The photosynthesis-irradiance response (PE) curve, in which mass-specific photosynthetic rates are plotted versus irradiance, is commonly used to characterize photoacclimation. The interpretation of PE curves depends critically on the currency in which mass is expressed. Normalizing the light-limited rate to chl $a$ yields the chl $a$:specific initial slope ($\alpha^{chl}$). This is proportional to the light absorption coefficient ($\alpha^{chl}$), the proportionality factor being the photon efficiency of photosynthesis ($\phi_m$). Thus, $\alpha^{chl}$ is the product of $\alpha^{chl}$ and $\phi_m$. In microalgae $\alpha^{chl}$ typically shows little (<20%) phenotypic variability because declines of $\phi_m$ under conditions of high-light stress are accompanied by increases of $\alpha^{chl}$. The variation of $\alpha^{chl}$ among species is dominated by changes in $\alpha^{chl}$ due to differences in pigment complement and pigment packaging. In contrast to the microalgae, $\alpha^{chl}$ declines as irradiance increases in the cyanobacteria where phycobiliproteins dominate light absorption because of plasticity in the phycobiliprotein:chl $a$ ratio. By definition, light-saturated photosynthesis ($P_m$) is limited by a factor other than the rate of light absorption. Normalizing $P_m$ to organic carbon concentration to obtain $P_m^{C}$ allows a direct comparison with growth rates. Within species, $P_m^{C}$ is independent of growth irradiance. Among species, $P_m^{C}$ covaries with the resource-saturated growth rate. The chl $a$:C ratio is a key physiological variable because the appropriate currencies for normalizing light-limited and light-saturated photosynthetic rates are, respectively, chl $a$ and carbon. Typically, chl $a$:C is reduced to about 40% of its maximum value at an irradiance that supports 50% of the species-specific maximum growth rate and light-harvesting accessory pigments show similar or greater declines. In the steady state, this down-regulation of pigment content prevents microalgae and cyanobacteria from maximizing photosynthetic rates throughout the light-limited region for growth. The reason for down-regulation of light harvesting, and therefore loss of potential photosynthetic gain at moderately limiting irradiances, is unknown. However, it is clear that maximizing the rate of photosynthetic carbon assimilation is not the only criterion governing photoacclimation.

In this article, we selectively review 50 years of research on photoacclimation of pigment content and the photosynthesis-irradiance response (PE) curve. The PE response curve is central to our analysis because it provides a convenient and objective means of differentiating between (and parameterizing) light-limited and light-saturated photosynthesis (Fig. 1A). In addition, the PE curve is the basis for models of phytoplankton productivity (Platt et al. 1977, Fasham et al. 1990). The shape and magnitude of the PE curve reflects the underlying biophysical, biochemical, and metabolic processes that regulate photosynthesis (Falkowski 1992, Falkowski and Raven 1997). Variability in the PE curve, together with variability in the ratio of chl $a$ to carbon (chl $a$:C), is used to assess photoacclimation.

Following Falkowski and La Roche (1991), the term photoacclimation refers to phenotypic adjustments that arise in response to variations of environmental factors. In contrast, the term photoadaptation is reserved for changes in the genotype that arise either from mutations or from changes in the distribution of alleles within a gene pool. Thus, acclimation does not involve a change in the genetic structure of the population under investigation whereas adaptation does. Photoacclimation is typically manifested as a graded reduction of photosynthetic pigment content in response to increased irradiance, although it can also involve changes in pigment complement, electron transfer chain components (Wilhelm and
Wild 1984, Dubinsky et al. 1986, Neale and Melis 1986, Sukenik et al. 1987, and Calvin cycle enzymes (Sukenik et al. 1987, Orellana and Perry 1992). As such, photoacclimation involves changes in the macromolecular composition and ultrastructure of the photosynthetic apparatus (Falkowski and Raven 1997, Dunford and Falkowski 1997). Photoacclimation should be differentiated from nonphotochemical dissipation of excitation energy (Demmig-Adams and Adams 1993) and the damage/repair processes involved in photoinhibition (Anderson et al. 1998). However, changes in the composition of the photosynthetic apparatus that modulate the capacity for nonphotochemical energy dissipation or the susceptibility to photoinhibition may be components of photoacclimation (Anderson et al. 1998).

