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Plenary Lectures

The dynamic coupling between photosynthesis and light in the phytoplankton environment

W. F. Vincent

Introduction

Lake ecosystems are driven by an energy supply that varies over the widest spectrum of timescales. The trophic processes of a lake ultimately depend upon the efficiency of the first step, the harvesting and conversion of sunlight into high energy chemical intermediates. Photosynthesis is the major coupling point between the lacustrine food web and its surrounding energy field, but that coupling must be extremely flexible. At one scale successional patterns in phytoplankton community structure can be viewed as an adjustment of the light harvesting system of a lake to seasonal changes in its environment. But there are periodic as well as irregular fluctuations in energy supply that must be adjusted to at longer and also much shorter timescales.

In recent years there has been a shift of focus toward the short-term dynamics of photosynthesis, stimulated in part by rapid advances in plant molecular biology especially in relation to the processes of energy capture and conversion. Of special relevance to limnology, this molecular research is revealing a cascade of mechanisms whereby the algal cell is able to tune its photosynthetic apparatus to the spectrum of variations which characterise the underwater light environment.

Scales of variation in energy supply

Substantial variations in photosynthesis from one year to another are often superimposed upon any long term trends such as eutrophication. This year-to-year variability can be initiated by meteorological factors especially at critical times in the successional or mixing cycle. For example, at Lake Tahoe (California-Nevada), GOLDMAN, JASSBY & POWELL (1989) have recently shown that the total annual production may be highly sensitive to local weather events over a period of less than one month when the water column is near isothermal. The depth of mixing during this brief window in time affects the entrainment of 'new' nutrients into the euphotic zone where there is an adequate light supply and where they can then be used for photosynthetic production. In Lake Tahoe there is a strong cross-correlation between annual photosynthesis and the maximum depth of mixing in spring.

This critical period of less than one month in Lake Tahoe is short relative to broader scale, synoptic weather patterns, such as those associated with the El Niño/Southern Oscillation cycle. The same authors have shown that this longer term meteorological forcing plays a role in the inter-annual variability of photosynthesis in Castle Lake. This effect may operate in part through the thickness and duration of winter snow and ice-cover. In ice-covered lakes in general the very high reflectivity of snow and certain types of ice coupled with the low solar angle in winter (alpine lakes) or throughout the year (polar lakes) make their underwater light field highly dependent on snowfall and the timing and extent of freezing and melting. Photosynthesis in ice-covered antarctic lakes, for example, may be especially sensitive to these interannual climate effects.

In the polar zones the annual radiation cycle from complete winter darkness to continuous light during summer, forces an extreme seasonality on phytoplankton photosynthesis. This relationship tends to be very poor for many tropical lakes (e.g. VINCENT et al. 1986), but in the temperate zone there is often a strong correlation between photosynthesis and light. For example, at Lake Constance the data presented in TILZER & BEESE (1988) give a close positive correlation between monthly photosynthesis and monthly irradiance ($r = +0.83$, $df = 10$, $p < 0.001$).

This correlation between means raises an important question. Are the phytoplankton simply adapting to average irradiance at these longer timescales, or is the community resolving and tuning itself to the energy supply entering the lake at a finer scale? At Lake Constance, for example, the mean monthly irradiance totals vary six-fold over the year but day-to-day differences up to a factor of ten can be recorded within certain

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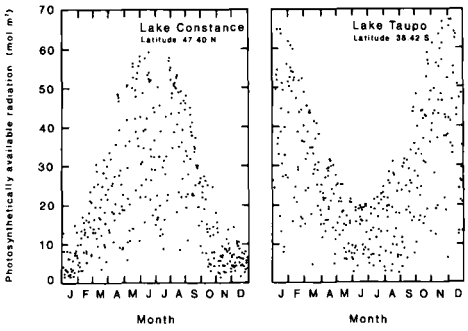

Fig. 1. Daily totals of radiation at Lake Constance and Lake Taupo during 1980. The Lake Constance data are reproduced courtesy of Prof. M. M. TILZER. The Lake Taupo data are for the central North Island, from VINCENT & DRYDEN (1989).

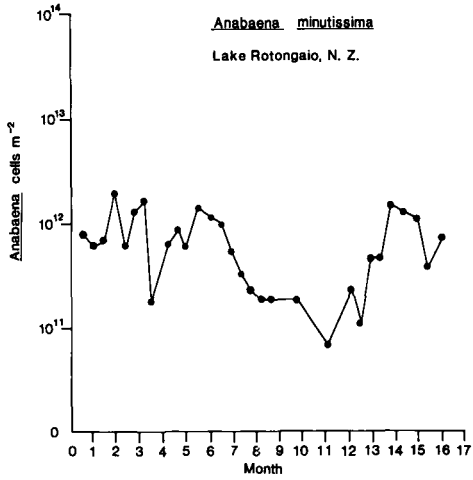

Fig. 2. Constancy of a cyanobacterial population in Lake Rotongaio, central North Island, New Zealand. The data have been replotted from VINER & KEMP (1983).

