Planktonic microalgae (phytoplankton) live in diverse and highly variable environments. Their photosynthetic apparatus is subject to significant stresses because of rapid changes or imbalances in irradiance and nutrient supply imposed by the physics and chemistry of natural water bodies. The ways in which the photosynthetic apparatus adjusts to these temporally variable and complex environments are of interest for both practical and fundamental reasons, because phytoplankton photosynthesis is responsible for ~50% of global productivity. Modern techniques for assessing productivity on global scales rely on remotely sensing plankton’s optical properties, using the signature of chlorophyll as an index of abundance (Fig. 1). The emphasis on chlorophyll is inevitable given chlorophyll’s distinctive optical characteristics, which enables plant material to be distinguished from other suspended matter. The relationship between chlorophyll and organic carbon (the desired currency for productivity models) is highly plastic, varying with growth, irradiance, nutrient availability and temperature. However, the variability is ordered, not random, and knowledge about the effects of environmental variables on the efficiency of light absorption and its conversion to biomass during photosynthesis allows estimates of chlorophyll abundance to be translated into carbon equivalents.

Understanding the effect of varying environmental conditions on photosynthetic rates can be considered in terms of the regulation of the amounts and the specific activities of components of the photosynthetic apparatus. Regulation can be accomplished by variations in the relative abundance of the constituents [e.g. chlorophyll and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco)] or, on a shorter timescale, by varying the efficiency of their coupling and activity (e.g. the activation state of Rubisco). The distinction is blurred at some levels but serves to distinguish between those means of photosynthetic regulation that depend on synthesis or turnover (usually of chlorophyll) in photoacclimation, and those that depend on more rapid changes in activation states or efficiencies, independent of turnover. Work in this area is complicated by the fact that phytoplankton include representatives of four kingdoms and are highly variable in their molecular, structural and optical properties. Whereas physiological studies have focused largely on taxa that are easy to maintain in culture, particularly chlorophytes and diatoms. It has been challenging to bring qualitative information on photosynthetic mechanisms together with quantitative kinetic information on rates of response to understand cellular photosynthesis in the natural environment. Here we review recent developments in our understanding of how phytoplankton photosynthesis adjusts to naturally variable environments.

The principal environmental factors that affect phytoplankton photosynthesis are light, nutrient availability and temperature. In nature, these factors operate independently on timescales that match photosynthetic physiology, presenting a complex and unpredictable environment to the cells. Phytoplankton respond to such stochastic environments using a variety of physiological processes that affect light harvesting efficiency and photosynthetic capacity. Two key issues are at the forefront of ecophysiological research:
• What are the kinetic constraints on processes that modulate photosynthesis in rapidly fluctuating environments?
• What are the mechanisms by which cells integrate multiple environmental factors in regulating their physiological responses? These questions are related to the photosynthetic mechanisms that modulate energy and material flow through the cell are common to phytoplankton in spite of their diversity. Significant conceptual advances have been made recently that tie whole-cell physiology with photosynthetic regulatory processes operating at the biochemical and biophysical levels.

Environmental control of photosynthetic processes
By definition, phytoplankton are incapable of sustained directed movement and therefore are subject to the environmental conditions in their parent body of water. Photosynthesis is responsive to changes in nutrient availability on short timescales but in marine systems the changes are more likely to occur over relatively long timescales (days to seasons). Although nutrient availability is critical for determining population dynamics and the ultimate determinant of the geographic abundance of phytoplankton (Fig. 1), nutrient availability is less likely to drive short-term changes in photosynthetic rates. Because of water’s capacity for high levels of latent heat, temperature is more likely to vary on daily to seasonal scales, and in a manner predictable from the balance of radiative transfer and evaporative cooling. By contrast, phytoplankton are subject to relatively rapid changes in both the intensity and the spectral quality of light as they move vertically in a water column (Box 1). In addition to the changes imposed by mixing, there are variations in the light field with timescales of hours, minutes and milliseconds as a result of changes in solar elevation, cloud cover and subsurface focusing by waves. Photosynthesis and growth rates appear to be insensitive to variability in the millisecond domain, therefore we will focus on variations that occur on a timescale of minutes and hours.