Previous investigators described two to five “strategies” of photoacclimation of the PE curve (Steemann-Nielsen and Jørgensen 1969, Prézelin 1981, Richardson et al. 1983). In contrast, we conclude that only one model is required to describe variations in the photosynthetic performance of cells acclimated to irradiances ranging from extreme light limitation to light saturation. This model assumes that light-limited photosynthesis rates are proportional to the cellular chl a content, whereas light-saturated rates are proportional to cellular carbon content.

The PE curve is a plot of mass-specific photosynthetic rate \( P^B \) versus irradiance \( E \). Net or gross gas exchange rates (designated \( P \) ) are divided by an index of mass (designated \( B \) ) to obtain mass-specific photosynthetic rates \( P^B = P/B \) (Table 1). In ecological studies, the most commonly used measure of mass is chl a concentration, because of the specificity of this readily measured variable to the phytoplankton. However, there are circumstances where cell abundance, particulate carbon concentration, or protein concentration would be more appropriate measures of mass. The unit of mass to which photosynthesis is normalized is commonly represented by a superscript; thus, \( P^G \) is the carbon-specific photosynthetic rate, \( P^{cell} \) the cell-specific rate, and \( P^{chl} \) the chl a-specific rate (Table 1).

Typically, the PE curve can be divided into light-limited, light-saturated, and photoinhibited regions. The light-limited and light-saturated regions can be characterized by three parameters: the light-limited initial slope \( \alpha^B \) ), the light-saturated maximum rate \( P^m_B \) ), and the light-saturation parameter \( E_s = P^m_B/\alpha^B \) (Talling 1957, Platt et al. 1977). Several forms have been used to describe the relationships (Jassby and Platt 1976, Eilers and Peeters 1988), but one that is commonly used (Platt et al. 1980) is

\[
P^B = P_s^B \left( 1 - \exp[-\alpha^B E/P_s^B] \right) \exp[-\beta^B E/P_s^B] \quad (1)
\]

Here, \( P_s^B \) is the photosynthetic rate at irradiance \( E \), \( \alpha^B \) is the light-limited initial slope, \( \beta^B \) is a parameter describing the reduction in photosynthetic rate at high irradiance, and \( P_s^B \) is a parameter equivalent to the light-saturated rate of photosynthesis, \( P^m_B \), when \( \beta^B = 0 \). Otherwise,

\[
P^B_m = P_s^B \left( \alpha^B / \left( \alpha^B + \beta^B \right) \right) \left( \beta^B / \left( \alpha^B + \beta^B \right) \right)^{\beta/\alpha} \quad (2)
\]

These parameters vary with growth rate in response to the environmental cues of irradiance, nutrient availability, and temperature. The responses to irradiance are ordered, and the parameters vary in predictable ways when described in terms of a second relationship, the growth-irradiance curve (Fig. 1B), which can be described using a Poisson function:

\[
\mu = \mu_m (1 - \exp[-E/K_E]) \quad (3)
\]

where \( \mu \) is the specific growth rate, \( \mu_m \) is the maximum growth rate, \( E \) is the growth irradiance, and \( K_E \) is a saturation parameter.

Photoacclimation continues to be an active area of research over 50 years after Myers published the first definitive studies in 1946. In fact, Myers (1946a,b) demonstrated all the essential features of photoacclimati-
PHOTOACCLIMATION: P vs E CURVES AND PIGMENTS

Table 1. Terminology.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Typical units</th>
</tr>
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<tbody>
<tr>
<td>(a_{chl})</td>
<td>Chl (a)-specific light-absorption coefficient</td>
<td>(m^2\cdot[g \text{ chl } a]^{-1})</td>
</tr>
<tr>
<td>(a_C)</td>
<td>Carbon-specific light-absorption coefficient</td>
<td>(m^2\cdot[g \text{ C }]^{-1})</td>
</tr>
<tr>
<td>(a_{cell})</td>
<td>Cell- or cell-volume-specific light-absorption coefficient</td>
<td>(m^3\cdot\mu m^{-3})</td>
</tr>
<tr>
<td>Chl (a:C)</td>
<td>Chl (a)-to-carbon ratio</td>
<td></td>
</tr>
<tr>
<td>(E)</td>
<td>Irradiance</td>
<td></td>
</tr>
<tr>
<td>(E_F)</td>
<td>Light-saturation parameter of the photosynthesis vs. irradiance curve</td>
<td></td>
</tr>
<tr>
<td>(K_F)</td>
<td>Light-saturation parameter of the growth rate vs. irradiance curve</td>
<td>(\mu mol\text{ photons }m^{-2}s^{-1})</td>
</tr>
<tr>
<td>(P)</td>
<td>Rate of photosynthesis</td>
<td></td>
</tr>
<tr>
<td>(P_B)</td>
<td>Mass-specific rate of photosynthesis</td>
<td></td>
</tr>
<tr>
<td>(P_m)</td>
<td>Light-saturated value of (P_B)</td>
<td></td>
</tr>
<tr>
<td>(P_{cell})</td>
<td>Cell-specific rate of photosynthesis</td>
<td></td>
</tr>
<tr>
<td>(a_{chl})</td>
<td>Chl (a)-specific initial slope of the PE curve</td>
<td></td>
</tr>
<tr>
<td>(a_{initial})</td>
<td>Chl (a)-specific initial slope of the PE curve</td>
<td></td>
</tr>
<tr>
<td>(\phi_m)</td>
<td>Maximum quantum yield of photosynthesis</td>
<td></td>
</tr>
<tr>
<td>(\mu)</td>
<td>Growth rate</td>
<td></td>
</tr>
<tr>
<td>(\mu_m)</td>
<td>Maximum growth rate</td>
<td></td>
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PHOTOACCLIMATION: P vs E CURVES AND PIGMENTS