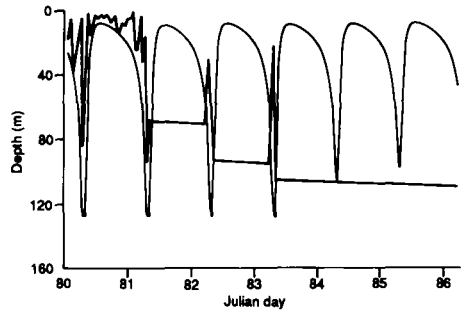

Fig. 3. The trajectory of an individual algal cell as it circulates through the diurnal mixed layer (bounded by the cyclic curve). At day 83 the cell sedimented below the zone of mixing. The energy status and productivity of a population of cells was tracked using this Lagrangian ensemble model. Redrawn from WOLF & WOODS (1988).

months (Fig. 1). At Lake Taupo, New Zealand, the mean monthly solar radiation varies by a factor of 3, but again differences can occur at an order of magnitude level between days (Fig. 1).

Although the solar energy incident on a lake surface is highly variable from day-to-day, average growth rates can be maintained at a seemingly constant value for prolonged periods, or a relative constant biomass can be maintained over periods of time. For example, during 17 months which included the year in Fig. 1, in a small lake adjacent to Lake Taupo, Lake Rotongaio, the populations of the blue-green alga *Anabaena minutissima* remained within an order of magnitude (Fig. 2). At what timescale is this organism perceiving and adapting to changes in the underwater light field? A series of photosynthetic assays over the course of several days suggested that this phytoplankton species was tracking relatively short-term variations in its environment (VINER 1989 b). Similarly, *Microcystis aeruginosa* in several lake environments is capable of maintaining its population size despite major seasonal, day-to-day and shorter-term variations in the environment but with considerable variations in its photosynthetic properties (e.g. ZOHARY & ROBARTS 1989). In Esthwaite Water in the English Lake District, the dinoflagellate *Ceratium hirundinella* maintains near-constant growth rates (HEANEY & TALLING 1981) during greatly changing irradiance conditions that can only partly be damped by its motility in the water column.

At the level of the individual algal cell the fastest and most severe variations in solar energy supply may be experienced during wind-induced mixing through the water column. Lagrangian simulation models have provided an approach towards describing the fluctuations in energy supply perceived by a phytoplankton cell as it is transported through the mixed layer (Fig. 3). Day-to-day variations in the mixing regime will further affect the average light intensity for the population, as well as the frequency of exposure to high and low light extremes. For example during the 2-week period of photosynthetic measurements by VINER

(1989 b) in Lake Rotongaio, IMBERGER & SPIGEL (1987) showed that there were considerable variations in the thermal structure and mixing dynamics of the lake from one day to another. These variations would affect the average light intensity experienced by the phytoplankton, as well as their frequency of exposure to high and low light extremes.

The photosynthetic membrane

To what extent can the phytoplankton adjust and optimise their efficiency in the face of this spectrum of variations in energy supply experienced within a lake? Physiologically it appears that much of this photo-adjustment takes place at the level of energy capture, and also to a lesser extent during the conversion of solar to chemical energy. These primary reactions of photosynthesis have been the subject of intense research over the last few years, and attention has focused in particular on the remarkable protein complexes located on the thylakoid membrane (Fig. 4). There are four classes of protein, each of is interconnected to the others via the transfer of some form of energy (STEINBACK et al. 1985):

(i) Light-harvesting pigment proteins. These bind the algal pigments in defined orientations to ensure the efficient transfer of the absorbed solar energy (known as excitation energy) to photosynthetic reaction centres. Some of these pigment proteins are inserted inside the membrane – for example light harvesting chlorophyll *a* and *b* proteins, and the proteins that bind fucoxanthin in diatoms or peridinin in dinoflagellates – while others are extrinsic to the photosynthetic membrane, such as the phycobilin pigments of cyanobacteria.

(ii) Reaction centre proteins. These specialised polypeptides create the chemical environment in which the water molecule can be split into oxygen and protons, and a charge separation accomplished and stabilised. This charge separation, that is the formation of an electrochemical potential, is the fundamental light reaction process. It takes place in two reaction centres which operate in series, photosystem II (PS II) where water is the primary electron donor, and photosystem I (PS I) which receives electrons from PS II.

(iii) Electron transfer proteins. These are the apoproteins that bind the co-factors such as hemes, quinones and iron-sulphur centres which shuttle electrons along the membrane between the two photosystems, and which transport protons across the membrane generating a potential that is then available to drive energy synthesis. One electron transport carrier, plastoquinone, remains dissolved in the lipid phase of the membrane, unassociated with the protein complexes. This plastoquinone pool plays an important regulatory role in the underwater light environment.

(iv) ATP-generating proteins. These polypeptides form the so-called coupling factors (the CF_1 and CF_0 complex) which utilize the proton gradient to drive ATP synthesis. The ATP generated by these proteins, coupled with the NADPH produced by the photosystem complexes together provide the energy and reducing power to fix carbon dioxide into the sugar intermediates required for phytoplankton growth.

