation in P_{max} under natural irradiance conditions: a model and it's implications. Mar. Ecol. Prog. Ser. 26:113–124.
Nultsch, W. and J. Pfau, 1979. Occurrence and biological role of light-induced chromatophore displacements in seaweeds. Mar. Biol. 51:77–82.
Nultsch, W., J. Pfau and U. Rüffer, 1981. Do correlations exist between chromatophore arrangement and photosynthetic activity in seaweeds? Mar. Biol. 62:111–117.
Pahl-Wostl, C. and D. M. Imboden, 1990. DYPHORA – a dynamic model for the rate of photosynthesis of algae. J. Plankton Res. 12:1207–1221.
Patterson, J. C., 1991. Modelling effects of motion on primary production in the mixed layer of lakes. Aquatic Sciences (in press, this volume).
Peterson, B. J., 1980. Aquatic primary productivity and the ^{14}C-CO_2 Method: a history of the productivity problem. Ann. Rev. Ecol. Syst. 11:359–385.
Pick, U., K. Gounaris and J. Barber, 1987. Dynamics of photosystem II and its light-harvesting system in response to light changes in the halotolerant alga *Dunaliella salina*. Plant Physiol. 85:194–198.
Platt, T. and C. L. Gallegos, 1980. Modelling primary production. Brookhaven Symposia in Biology 31:339–362.
Powles, S. B., 1984. Photoinhibition of photosynthesis induced by visible light. Ann. Rev. Plant Physiol. 35:15–44.
Post, A. F., Z. Dubinsky, K. Wyman and P. G. Falkowski, 1984. Kinetics of light-intensity adaptation in a marine planktonic diatom. Mar. Biol. 83:231–238.
Prézelin, B. B. and H. A. Matlick, 1980. Time course of photoadaptation in a photosynthesis-irradiance relationship of a dinoflagellate exhibiting photosynthetic periodicity. Mar. Biol. 58:85–96.
Prézelin, B. B., M. M. Tilzer, O. Schofield and C. Haese, 1991. The control of the production process of phytoplankton by the physical structure of the aquatic environment. Aquatic Sciences 53:136–186.
Randall, J. M. and J. W. Day Jr, 1987. Effects of river discharge and vertical circulation on aquatic primary production in a turbid Louisiana (USA) estuary. Neth. J. Sea Res. 21:231–242.
Raven, J. A., 1984. Energetics and transport in aquatic plants. MBL lectures in biology. Alan R. Liss, New York, 587 pp.
Raven, J. A., 1989. Fight or flight: the economics of repair and avoidance of photoinhibition of photosynthesis. Functional Ecology 3:5–19.
Reynolds, C. S., R. L. Oliver and A. Walsby, 1987. Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. In: W. F. Vincent (ed.), N. Z. J. Mar. Freshw. Res. 21: Dominance of Bloom-forming Cyanobacteria (Bluegreen Algae), pp. 379–390.
Richardson, K., J. Beardall and J. A. Raven, 1983. Adaptation of unicellular algae to irradiance: an analysis of stategies. New Phytol. 93:157–191.
Rivkin, R. B., H. H. Seliger, E. Swift and W. H. Biggley, 1982. Light-shade adaptation by the oceanic dinoflagellates *Pyrocystis notiluca* and *P. fusiformis*. Mar. Biol. 68:181–191.
Savidge, G., 1988. Influence of inter- and intra-daily light-field variability on photosynthesis by coastal phytoplankton. Mar. Biol. 100:127–133.
Schanz, F. and Z. Dubinsky, 1988. The afternoon depression in primary productivity in a high rate oxidation pond (HROP). J. Plankton. Res. 10:373–383.
Spalding, M. H., 1989. Photosynthesis and photorespiration in freshwater green algae. Aquatic Botany 34:181–209.
Spigel, R. H. and J. Imberger, 1987. Mixing processes relevant to phytoplankton dynamics in lakes. In: W. F. Vincent (ed.), N. Z. J. Mar. Freshw. Res. 21: Dominance of Bloom-forming Cyanobacteria (Blue-green Algae), pp. 361–377.

Stone, S. J. L. and G. G. Ganf, 1981. The influence of previous light history on the respiration of four species of freshwater phytoplankton. Arch. Hydrobil. 91:435–462.
Takahashi, M., S. Shimura, Y. Yamaguchi and Y. Fujita, 1971. Photoinhibition of phytoplankton photosynthesis as a function of exposure time. J. Oceanogr. Soc. Japan 27:43–49.
Talling, J. F., 1957. The phytoplankton population as a compound photosynthetic system. New Phytol. 56:133–149.
Tett, P. and A. Edwards, 1984. Mixing and plankton: an interdisciplinary theme in oceanography. Oceanogr. Mar. Biol. Ann. Rev. 22:99–123.
Thornley, J. H. M., 1976. Mathematical models in plant physiology. A quantitative approach to problems in plant and crop physiology. Academic Press, London, 318 pp.
Tilzer, M., 1987. Light-dependence of photosynthesis and growth in cyanobacteria: implications for their dominance in eutrophic lakes. In: W. F. Vincent (ed.), N.Z. J. Mar. Freshw. Res. 21: Dominance of Bloom-forming Cyanobacteria (Blue-green Algae), pp. 401–412.
Tolbert, N. E., 1974. Photorespiration. In: W. D. P. Stewart (ed.), Bot. Monogr. 10: Algal Physiology and Biochemistry, pp. 474–504.
Walsh, P. and L. Legendre, 1983. Photosynthesis of natural phytoplankton under high frequency light fluctuations simulating those induced by sea surface waves. Limnol. Oceanogr. 28:688–697.
Walsh, P. and L. Legendre, 1988. Photosynthetic responses of the diatom *Phaeodactylum tricornutum* to high frequency light fluctuations simulating those induced by sea surface waves. J. Plankton Res. 10:1077–1082.
Weger, H. G., R. Herzig, P. Falkowski and D. H. Turpin, 1989. Respiratory losses in the light in a marine diatom: measurements by short-term mass spectrometry. Limnol. Oceanogr. 34:1153–1161.
Winter, K. and B. Demmig, 1987. Reduction state of Q and nonradiative energy dissipation during photosynthesis in leaves of a crassulacean acid metabolism plant, *Kalanchoë daigremontiana* Hamet et Perr. Plant Physiol. 85:1000–1007.
Woods, J. P. and R. Onken, 1982. Diurnal variation and primary production in the ocean preliminary results of a Lagrangian ensemble model. J. Plankton Res. 4, 22 pp.
Yentsch, C. S., 1980. Light attenuation and phytoplankton photosynthesis. In: I. Morris (ed.), Blackwell Scientific Publ., Oxford: The physiological ecology of phytoplankton, pp. 95–127.
Yoder, J. A. and S. S. Bishop, 1985. Effects of mixing induced irradiance fluctuations on photosynthesis of natural assemblages of coastal phytoplankton. Mar. Biol. 90:87–93.
Zimmerman, R. C., J. Beeler SooHoo, J. N. Kremer and D. Z. D'Argenio, 1987. Evaluation of variance approximation techniques for non-linear photosynthesis-irradiance models. Mar. Biol. 95:209–215.

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