In this review, we consider some of the methodological factors that can affect the values of the PE curve parameters here because the PE curve is central to our analysis. A PE curve is obtained either by sequentially measuring oxygen exchange at a number of irradiances or simultaneously measuring \(^{14}\)C incorporation into organic matter in a set of samples exposed to constant irradiances (Fig. 3). Carbon dioxide and oxygen exchange rates are related through the photosynthetic quotient (Laws 1991). There have been very few direct comparisons of PE curves determined by carbon assimilation and oxygen evolution (Platt et al. 1987, Kana 1992). However, photosynthetic rates measured by short-term \(^{14}\)C incorporation are generally found to be within 15% of net oxygen evolution rates for a range of taxa (e.g., Fig. 3; Kana 1992, Williams et al. 1996). The true gross oxygen evolution rate in microalgae, as measured by the \(^{18}\)O/\(^{16}\)O technique, can exceed the net oxygen evolution rate by 10% to >50%, depending on the capacity of the cells to support Mehler reaction activity (oxygen reduction by PSI). This “excess” PSII activity provides electrons to an alternative electron sink (i.e., oxygen) and is not related to carbon assimilation (Kana 1992, Lewitus and Kana 1995). Thus, PE curves determined by \(^{14}\)C or conventional net oxygen flux techniques should lead to similar conclusions regarding the interpretation of PE
determination of the PE parameters

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curves, although they may diverge from curves based on true gross $O_2$ evolution rates.

That said, the oxygen exchange and $^{14}$C uptake methods measure different responses where there is any time dependence of photosynthetic rate. The rate measured by oxygen uptake is obtained by regressing repeated estimates of oxygen concentration on time over a relatively short interval (seconds to minutes) and is almost always measured after verification that a steady-state rate has been achieved. In contrast, the rate measured by $^{14}$C uptake is usually determined from a single observation, as the integral of uptake over the duration of an incubation normalized to its duration (Fig. 4, A and B). Where there is a pronounced time dependence to the response, as for instance during photoinhibition or photosynthetic induction, the estimate is strongly dependent on the length of the incubation (Harris and Piccinin 1977, Marra 1978, MacIntyre et al. 1996, 2000, Hassidim et al. 1997). This is illustrated in Figure 4, which shows the time dependence of the PE response for two assemblages, a Skeletonema-dominated spring bloom assemblage from Delaware Bay and a Synechococcus-dominated spring bloom assemblage from the eastern North Atlantic. The Skeletonema-dominated assemblage was dark adapted for an hour before measuring PE curves of 5- to 60-min duration (Fig. 4, C and E) and the resulting curves show an increase in the light-saturated rate of photosynthesis over the first 20 min and a subsequent decline over the next 40 min. The kinetics of this are consistent with the activation of RUBISCO followed by the onset of feedback limitation of photosynthesis and/or photoinhibition (MacIntyre et al. 1996, 2000). In the Synechococcus-dominated spring bloom assemblage, the samples were not dark adapted before incubation, and the PE curve was stable for the first 60 min but showed a pronounced decline in the light-saturated rate of photosynthesis over the following hour (Fig. 4, D and F). This is consistent with the accumulation of photoinhibition.