Photoacclimation of pigment content
For a given temperature and nutrient status, photoacclimation in phytoplankton can be described in terms of regulation of the cell concentrations of the catalysts that determine light-limited and light-saturated photosynthetic rates. The rate of light absorption, which co-varies with a cell’s chlorophyll concentration, is often the primary determinant of light-limited photosynthesis, whereas the maximum rate of carbon dioxide fixation, which co-varies with a cell’s chlorophyll concentration, is often the primary determinant of light-saturated photosynthesis. The cell chlorophyll content is usually higher in cells that have grown under low light. Variations in other constituents of the photosynthetic apparatus appear to be taxon-specific: two studies of cells grown under nutrient-replete conditions, the concentration of Rubisco decreased at low growth irradiance in a diatom whereas it remained unchanged in a chlorophyte. Synthesis of pigment-protein complexes appears to be transcriptionally regulated by a mechanism that is under the control of the redox state of the plastoquinone pool. Under low-light conditions, plastoquinone is largely oxidized, and transcription of the mRNAs that code for the proteins that bind chlorophyll in the antenna occurs at maximal rates. As irradiance increases, photo-synthesis control passes from light harvesting to the maximum capacity for carbon dioxide fixation, the plastoquinone becomes increasingly reduced, and transcription of the mRNAs for pigment-protein complexes declines. The end results of this mode of regulation can be mimicked by ‘energy balance’ models developed recently. These are based on the concept of a physiological light sensor that regulates the pigment quota to maintain a balance between the harvesting of excitation energy by means of light absorption and photochemistry on the one hand and the energetic demands of growth on the other. Conceptually, this is comparable to the redox regulation of the antenna protein LH2 (Refs 9,12). These models can account for steady-state responses and for the differences in the rates of acclimation that are observed following shifts from low-to-high versus high-to-low irradiance, without the potential errors imposed by specifying a mathematical function to describe the kinetics of photoacclimation.

Photosynthetic induction
The time-course of light intensity changes in estuarine waters is much faster than in coastal or open-ocean waters because both the rate of light attenuation and the rate of mixing are much higher (Box 1). Two mechanisms, the activation and deactivation of Rubisco and state transitions, have time constants that are comparable to the timescale of mixing in estuarine waters and probably dominate short-term rates of photosynthesis (Fig. 2).

Photosynthetic regulation operating by means of the catalytic activity of Rubisco can be controlled by variations in the enzyme concentration or, in the short-term, by its activation state. Although the enzyme catalytic concentration might not be regulated during photoacclimation under nutrient-replete conditions, depending on the taxon, it is regulated in response to chronic phosphorus or nitrogen limitation. Because there is a correlation between the maximum quantum efficiency (φp) and the ratio of Rubisco to the PSII reaction center protein D1, changes in the pool size of Rubisco might play a role in regulating acclimated photosynthetic rates during nutrient-limited growth.

A potential role for activation and deactivation of Rubisco in the short-term limitation of photosynthetic rates hinges on the assumption that at light saturation, the rate of photosynthetic activity depends on the enzyme’s activity. Broad conclusions are complicated by the diversity in microalgal Rubisco structure and function to describe the kinetics of photoacclimation. The time-course of light intensity changes in estuarine waters is much faster than in coastal or open-ocean waters because both the rate of light attenuation and the rate of mixing are much higher (Box 1). Two mechanisms, the activation and deactivation of Rubisco and state transitions, have time constants that are comparable to the timescale of mixing in estuarine waters and probably dominate short-term rates of photosynthesis (Fig. 2).

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catalytic characteristics. However, activity changes in those few microalgae that have been studied are consistent with models of regulation by means of carbamylation–decarbamylation and, in addition, possibly, by a tight-binding inhibitor, such as carbonyl-arabinitol-1-phosphate. The kinetics of activation and deactivation could affect photosynthetic rates in response to rapid increases and decreases in light intensity. Because activation is much faster than deactivation, the effect is less pronounced during rapid mixing because the interval between decreases in illumination as it is mixed back up are insufficient to allow much deactivation.

There appears to be little role for Rubisco oxygenase activity in phytoplankton. Although the abundance of free CO₂ in seawater (~10–15 μM) is well below the half-saturation concentration of Rubisco (30–170 μM)23, carbon concentrating mechanisms that involve either active transport of HCO₃⁻, or coupled dehydration of HCO₃⁻ by a cell-surface carbonic anhydrase and CO₂ transport, have been documented for cyanobacteria, chlorophytes, diatoms20 and dinoflagellates21,22. In addition, microalgal Rubiscos have high CO₂ specificities compared with those from terrestrial plants. This might be because of differences in the structure of the loop-6 region25 or in the length of the large subunit C-terminus27, both of which appear to play a role in the conformation of the active site during catalysis. The dinoflagellates are distinct from all other eukaryotes in having a prokaryotic-type form II Rubisco26 (i.e. one lacking the small subunit characteristic of the eukaryotic form II). Although the specificity of dinoflagellate form II Rubisco is higher than bacterial form II Rubisco26, it is unlikely that it could support measured rates of photosynthesis without the presence of a carbon-concentrating mechanism.