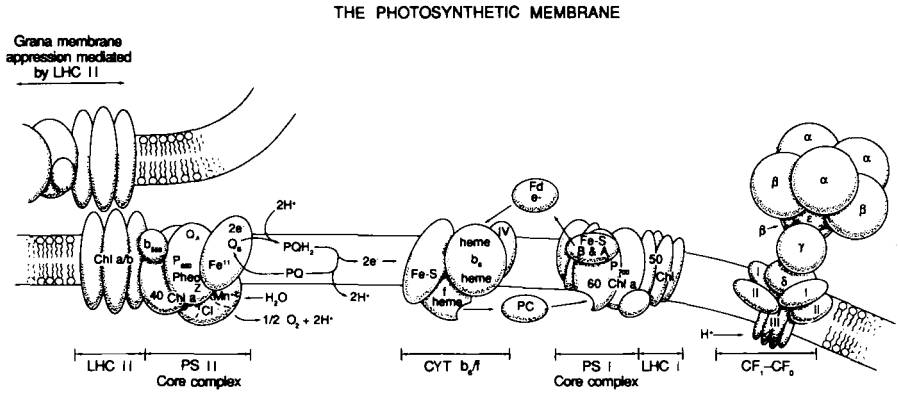

Fig. 4. The major protein complexes and reactions associated with the photosynthetic membrane. Redrawn from STEINBACK et al. (1985). LHC = light harvesting complex; PQ = plastoquinone; PC = plastocyanin.

The light harvesting complex

A major theme that has emerged from the last decade of photophysiological research is the great flexibility of this apparatus in response to changes in the environment. This flexibility is manifested through the full spectrum of time scales.

The light harvesting complexes come in a wide assortment of molecular forms and spectral capabilities (Table 1). Phytoplankton succession provides one of the most graphic examples of photo-adjustment at a community level, involving species-related shifts in the light harvesting pigment-proteins in response to changes in the lake environment.

The efficiency of light harvesting by these pigment-protein complexes dictates the areal absorption coefficient of the cell, usually normalised to Chl*a* and referred to as k_c. The efficiency of coupling between the light energy absorbed and the production of chemical potential energy is the quantum yield, Φ_c. For a range of diatoms, dinoflagellates, chrysophytes and chlorophytes, k_c has been found to average 0.0075 m^2 (mg Chl*a*)$^{-1}$, while Φ_c averaged 0.064 mol C · (mol · photons)$^{-1}$, with both parameters varying by about a factor of three between species (Langdon 1988). The product $k_c \Phi_c$ is equivalent to α, the photosynthetic efficiency in P versus I formulations. Phytoplankton in culture typically have α values around 0.02 to 0.03 mg C (mg Chl*a*)$^{-1}$ (μmol photons $m^{-2} \cdot s^{-1}$)$^{-1}$ but cyanobacteria specifically the phycoerythrin-rich picoplankton, have an unusually high α, up to 0.13 (Langdon 1988).

Cyanobacteria or blue-green algae have a light capturing system especially adept at functioning under the unusual spectral conditions that operate inside a bloom. For example, in Lake Rotongaio, New Zealand, the spectral distribution in a bloom of *Anabaena* varied greatly (Walsby et al. 1989) over the 1 m-deep mixed layer revealed by the physical measurements (Imberger & Spigel 1987). The spectral absorption capability of cyanobacteria is suggested by the wide range of distinctive colours of their photosystem II light harvesting pigments, the phycobiliproteins. These colours depend upon the specific tetrapyrrole or bilin group which is attached covalently to the polypeptide chain. Yet the enormous differences in absorbance maxima, from 495 nm for phycourobilin to 620 nm for phycocyanobilin are simply dictated by the arrangement of double bonds; despite the chromatic diversity all of the tetrapyrrole groups are isomers. These bilins are then further tuned to their environment by the larger proteins that surround them, and their organisation into functional units, the phycobilisomes. The α and β proteins carrying the bilins modify their absorbance maxima (λ_{max}); for example, both C-phycocyanin and allophycocyanin carry phycocyanobilin groups, but the former has λ_{max} at 620 nm, the latter at 650 nm. The aggregation of the $\alpha\beta$ complexes further affects their properties; for example the monomeric form of allophycocyanin has λ_{max} at 615 nm, whereas the trimeric form $(\alpha\beta)_3$ has a λ_{max} at 650 nm (Glazer 1989).

Inside the phycobilisome the proteins are arranged in a series of rods and discs in such a way that the fluorescence properties of one unit are directly coupled to the absorbance properties of the next. The phycobiliproteins with the shortest λ_{max} are located at the outside of the complex. (e.g. 495 nm for PUB phycoerythin in the outer rod region) and those with the longest λ_{max} are located internally (670 nm for terminal acceptor bilins at the core), ultimately coupling into the photosystem II reaction centre (λ_{max} = 680 nm). Light can be absorbed by any part of this spectrally broad system, but the molecular arrangement of acceptors and donors ensures that the captured solar energy is transferred in one direction with high efficiency (> 95 %) from the rods to the core complex and thence to the photosystem II reaction centre (Glazer 1989).

Table 1. Peripheral light-harvesting pigment-protein complexes isolated from some phytoplankton classes, from Owens (1988). MW = molecular weight.

Phytoplankton class	Pigment	Apoprotein polypeptides	
		Number	MW (kDa)
Chlorophyceae	Chl *a*/*b*-lutein		
Prymnesiophyceae	Chl *a*/*c*-fucoxanthin	1	21
Bacillariophyceae	Chl *a*/*c*-fucoxanthin	2 – 3	18 – 20
	Chl *a*/*c*	2	18 – 20
Eustigmatophyceae	Chl *a*/*c*-violaxanthin	1	20 – 22
Dinophyceae	Chl *a*-peridinin	–	19 – 49
	Chl *a*/*c*	–	19 – 24
Cryptophyceae	Phycobiliproteins Chl *a*/*c*	3	18 – 22
Cyanobacteria	Phycobiliproteins Chl *a*		

Sun-shade adaptation

It is well known that low light typically results in an increase in cellular chlorophyll *a*, accompanied by a decrease in maximum photosynthesis per unit chlorophyll. Most recent evidence indicates that these changes are brought about not only by variations in the total concentration of light

harvesting protein complexes at PS I and PS II (or the number and stoichiometry of reaction centre-light harvesting complexes, e.g. FRIEDMAN & ALBERTE 1986, NEALE & MELIS 1986), but also by the differential accumulation of complexes with distinct pigment compositions.