Progressive time-dependent inhibition of light-saturated photosynthesis is not evident in nutrient-replete cells except when the experimental irradiance exceeds the growth irradiance by a factor of 10 or more (Fig. 1A). Thus, cells growing at an irradiance of 100 $\mu$mol photons·m$^{-2}$·s$^{-1}$ are not likely to experience photoinhibition unless exposed to irradiances in excess of 1000 $\mu$mol photons·m$^{-2}$·s$^{-1}$. In nature, pronounced photoinhibition in PE curves is commonly observed only in samples collected from below the surface wind-mixed layer (Platt et al. 1980). Such populations are likely to be low-light acclimated and cannot adequately dissipate the excessive photon flux provided by the experimental condition. This is distinct from photoinhibition in situ, which is most likely to be found in populations from surface waters recently subject to diel mixing and stratification (Neale and Richerson 1987) or from rapidly mixed shallow waters where the mean water column irradiance is greater than $E_k$ (MacIntyre and Cullen 1996). Under nutrient-limited conditions, there may be an increase in susceptibility to photoinhibition and consequent time-dependent changes in $P_m^{\text{chl}}$. This is likely due to a shift in control of $P_m^{\text{chl}}$ from carbon assimilatory reac-
tions to the light reactions and, in particular, the turnover capacity of PSII. Thus, the stability of the PE curve within the time domain of the measurement should be evaluated if the physiological state of the population or assemblage is unknown.

It is not our intention to delve into the pros and cons of different models for fitting PE curves, which have already been covered in depth elsewhere (Jassby and Platt 1976, Platt et al. 1980, Eilers and Peeters 1988, Frenette et al. 1993). The consensus of these workers is that the choice of model has a profound effect on the estimate of the light-limited rate of photosynthesis, α, but that most models return similar (and reliable) estimates of the light-saturated rate, Pm. Consequently, where photoacclimation of the PE response has been reported after growing a culture under a variety of conditions, there is likely to be an internal consistency in the parameters that are reported, assuming that they were estimated using the same model. This does not hold necessarily for comparisons between reports, which may be based on different models and fitting protocols. However, even internal consistency may be lost where data are compared across a range of growth irradiances because of the effect that changes in the shape of the PE curve have on the estimated parameters. A pronounced downturn of P0 at high irradiance is often observed in cells grown at low irradiance, whereas Pm may not be reached in cells grown at high irradiance (Fig. 1A). In the latter case and/or where cells are grown at high temperature, the fit parameters are frequently extrapolations of the declining curvature to an asymptotic value that may not be achieved except at an irradiance of dubious biological significance. This artifact of curve fitting can result in an estimate of Pm that is higher than any observed rate of fixation (Fig. 5).

The data shown in Figure 5 were measured for an assemblage that was sampled from a warm (29–30°C) and shallow (1.7 m) bay. The water was well mixed, and the depth of the 1% isolume was 0.6 m or less over the previous 24 h, so that the highest mean irradiance in the water column had been less than 170 μmol photons·m−2·s−1. This is <10% of the maximum irradiance over which the curve was measured (2200 μmol photons·m−2·s−1). For comparison, when the PE curve is fitted over the full range of irradiances, 99% of the asymptotic value (which is still below the irradiance at which Pm occurs) is reached only at 2700 μmol photons·m−2·s−1 for a model without a β term. The extrapolation is more extreme, and the overestimate of Pm more pronounced, if the data set has fewer values closer to saturation, as indicated by fitting to successively more truncated subsets of the data (Fig. 5A). There was a corresponding and compensatory fall in α over the same range, illustrating the covariation of the two parameters when both are determined simultaneously by using an iterative protocol (Zimmerman et al. 1987). We note that the variation in the estimates is not apparent from the fitted curves, which differ by only minute amounts over the range in which they were fitted, nor from the goodness of fit: all curves had values of R2 in excess of 0.99. The overestimate was less pronounced and less sensitive to the degree of saturation that the data exhibit when the model included a β term (Fig. 5B). There is no statistical justification for including the term, but it may re-
duce the potential overestimate of $P_m$ in cells acclimated to high temperature or irradiance, which can otherwise complicate discussion of photoacclimatory changes.

Despite the uncertainties introduced by differences in methodology, the PE curve is widely accepted as a useful relationship for examining the photosynthetic physiology of microalgae and cyanobacteria (Henley 1993). In particular, the relative short-term stability of the PE curve allows it to be used to interpret the "physiological state" of the photosynthetic apparatus on a time scale of minutes to hours. Environmentally induced changes in the parameters of the PE curve that occur on longer time scales reflect acclimatory processes. We discuss these below.