A second phenomenon that might drive the short-term photosynthetic response in estuarine waters is the occurrence of state transitions25, which are rapid adjustments in the relative magnitudes of the photosystems I (PS I) and photosystem II (PS II) antenna. State 2 (preferential excitation of the short-wavelength sensitive PS I) is favored under conditions of high absolute irradiance and under darkness, whereas State 1 (preferential excitation of PS II) is favored under conditions in which the spectrum is dominated by red light. Consequently cells in estuarine waters are driven to State 2 at aphotic depths (depths to which light does not penetrate because of complete attenuation by the overlying water), to State 1 at intermediate depths where the spectrum is weighted towards long wavelengths (Fig. 3), and back to State 2 at the surface25. It is not clear what effect, if any, state transitions have on photosynthetic rates, but the interchange time constants are close enough to the rate of mixing that the transitions can be observed in cyanobacteria and chlorophytes from turbid waters25. State transitions are unlikely to limit photosynthetic rates in the ocean because the timescale of mixing is slower, and because red light is more rapidly attenuated than blue light (Fig. 3). State transitions have yet to be documented from chromophytic microalgae.

**Photoprotection**

The most complex group of photosynthetic responses includes the transients associated with photoprotection and photoinhibition.
Photoprotective mechanisms can broadly be described as those that either decrease the absorption of light energy (by reducing the absorption cross section or effective photosynthetic cross-section of the reaction centers), or provide alternative energy sinks when photosynthetic capacity is exceeded. Change in the excitation delivery includes rapid responses, such as induction of energy dissipating pigments in xanthophyll cycles26,27, and slower responses, such as photoacclimative changes in the size and pigment composition of the antennae (Fig. 2). Two different xanthophyll cycles are found in chlorophylls and chlorophylls: in chlorophylls, violaxanthin is de-epoxidated to zeaxanthin in a two-step pathway, with antheraxanthin as an intermediate, in chlorophylls diadinoxanthin is de-epoxidated to diatoxanthin in a single step. Although the chlorophylls have a pathway that is structurally similar to vascular plants, the relationship between non-photocatalytic energy quenching and the level of de-epoxidation is different28. Conversely, although chlorophylls have a different pathway, the relationship between non-photocatalytic energy quenching and the level of de-epoxidation is comparable to that in vascular plants.

Other electron sinks

In addition to xanthophyll cycling, there are other mechanisms that might act as sinks for electrons when PS II activity exceeds photosynthetic capacity. For example, cyanobacteria lack a xanthophyll cycle but exhibit strong Mehler activity at light saturation29, and diatoms appear to be unique in using non-assimilatory nitrate reduction as a sink30. Both pathways bled off excess energy from the electron transport chain when NADPH turnover is operating at the maximum rate, preventing over-excitation of the photosynthetic antennae.

Photoinhibition

When the photoprotective mechanisms already described are exceeded, damaged PS II reaction centers, lacking a functional D1 protein, can accumulate. The reconstitution of functional PS II reaction centers can be described by first-order reaction kinetics when cells are moved to non-inhibitory irradiance31. Modeling the accumulation of damaged D1 might be more difficult because of the diversity of photoprotective responses, the protective capacity of which depends on both the light history and nutrient status of the cell26. However, photo-inactivation of D1 can be modeled by target theory32, opening the possibility that photosynthesis could then be described using the relationship between the proportion of inactive PS II reaction centers and the quantum efficiency.

Kinetic models and the time-dependence of photosynthetic physiology

Short-term variability in photosynthetic rates can be accounted for in productivity models using time-dependent relationships. Generally, two assumptions are made, namely that the ocean can be considered as a one-dimensional system in the vertical and (in many models) that the time-dependence of photosynthetic processes follow first-order reaction kinetics. With an adequate understanding of the vertical variation in mixing rate, the trajectories of groups of cells can be described by a random walk simulation (the vertical steps of which are defined in time by the local turbulent diffusivity) using a Lagrangian ensemble model. Given the rate of light attenuation, changes in light intensity can be described as a function of depth and time (Fig. 3). The sensitivity of photosynthesis to mixing can then be described by specifying the time-dependence of the response to changes in light intensity with one or more time constants (Fig. 2). Separate time constants for upward and downward movements are usually employed to account for different physiological rate constants associated with responses to increases and decreases in irradiance.