When the green algal flagellate *Dunaliella tertiolecta* is transferred from high light to low light there is an increase in the amount of chlorophyll *a* and the number of reaction centres per cell (SUKENIK et al. 1987). The total number of chl*a* molecules serving each reaction centre remains relatively constant, but the number of chl*b* molecules increases by a factor of 2–3. It appears that the different light-harvesting protein complexes have different complements of the two pigments. Low light selects for light harvesting apoproteins at photosystem II with a high Chl*b* content (average of 5 Chl*a*, 2 Chl*b* and 2 lutein). The transfer of excitation energy by Chl*b* to Chl*a* is higher than from lutein to Chl*a* and the Chl*b* enriched complex is therefore an advantage under low light conditions. At high light intensities the lutein is likely to function as a protective screen for the reaction centres against photo-oxidative damage.

The increase in the carotenoid content of the light-harvesting complex may be especially important in brightly lit environments. PAERL et al. (1983) have shown the differential accumulation of the carotenoid pigments zeaxanthin and myxoxanthophyll in bloom-forming cyanobacteria which may reduce the damaging effects of bright light when they float near the surface. Zeaxanthin is known to be effective in higher plants in protecting the cell against photoinhibition (DEMMIG et al. 1987).

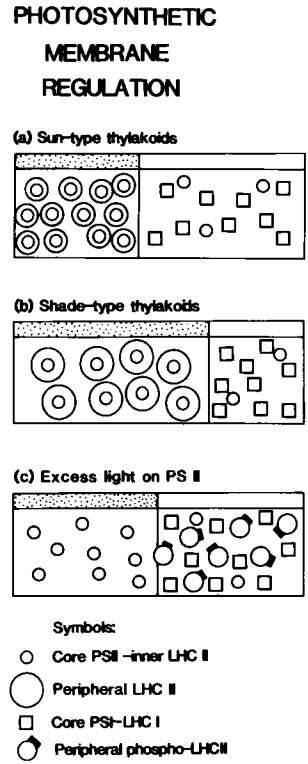

Fig. 5. Changes in the light harvesting complexes (LHC) on the photosynthetic membrane in response to variations in light. Prolonged high (a) or low (b) light result in a modification of LHC size. Under transient bright light (c) the LHC pigment-proteins detach from the photosystem II reaction centre cores and migrate to the non-appressed part of the membrane. Modified from ANDERSON & ANDERSSON (1988).

Short-term photoadaptation

The biosynthetic processes associated with sun-shade adaptation allow the phytoplankton community to adjust to mean irradiances over a timescale of hours to days, but for an algal cell circulating through the mixed layer of a lake, or exposed to changing cloud conditions, a more urgent photoadaptive response is required. It is now known that the protein complexes on the thylakoid membrane can respond very rapidly to this sort of natural variation.

Firstly, the chloroplast is capable of rapidly (seconds to minutes) changing its shape and position in the cell (e.g. HARRIS & PICCININ 1977). The exact implications of these movements in terms of quantitative changes in k_e still remain poorly known.

Secondly, the light-capturing system can be rapidly re-configured (Fig. 5). Too much light sets off a train of events that reduces the flow of energy to reaction centres, while preserving the ability to efficiently harvest light at low irradiance (STAEHELIN & ARNTZEN 1983, ANDERSON & ANDERSSON 1988). Bright light results in the over production of the plastoquinone pool which links the two photosystems. This activates a membrane-bound kinase which phosphorylates the proteins on the outside of the light harvesting complex attached to the photosystem II reaction centres. This in turn results in a net increase in repulsive charges which forces the light harvesting proteins to dissociate. The increase in charge also loosens the thylakoid

membranes which allow the light harvesting complex units to migrate laterally into regions away from the photosystem II cores which remain behind. The lipid bilayer of the membrane is very fluid and this migration of complexes requires only 20 s. This decoupling between light absorption and photochemistry is reversible: when the light stress is removed the peripheral light harvesting proteins are dephosphorylated which causes them to migrate back into the appressed thylakoid regions where they rejoin the photosystem II cores.

These phosphorylation responses (but also changes in the electric field around the thylakoid membrane, FORK & SATOH 1986) may play a major role in light state transitions whereby the phytoplankton cell rapidly changes its ability to redistribute excitation energy between the two photosystems. The light reactions of photosynthesis require the operation of photosystem I and photosystem II in series, and therefore to achieve maximum efficiency each of the photosystems must receive equal amounts of the captured energy. However, in the underwater environment, the greater portion of light harvesting by the phytoplankton is with the specialised accessory pigments in photosystem II. In green algae, for example, below 670 nm photosystem II absorbs more light than photosystem I, and at wavelengths longer than this photosystem I absorption becomes predominant. This unbalanced absorption is especially pronounced for cyanobacteria, in which photosystem II can absorb more than 80 % of the waveband 470–660 nm (SATOH & FORK 1986).