PHOTOACCLIMINATION AND BALANCED GROWTH

Photoacclimation is complete only when a condition of "balanced" growth has been achieved. Under balanced growth, the specific rate of change of all measures of cell mass are equal (Eppley 1981). Thus, balanced growth occurs when

$$\mu = \frac{1}{X} \frac{dX}{dt} \text{ for all variables } X$$

In this equation, $\mu$ is the specific growth rate (units of d$^{-1}$) and $X$ is any measure of cell abundance or mass. For example, $X$ could be cell numbers, particulate organic carbon, or chl $a$. For cells growing under a light:dark cycle, balanced growth is achieved when

**Fig. 4.** Time dependence of photosynthesis and the PE curve. (A) Time course of $^{14}$C fixation for a *Skeletonema costatum*-dominated spring bloom assemblage from Delaware Bay (39° N, 73° W), dark adapted for 1 h, then exposed to saturating irradiance (500 $\mu$mol photons·m$^{-2}$·s$^{-1}$). Samples were taken every 15 s for the first 5 min and every minute thereafter. (B) Estimate of the photosynthetic rate. Open squares are the slopes of three-point regressions for each successive trio of data. This is analogous to the rate measured by an oxygen electrode. Closed circles are mean rates over successive periods, obtained by dividing cumulative fixation over time $t$ by $t$. This is the way in which $^{14}$C uptake is usually measured. (C) $^{14}$C uptake vs. irradiance curves for the same sample based on 15-, 40-, and 60-min incubations. Rates at each irradiance are based on cumulative uptake averaged over the duration of the incubation. For details of methodology see MacIntyre et al. (1996). (D) $^{14}$C uptake versus irradiance curves for a *Synechococcus*-dominated spring bloom assemblage from the eastern North Atlantic (40° N, 20° W) based on 30-, 60-, and 120-min incubations (Suggett et al. 2001). (E) Time dependence of the light-saturated rate of photosynthesis for the *Skeletonema*-dominated assemblage. The circles are estimates of $P_m$ for curves of 5- to 60-min duration and are plotted against the time for which they were incubated. The solid line is the mean value of $P_m$ for each interval, obtained by difference. Note the relative insensitivity of the cumulative estimates to short-term changes in rate, as shown in B. (F) Time dependence of the light-saturated rate of photosynthesis for the *Synechococcus*-dominated assemblage. Symbols are as for E.
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Fig. 5. The effect of irradiance range on estimates of \( P_{\text{m}} \) and \( \alpha \) for \(^{14}\text{C} \) uptake vs. irradiance curves for a natural assemblage from San Antonio Bay (28 N, 97 W) based on a 30-min incubation (data from MacIntyre and Cullen 1996). In both panels, the data (open circles) have been fit to an exponential model of the PE response. (A) Equation 1 in which \( \beta \) has been set at 0, so that \( P_{\text{m}} = P_e \). (B) Equation 1 in which \( \beta \) was fitted simultaneously with the other parameters. \( P_{\text{m}} \) is obtained from Equation 2. The estimates of \( P_{\text{m}} \) (solid circles) and \( \alpha \) (squares) were obtained by repeatedly truncating the highest light intensity and refitting the data. Each estimate is plotted against the maximum irradiance in the subset of data for which it was fitted. Three of the fitted curves are also shown on each panel, for those data subsets in which the highest irradiance is indicated by the arrows.

Ensuring that cells are in balanced growth is essential for unambiguous assessment of photoacclimation (Beardall and Morris 1976). For example, the cyanobacterium Synechococcus is unable to tolerate high photon flux densities when transferred directly from low to high light (Barlow and Alberte 1985), although it is capable of growing in full sunlight (2000 \( \mu \)mol photons-m\(^{-2}\)-s\(^{-1}\)) when transferred through intermediate irradiances (Kana and Gilbert 1987a). We take a reductionist approach in arguing that the photosynthetic responses of fully acclimated microalgae and cyanobacteria are general and predictable. A logical corollary, which extends the treatment into the realm of physiological ecology, is that the response to environmental perturbation can then be predicted, given

\[ \text{the tendency of the response toward a new acclimated state, when the frequency and magnitude of the perturbation are matched to the time scale of response (reviewed by MacIntyre et al. 2000).} \]