Fig. 3. Light absorption in oceanic waters (a) is almost wholly dependent on phytoplankton (black line) and water itself (gray line), in contrast with estuarine waters (b), where detritus (broken black line) and chromophoric dissolved organic material (bold, black line) also make a substantial contribution (note different scales). As a consequence, both the magnitude and spectral dependence of underwater light are different. (c) The attenuation of incident sunlight (0 m) is more pronounced in red light (depicted by light gray) than blue light (depicted by dark gray) in oceanic water, in contrast with estuarine water (d), where blue light is attenuated more rapidly than red light. Light intensity is expressed as PAR (photosynthetically active radiation), which is the integral of irradiance between 400 and 700 nm. The blue and red absorbance peaks of plant pigments are shown. The spectral composition of light is shown at different depths that correspond to either a doubling or a halving in the intensity of PAR. Higher turbulence and more rapid attenuation in the estuarine water results in entrained cells experiencing more rapid transients in light intensity (f) than in the oceanic water (e). Note the difference in scales. Exposure was calculated from the spectrally dependent attenuation coefficient for a cell that was released into the middle of a mixed layer and whose trajectory was based on a random walk model.
The approach has been used to model the sensitivity of photosynthesis to changes that are characteristic of photoacclimation, photoinhibition, and photosynthetic induction. The relative importance of different photosynthetic mechanisms depends on the timescale and the magnitude of the changes in the light field (i.e. if the time constant for the metabolic response is longer than the characteristic timescale of change, the mechanism has the potential to limit the reaction rate). Constructing a general model of the effect of mixing on photoinhibition that is analogous to the acclimative models depends on a somewhat arbitrary level of calibration because both the degree and rate of accumulation of photoinhibitory damage are less constrained than acclimative changes.

A description based on energy-balance models is an alternative to the descriptions of photoacclimation based on explicit time-constants of chlorophyll-specific photosynthetic responses. In energy-balance models, a physiological sensor regulates the pigment quota as a means of balancing excitation-energy harvesting with the energetic demands of growth. By specifying both as rates and units of inverse time (which necessitates converting the currency of electrons to carbon equivalents), the imbalance can be related to the energetic demands of growth. By specifying both as rates and units of inverse time (which necessitates converting the currency of electrons to carbon equivalents), the imbalance can be related to the energetic demands of growth.

The future

It is now possible to evaluate how the photosynthetic apparatus is regulated under complex environmental forcing. The complexity of the environment-photosynthesis relationship is tractable using the notion of energy-balance regulation: the redox state of the light reactions is a universal signal in microalgae for regulating cellular light harvesting efficiency. The success of recent pigment-photoacclimation models that incorporate an energy balance regulatory ‘signal’ based on the redox state, holds promise for more sophisticated models that incorporate short-term energy modulation mechanisms. These models can be made species-specific by setting parameters according to the specific energy modulation processes that are present. Future work on environmental effects will distinguish short-term kinetic from long-term energy-balance–constrained responses. This will clarify the relative importance of kinetic versus acclimative responses to particular environments.

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References

Floral induction and determination: where is flowering controlled?

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Floral induction is the process by which stimuli originating outside the shoot apex induce the formation of flower primordia (Fig. 1). The photoperiodic induction of flowering was discovered 86 years ago by Julien Tomlin in hops1. Shortly afterwards, additional experiments suggested that the photoperiodic control of flowering was a general phenomenon, which controlled flowering in most plants2. Later, focused-light experiments showed that leaves perceive photoperiodic signals3. These studies, and numerous grafting experiments, indicate that the production of the photoperiod-induced floral stimulus4 occurs in the leaves of a wide variety of flowering plants4–7.

In contrast with floral induction, floral determination can be defined as the assignment of flowering fate, which is persistent even when the flower-inducing conditions no longer exist8,9. Assays for floral determination include:

- Changing environmental conditions (from inductive to non-inductive).
- Microsurgical removal of shoot apices, and the placement of those apices into neutral environments.
- Inductive leaves are removed from the plant following an inductive treatment11.

However, both types of determination assay have limitations, and it is important to note that different determination assays might yield alternative conclusions for the same primordia (the caveats associated with determination experiments are discussed in Ref. 11). A third type of assay has been used to test leaf commitment to the continued production of floral stimulus: in this assay, photo-induced leaves are removed from the plant following an inductive treatment11.

In this review we discuss firstly a variety of experiments that indicate the site(s) that control flowering. Secondly, we review recent studies that indicate how a few molecular players regulate the specification of flower primordia in Arabidopsis.

Floral determination assays

Photoperiodic assays for floral determination

The simplest type of determination assay is one in which plants are moved to non-inductive conditions after various lengths of time under inductive conditions. Using this method, the duration of photoinduction treatment required to produce flowers can be


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