The required balance between the photosystems can be reestablished by the direct transfer of excitation energy from photosystem II to I (spillover), and/or by differential changes in the optical cross-section of photosystem I versus photosystem II. There are two major adaptational states, but in aquatic environments a vertical gradation from one to the other is likely to be encountered in the mixed layer. State I, the highly fluorescent state, results from over-excitation of PS I by far red light (green algae) or blue or red light (cyanobacteria). The absorption cross section of photosystem I is decreased and the spillover from photosystem II to I is retarded. In State II the absorption cross-section of photosystem I is increased, and/or spillover enhanced.

This process is important for phytoplankton circulating through a mixed layer, particularly in bloom environments where there are major changes in spectral composition over relatively short length scales. As the bloom develops, phytoplankton will be exposed to a narrow band of wavelengths (typically green) for longer periods of time during mixing. Cyanobacteria appear to be especially adept at matching their photosynthetic system to this sort of underwater light spectrum. POST et al. (1989) have shown that when a cyanobacterium was cultured under green light (560 nm) there was a large increase in the phycobilin content (a tenfold increase in phycoerythin relative to 630 nm light) accompanied by a small increase in Chl *a* (20 % relative to 630 nm). This chromatic response allowed the cells to maintain as high a photosynthetic efficiency (α) at 560 nm as at 630 nm or 680 nm. The phycobilins are entirely associated with the light harvesting complex at photosystem II, while about 75 % of the Chl *a* in cyanobacteria is associated with that at photosystem I. This differential pigment adjustment thus resulted in a large absorption cross-section (σ) for photosystem II (σ_{II} = 36.1 nm^2) relative to photosystem I (σ_I = 0.9 nm^2). However, the species had a very large capacity for energy spillover and in State II could redistribute up to 48 % of the energy absorbed by the light harvesting complex at photosystem II to photosystem I. This capacity for spillover was greatly reduced in red-light grown cells (8 % spillover in State II), but under these growth conditions a much more balanced absorption cross-section of the two photosystem light harvesting complexes was achieved.

A novel form of short-term regulation of bright light effects has recently been reported by NEALE (1989) in *Chlamydomonas reinhardtii*. This green algal species (along with most other Chl*a/b* containing organisms) has a reserve pool of reaction centre-light harvesting complexes which is inactive under most irradiance conditions (referred to at PS II_β). Under bright light intensities, the PS II_β reserves are activated, and this partially offsets the photoinhibitory damage to the main functional pool of light-harvesting-photosystem II complexes PS II_α).

Measurement of photoadaptation in lakes

Many of these adaptational processes operate at photosystem II which at ambient temperatures is highly fluorescent. *In vivo* fluorescence has proved to be a valuable probe in measuring the energy capturing process in natural waters, but variations during the 'observational' time scale (NEALE et al. 1989) and the many sources of variation in

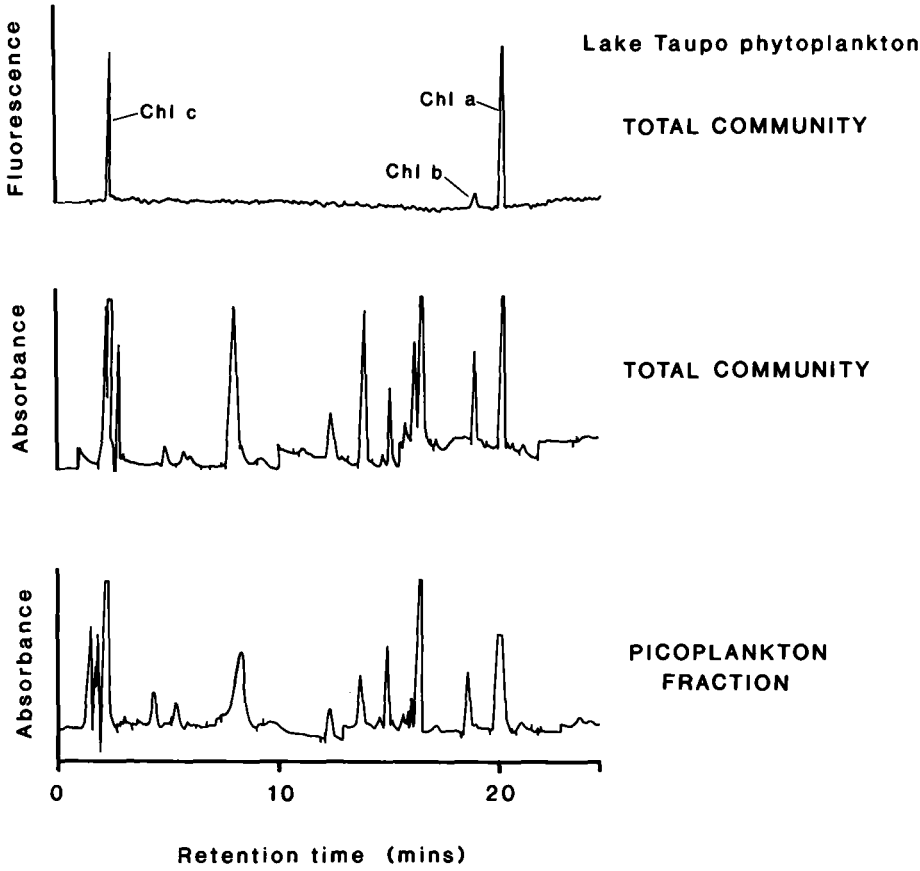

Fig. 6. The diversity of light harvesting pigments in the picoplankton as well as the total community of lakes is increasingly revealed by HPLC. These chromatograms are for near surface water from Lake Taupo, New Zealand, during the winter bloom (11 July 1989). Top: fluorescence chromatogram resolving the major chlorophyll peaks; middle, absorbance chromatogram for the whole community; bottom, absorbance chromatogram for the fraction which passed a 2 μm Nuclepore filter.