INTERPRETATION OF THE PE CURVE DEPENDS ON THE VARIABLE TO WHICH PHOTOSYNTHESIS IS NORMALIZED

PE curves constructed using carbon, cells, or chl \( \alpha \) as the measure of mass provide strikingly different impressions of photoacclimation (Kana and Gilbert 1987b, Anning et al. 2000). The rate of photosynthesis of microalgae is commonly expressed on a unit chl \( \alpha \) basis (units of g C fixed-[g chl \( \alpha \)]\(^{-1}\)-h\(^{-1}\)) for several reasons, including ease of measurement. When chl \( \alpha \)-specific photosynthetic rates (\( P_{\text{chl}}^\alpha \)) are plotted against irradiance, the initial slopes of high-light and low-light acclimated cells are often similar, although the light-saturated rates vary markedly (Fig. 6A). High-light acclimated cells have higher chl \( \alpha \)-specific light-saturated photosynthetic rates than low-light acclimated cells. This pattern should not be interpreted to mean that high-light acclimated cells will outperform low-light acclimated cells at light-saturating irradiances (Fig. 6B) because chl \( \alpha \) is a much lower proportion of total mass in high-light cells (see below).

Photosynthetic rates are also expressed per cell because cells are the basic unit that must reproduce for a phytoplankton lineage to continue and because cell abundance is relatively easy to determine. However, changes in the average mass of a cell can occur under different environmental conditions (Myers and Graham 1971, Thompson et al. 1991) and can confound attempts to assess the relationship between growth rate and cell-specific photosynthetic rate. This is analogous to the difficulties of interpretation associated with relating photosynthetic rates to growth rates when photosynthesis is expressed as a function of chl \( \alpha \) (Eppley 1981), another parameter that is affected by the environment.

An alternative, but less frequently used, basis for expressing photosynthetic rates is cellular carbon (Fig. 6C). Carbon-specific photosynthesis can be compared directly with balanced growth rates (i.e. photosynthetic rates have units of mol CO\(_2\) assimilated-[mol cell carbon]\(^{-1}\)-h\(^{-1}\) = h\(^{-1}\), which are the same units as are used for specific growth rate). That is,

\[ \mu = P_C^\text{cell} - R_C^\text{cell} \]

where \( R_C^\text{cell} \) is the carbon-specific respiration rate. This approach allows one to constrain photosynthesis in terms of growth and the conservation of carbon by the cell. Evaluating \( P_C^\text{cell} \) allows assessment of how variations in PE curves relate to the rate of incorporation of C into biomass under balanced growth conditions (Kana and Gilbert 1987a, b). Significantly, previous attempts to classify “photoadaptation strategies” were based on chl \( \alpha \)-specific and cell-specific data (Steenmann-Nielsen and Jørgensen 1969, Prézelin 1981, Richardson et al. 1983), which did not account for possible variations in cell volume or mass.
The rate of light absorption is a major determinant of light-limited photosynthesis. In many microalgae the rate of light absorption is broadly correlated with the chl a content. Not surprisingly, the carbon-specific initial slope ($\alpha^{C}$) is also correlated with chl a:C (Fig. 7A). The carbon-specific initial slope equals the product of the maximum quantum efficiency of photosynthesis ($\phi_m$) and the cellular light absorption efficiency. When light absorption is expressed as $\alpha^{chl}$ (the chl a-specific absorption coefficient) the carbon-specific initial slope is

$$\alpha^{C} = \frac{\alpha^{chl}}{\phi_m}$$

Dividing both sides of this equation by chl a:C yields the chl a-specific initial slope ($\alpha^{chl}$),

$$\alpha^{chl} = \alpha^{chl} \phi_m$$

We now turn to a consideration of the contributions of $\phi_m$ and $\alpha^{chl}$ to $\alpha^{chl}$. The proportionality between $\alpha^{C}$ and chl a:C (Fig. 7A) suggests that $\alpha^{chl}$ shows limited phenotypic variability (Geider et al. 1985, Dubinsky et al. 1986, Fisher et al. 1996). As expected, there was no significant trend in $\alpha^{chl}$ with irradiance ($P > 0.05$, Bartlett’s type II regression) in seven of nine data sets reported for eukaryotes (Fig. 7B). There was a significant decline in one of two reports of *Thalassiosira pseudonana* and in one of three reports of *Emiliania huxleyi*. In contrast, there were significant ($P < 0.05$) declines in $\alpha^{chl}$ with irradiance in all four data sets reported for cyanobacteria (Fig. 7C). However, chl a is not the dominant light-harvesting pigment in these species nor is it the pigment whose quota is most highly regulated in photoacclimation (see below).

**Quantum Yield**

The quantum yield has a theoretical upper limit of 0.125 mol O$_2$·[mol photons]$^{-1}$, based on the Z scheme for photosynthetic electron transfer (Falkowski and Raven 1997). This value will only be observed if all absorbed photons are used for photochemistry. Lower values are expected because light can be absorbed by pigments that are not associated with photosynthesis and because excitation energy may be dissipated as heat in the light-harvesting antennae or the reaction centers (Anderson et al. 1995). The processes that lead to conversion of excitation energy to heat are collectively referred to as nonphotochemical quenching. Nonphotochemical quenching can arise from processes that are associated with interconversion of xanthophyll cycle pigments in the antennae of PSII, with acidification of the thylakoid lumen, and/or with processes that affect the functional state of the PSII reaction center.

Conventionally, $\phi_m$ is obtained indirectly by dividing measured values of the initial slope of the PE curve by measured values of the rate of light absorption. An exception is the work of Welschmeyer and Lorenzen (1981) in which $\phi_m$ was determined by measuring $^{14}$C assimilation of an algal suspension contained within an integrating sphere. The maximum quantum efficiency is often constant in cultures grown at light-limiting irradiances (i.e. at irradiances that are less than or equal to about 2 K$_E$) (Geider et al. 1985), although reductions of $\phi_m$ are observed in cultures acclimated to very high irradiance (Dubinsky et al. 1986, Fisher et al. 1996). Significantly, reduction...
PHOTOACCLIMATION: P vs E CURVES AND PIGMENTS

of $\phi_m$ may not be accompanied by reductions of the photochemical efficiency of PSII ($\Phi_{PSII}$) as measured by the ratio of variable to maximum fluorescence ($F_v/F_m$) of dark-acclimated cells (Kolber et al. 1988). Although Dubinsky et al. (1986) report declines of $\phi_m$ in cultures acclimated to 600 $\mu$mol photons·m$^{-2}$·s$^{-1}$, Kolber et al. (1988) show that $F_v/F_m$ retains its maximum value even in cells acclimated to 1000 $\mu$mol photons·m$^{-2}$·s$^{-1}$. Thus, declines of $\phi_m$ at high irradiance in nutrient-replete cultures are most likely due to accumulation of pigments that do not contribute to excitation energy transfer to reaction centers rather than to reduction in the maximum photochemical efficiency of the reaction centers (see below and Fig. 9, G and H). Severe depression of $\phi_m$ (to 0.01 mol CO$_2$·[mol photons]$^{-1}$) is only reported for nutrient-starved stationary phase cultures (Welschmeyer and Lorenzen 1981, Cleveland and Perry 1987) in which accumulation of damaged PSII reaction centers is likely (Kolber et al. 1988).

There is some evidence for limited interspecific variability of $\phi_m$. For example, $\phi_m$ varied from 0.077 to 0.091 mol O$_2$·[mol photons]$^{-1}$ in light-limited cultures of three species of marine microalgae (Dubinsky et al. 1986). However, a summary of data for 13 species of algae compiled by Langdon (1988) indicated a range from 0.034 to 0.10 mol CO$_2$·[mol photons]$^{-1}$. The lowest values reported by Langdon (1988) were for the dinoflagellates *Prorocentrum micans* and *Alexandrium* sp., and the highest values were found in diatoms. The photochemical efficiency of PSI, as assessed from variable to maximum fluorescence ($F_v/F_m$), shows much

**Fig. 7.** Relationship between (A) the carbon-specific initial slope of the PE curve and chl $\alpha$·C and (B and C) the chl $\alpha$-specific initial slope and growth irradiance. Although there is potential for a spurious correlation in A because both variables are normalized to carbon, the wider dynamic range of chl $\alpha$ indicates a meaningful relationship. The data in B are for eukaryotic species. Data in C are for cyanobacteria, in which the dominant light-absorbing pigments are phycobilins rather than chl $\alpha$. Irradiance (B and C) is shown in dimensionless form as the ratio of growth irradiance to $K_E$, the saturation parameter of the growth rate vs. irradiance curve (Eq. 3). $\alpha_{ch}$ in B and C is normalized to the mean value across all irradiances (Table 2).
less interspecific variability than does \( \phi_m \) (Kolber et al. 1988). This suggests that most interspecific variability in \( \phi_m \) is due to variations in the proportion of pigments that are capable of transferring excitation energy to the reaction centers. For example, in cyanobacteria, zeaxanthin can account for a large proportion of the light absorbed by a cell, but because zeaxanthin is associated with the cell wall, this light energy cannot be used for photosynthesis (Kana et al. 1988, Bidigare et al. 1989).