fluorescence (SIVAK & WALKER 1985, CULLEN et al. 1988) sometimes limits the usefulness of this parameter.

The fluorescence signal can be manipulated and measured in a variety of ways to generate different sorts of information about the phytoplankton community. For example, DCMU-induced fluorescence has been used as a measure of operational photosystem II reaction centres (e.g. NEALE et al. 1989), while fluorescence transients over the first 20 s of assay have been used to detect the short-term adaptational responses associated with the dynamics of the thylakoid membrane (e.g. VINCENT 1979). Field assays of *in vivo* fluorescence have been especially informative when coupled with detailed measurements of temperature structure and other hydrodynamic properties of the water column (e.g. VINER 1989 a).

Towards the longer end of the spectrum of timescales of photoadaptation, high performance liquid chromatography (HPLC) is playing an increasing role for the tracking of shifts in the light-harvesting pigments in natural waters. This technique is proving especially valuable for monitoring the successional changes in the picoplankton (Fig. 6), a phytoplankton group which for the most part lack morphological attributes that can be used for their identification.

Photoinhibition

If the strong light is above a certain threshold and it persists for long periods of time then the effects become increasingly serious. Any limnologist who has conducted an *in situ* bottle assay in a lake to measure oxygen production or ^{14}C-CO_2 fixation is familiar with the strong inhibitory effects of bright light at the surface. This process of photoinhibition is emerging to be the net effect of a complex balance between photo-protection, damage and repair with the primary site of damage at the photosystem II reaction centre.

The last half decade has seen a very rapid advance in knowledge about how the photosystem II reaction centre is organised and the associated water splitting process (Barber 1987). A coupled assemblage of proteins (D 1, D 2 and cytochrome b_{559}) spans the photosynthetic membrane and holds and stabilizes the various intermediates. The primary electron donor is P 680, believed to be a special pair of chl*a* molecules, and the primary electron acceptor is pheophytin located on the D 1 protein. Electrons are then transferred to two plastoquinone molecules Q_A and Q_B. On the oxidising side of P 680, a cluster of 4 manganese atoms is held by another protein (an extrinsic 33 kDa polypeptide), and these build up the necessary oxidising power by electron transfer to P 680, to catalyze the oxidation of 2 water molecules to one molecule of oxygen.

The primary charge separation within the reaction centre II complex can therefore be summarized as:

$$P680\ PheoQ_A + h\nu \rightarrow P680^*PheoQ_A \rightarrow P680^+Pheo^-Q_A \rightarrow P680^+PheoQ_A^- \cdot P680^+$$

is re-reduced to P 680 by electrons from H_2O, and Q_A^- passes its electron to Q_B, and ultimately to $NADP^+$ to be used in the dark reactions of photosynthesis.

Of the various candidates for the primary site of photoinhibition the most likely appears to be oxidised P 680, i.e. $P680^+$ (Cleland 1988, Demeter et al. 1987). However, the initial damage at this reaction centre ramifies through the whole complex and inactivates other components including the oxygen evolving system, the electron carriers and the D 1/D 2 proteins to which they are bound. The cell contends with this damage by rebuilding the reaction centres *de novo*, a slow (of order hours), biosynthetic recovery process. Enhanced rates of protein turnover have thus been reported during photoinhibition in a wide range of higher plants and algae (e.g. Samuelsson et al. 1987). In cultures of the cyanobacterium *Synechococcus* exposed to bright light, the synthesis of the D 1 protein alone during this photoinhibition repair process accounts for 10 % of the total protein synthesis in the cell (Raven & Samuelsson 1986). Algae exposed to high irradiances in the surface waters of lakes must therefore allocate a large proportion of their energetic and cellular reserves simply to keep pace with the damage incurred by photoinhibition.

How important is the photoinhibition process? Diel thermoclines are a common feature of lakes and act to trap cells at high light intensity for prolonged periods. This phenomenon may encourage photoinhibitory responses in a variety of environments (e.g. Neale & Richerson 1987). Although photoinhibition is restricted to the surface waters it may play a critical role in aspects of community succession, tipping the balance towards species that are less prone to these effects. For example, *Asterionella formosa* rises towards dominance in the spring diatom bloom of Lake Windermere under conditions of extreme light limitation. Application of *in vivo* fluorescence assays to this community revealed that during the latter stages of the spring maximum there was a loss of photosystem II function during days of sunny, calm weather. In addition to impaired photosynthesis, the photoinhibited cells had sinking rates 1.5 to 3.0 times faster than uninhibited cells. In Lake Windermere photoinhibition may accelerate the decline and replacement of the dominant species in the spring bloom by these combined effects on productivity and sedimentation (Neale et al. in prep).

Models of photosynthesis and adaptation

The rapid advance in knowledge of photosynthetic dynamics has accelerated the search for quantitative models to describe the processes of photosynthesis and photoadaptation. The models to date have varied greatly in their level of complexity and mechanistic detail.

A simple and conceptually reasonable expression of photoadaptive state has been formulated by Wolf & Woods (1988) in their Lagrangian ensemble model. A multiplicative photoadaptation parameter referred to here as Γ (standardising to the terminology of Cullen & Lewis 1988) is used to define the amount of light absorbed by an algal cell for photosynthesis (I_{abs}):

$$I_{abs} = k_c I(z, t) \Gamma \qquad (1)$$

where k_c is the effective absorption area of one cell, and irradiance varies with depth (z) and time (t). Each cell has a value of Γ dictated by its own recent light history:

$$\Gamma = \exp(-I/I_m) \quad (2)$$

where I_m is the average irradiance over an adaptation period, taken to be 5 h. This function may adequately describe the physiology of transition from dim to bright light, but in the reverse transition it generates an unrealistic rise in photosynthetic capacity.

CULLEN & LEWIS (1988) examined two models of photoadaptation in the context of vertical mixing, a first order relationship of the form:

$$\frac{\partial \Gamma}{\partial t} = \gamma(\Gamma_m - \Gamma_t) \quad (3)$$

where Γ_m is the asymptotic maximum Γ (most adapted state) and Γ_t is the current state of adaptation; and secondly a logistic relationship of the form:

$$\frac{\partial \Gamma}{\partial t} = \varrho\, \Gamma_t(\Gamma_m - \Gamma_t)/\Gamma_m \quad (4)$$

The former model is especially appealing given that many of the adaptational processes described above follow first order rate kinetics. However, CULLEN & LEWIS (1988) found that some photoadaptive characteristics of a diatom culture exposed to changes in light were better described by the logistic function; for example, the carbon to chlorophyll *a* ratio.

The logistic equation has important implications for algal photosynthesis in the mixed layer because it yields a strong hysteresis in response to the changing light field. Such effects have been reported from a range of lake and ocean environments, but alternative explanations to the logistic model are possible. The description of photoadaptational processes above has shown that the molecular events accompanying the transition from dim to bright light are often not simply the reverse of the bright to dim light transition. These coupled protection-recovery processes are likely to have different rate constants. Photoinhibition provides one of the clearest examples: Reaction centre II inactivation is photochemically mediated and very fast, but recovery requires the slow resynthesis of RC II proteins. In the diurnal mixed layer of Lake Titicaca, for example, the rapid photoinhibition of DCMU-induced fluorescence, and the slow recovery were both described by first order kinetics. The rate constants (γ in eq. 3) differed greatly and gave rise to a pronounced hysteresis in the fluorescence and photosynthetic parameters (VINCENT et al. 1984).

A model describing the photoinhibition effect on photosynthesis in Lake Titicaca has been developed by NEALE & RICHERSON (1987). The model incorporates a photoinhibition function, F:

$$P'_{max} = P_{max} \cdot F(I, \beta, I_T) \quad (5)$$

where P_{max} is the maximum attainable photosynthetic rate and F is the photoinhibition function. At light intensities below a threshold irradiance for photoinhibition I_T, F is set to 1. At light levels above I_T this parameter is given as an exponential function of irradiance:

$$F = \exp(-\beta(I - I_T)) \quad (6)$$

where β determines to what extent photosynthesis is depressed once the irradiance becomes inhibiting.

Photosynthetic models more commonly define Γ in terms of known physiological parameters such as α (light limitation), β (light inhibition) and P_s (light-saturated photosynthetic maximum) with no attempt to include a time or light history dependence for these parameters. Extremely complex models have been formulated to incorporate some of the mechanistic (although not kinetic) concepts described above. For example, FASHAM & PLATT (1983) proposed a model of the form:

$$\begin{aligned} 2P^* = {} & \mu_o\mu^*/P_o + (\exp(\beta_o I_o \beta_o {}^*I^*)\chi_o I_o \chi^*/P_o \\ & + \alpha_o I_o \alpha^*/P_o)I^* - [\mu_o\mu^*/P_o \\ & + (\exp(\beta_o I_o \beta^* I^*)\chi_o I_o \chi^*/P_o \\ & + \alpha_o I_o \alpha^*/P_o)I^*)^2 - 4\,\alpha_o\mu_o I_o \alpha^* \mu^* I^*/P_o{}^2]^{0.5} \end{aligned} \quad (7)$$

In this expression P is photosynthesis: μ, α, β and χ are defined in terms of kinetic parameters derived from a simplified model of charge separation at RC II; superscript* refers to dimensionless quantities and subscript o refers to scale factors.

A much simpler model that appears to describe a large amount of photosynthetic behaviour including photoadapted photosynthesis, has been derived by considering each light harvesting-reaction centre complex (often referred to as the photosynthetic unit, PSU) in the phytoplankton cell as a target that is hit by incoming photons. When the unit is successfully hit it remains closed to further incoming photons until the excitation energy can be processed, i.e. until the charge separation is completed, $P680^+$ is reduced, and the reaction centre re-opened.

The photons absorbed during this period of closure are given by $\sigma \tau I$ where σ is the absorption cross section of the PSU, τ is its turnover time (i.e. time from closure to re-opening), and I is the irradiance (photon flux density). The number of first strikes during the turnover time is described by a POISSON function: $(1 - \exp(-\sigma \tau I))$ (DUBINSKY et al. 1986). Quantum yield (Φ) is defined as the maximum yield (Φ_m) times the Poisson probability that a PSU is open when it is hit:

$$\Phi(I) = \Phi_m (1-\exp(-\sigma\tau I))/(\sigma\tau I) \quad (8)$$

SAKSHAUG *et al.* (1989) applied this formulation to the growth and light absorption of the diatom *Skeletonema costatum* under varying day lengths and found the data could be closely described by

$$\mu_g = \Phi I)\,[\text{Chl}\,a/C]\,k_c\,D\,I \quad (9)$$

where μ_g = gross growth rate (sum of specific growth and respiration rates)

$\Phi(I)$ = Poisson corrected yield as in eq. 8.

k_c = specific absorption coefficient for chlorophyll *a*

D = daylength

I = irradiance

One of the attractions of this expression is that nutrient-limited growth, incident light and variable daylength are all encompassed in a single equation. Moreover, CULLEN (1989) has shown that the equation can be re-arranged to describe the adapted rate of photosynthesis (P_B^*) as a function of irradiance:

$$P_B^* = (\mu_g/D)\,[C/\text{Chl}\,a] = [k_c\Phi_m(1-\exp(-\sigma\tau I))]/\sigma\tau \quad (10)$$

where P_B^* is the rate of the photosynthesis (per unit chlorophyll) by a phytoplankton population at the light intensity to which it is adapted. CULLEN (1989) points out that this relationship is analogous to that of PLATT et al. (1980)

$$P^* = P_s^*(1-\exp(-\alpha I/P_s))(\exp(-\beta I/P_s)) \quad (11)$$

where β is set to zero. P_s is the maximum rate of photosynthesis at light saturation. By comparing Eq. 10 and 11 he notes that

$$P_s^* = k_{chl}\Phi_m/(\sigma\tau) \quad (12)$$

and

$$\alpha = k_{chl}\Phi_m \quad (13)$$

The parameter of light saturation I_k (TALLING 1957) is given by P_s/α and thus from Eq. 12 and 13:

$$I_k = (\sigma\tau)^{-1} \quad (14)$$

Substituting into Eq. 11 gives the expression

$$P^* = P_s^*(1-\exp(-I/I_k)) \quad (15)$$

The mechanistic origins of this model are misleading because as a description of photoadapted photosynthesis it encompasses a broad range of effects (CULLEN 1989). Nonetheless this expression has been shown to closely describe P (not necessarily photoadapted P) as a function of I for a remarkably wide range of aquatic and terrestrial photosynthetic systems, with the parameters P_s and I_k (and thus α as P_s/I_k)readily determined by non-linear regression (PETERSEN et al. 1988).

The photosynthesis-light cascade

None of the models described above have attempted to incorporate the spectrum of adjustments, adaptations and damage/repair responses which characterise phytoplankton photosynthesis. Thirty years ago Jack Talling referred to the phytoplankton community of a lake as a compound photosynthetic system (TALLING 1957) – a multi-cellular entity with its own characteristic set of integrated properties. Increasingly we are beginning to view the individual algal cell as a compound system with a cascade of physiological responses to its environment (Table 2). These processes have kinetics that range from tens of seconds in the case of thylakoid dynamics, through to 10^5 seconds at the level of successional adjust-

Table 2. The dynamic coupling between photosynthesis and light in the phytoplankton environment. $T_{0.5}$ is the time to achieve half the maximum adjustment of the light-capturing process. L = low light, H = high light. *Note that for several of the lake phytoplankton measurements in ELSER & KIMMEL (1985), $T_{0.5}$ was approximately the same (c. 10^3 s) for L→H and H→L.

Process	$T_{0.5}$ (seconds)	Reference
Reaction centre turnover	$\leq 10^{-2}$	POST et al. 1989
Thylakoid dynamics		
L→H	5×10	VINCENT 1979
H→L	3×10^2	VINCENT 1979
Chloroplast contraction/ orientation	5×10^2	LECHOWSKI & BIALCZYK 1988
Reaction centre damage/repair*		
L→H	5×10^2	ELSER & KIMMEL 1985
H→L	2×10^3	VINCENT et al. 1984
PSU size/number		
L→H	3×10^4	POST et al. 1984
H→L	5×10^5	POST et al. 1984
PSU composition Chl *a*/Chl *b*	4×10^3	SUKENIK et al. 1990
Carotenoids	5×10^5	
Successional change	$\geq 6\times10^5$	HARRIS 1986

ment. For many of these processes there is a strong hysterisis between the responses to different directions of change in light intensity. At the short-term end of the spectrum responses can be tracked with *in vivo* fluorescence; towards longer time scales some of the responses can be followed closely with HPLC.

The next decade of physiological limnology offers the chance to better resolve 3 important aspects of these processes: firstly, the link between photoadaptation and lake hydrodynamics; secondly, to more fully understand the tolerance limits of these processes, for example in the context of algal succession; and thirdly, to integrate quantitatively this cascade of processes whereby solar energy capture and conversion is dynamically coupled to the underwater light field.

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Author's address:

Dr. W. F. VINCENT, Taupo Research Laboratory, DSIR, P.O. Box 415, Taupo, New Zealand.