**CHL \( a \)-SPECIFIC LIGHT ABSORPTION EFFICIENCY**

The chl \( a \)-specific light absorption coefficient (\( a_{\text{chl}} \)) is expected to vary with the ratio of accessory pigments to chl \( a \) and cell size (Morel and Bricaud 1981, Berner et al. 1989). In some species, \( a_{\text{chl}} \) is virtually constant over a wide range of growth conditions (Geider et al. 1985, Nielsen and Sakshaug 1993). In others, \( a_{\text{chl}} \) may increase at growth irradiances greater than \( K_a \) (Dubinsky et al. 1986). Increases of \( a_{\text{chl}} \) in high-light acclimated conditions (i.e. in cells with low chl \( a/C \)) may be due to a reduction in the package effect (Morel and Bricaud 1981) and/or increases in the ratios of carotenoids and/or xanthophylls to chl \( a \). In the relatively large and heavily pigmented species, *Dunaliella tertiolecta*, 24-fold variability in \( a_{\text{chl}} \) could be partitioned almost equally between contributions due to the package effect and contributions due to changes in pigmentation (Berner et al. 1989).

Although chl \( a \) is commonly used as a measure of pigment content, other pigments can contribute significantly to light absorption (Sathyendranath et al. 1987). These accessory pigments may contribute to light harvesting or to the dissipation of excitation energy (photoprotection). Pigments are bound to proteins *in situ* as part of reaction center complexes, peripheral complexes, and light-harvesting complexes (Yamamoto and Bassi 1996). The reaction center complexes are highly conserved across phyla and contain chl \( a \) and \( \beta \)-carotene (Fig. 8). The peripheral complexes contain chl \( a \) and \( \beta \)-carotene but may also contain chl \( b \) and/or \( c \) and xanthophylls. The light-harvesting complexes are extremely diverse and account for some of the differences in thylakoid structure that are used as criteria for differentiating among algal taxa. Included in the light-harvesting complexes are the chl \( a/b \) complexes of green algae, fucoxanthin-chl \( a/c \) complexes of chromophytes, and peridinin–chl complexes of dinoflagellates as well as the phyobiliproteins of cyanobacteria, rhodophytes, and cryptophytes.

Microalgae also contain pigments that quench (or dissipate) absorbed energy before it can be used in photosynthesis. These pigments may be associated with photosynthetic pigment–protein complexes (Fig. 8). An important short-term (minutes scale) modulator of energy flow to the photosynthetic reaction centers involves an enzymatic de-epoxidation reaction of specific xanthophylls pigments. In chromophytes, the so-called xanthophyll cycle involves the conversion of diadinoxanthin to diatoxanthin, the quenching form (Arsalane et al. 1994, Olaizola et al. 1994). In chlorophytes and chrysophytes, the xanthophyll cycle involves the reversible conversion of violaxanthin (non-quenching) to antheraxanthin (quenching) and of antheraxanthin to zeaxanthin (quenching) (Demmig-Adams and Adams 1993, Casper-Lindley and Björkman 1998). In addition, \( \beta \)-carotene may serve as an energy quencher in the reaction center antennae, through it is not regulated in the manner of the xanthophyll cycle pigments.

**CELL PIGMENT CONTENT: CHL \( a \)**

Although there is a high diversity of light-harvesting pigments in algae and cyanobacteria, initially chl \( a \) will be used as an index of the abundance of all light-harvesting pigments. The cellular quota of chl \( a \) varies widely, both between species and within species (Geider et al. 1997). However, the quota of this pigment is highly regulated and responds in predictable ways to variations of irradiance, nutrient supply, and temperature in all taxa examined.

The maximum growth rate and the irradiance at which growth saturates, \( \mu_m \) and \( K_a \), vary widely between species (Table 2). However, the variation can be collapsed by expressing both growth and irradiance on dimensionless scales to provide plots of relative growth rate, \( \mu/\mu_m \), versus relative growth irradiance, \( E/K_a \) (Fig. 9A). The reduction in the cellular quota of chl \( a \) can be treated in a similar way, by normalizing the cellular quota to its maximum value (Fig. 9B). A more complete description, which also accounts for variations in the mass of the cells across the gradient of growth irradiance (e.g. Fig. 2C), is to standardize the chl \( a \) quota to cellular carbon. The response of chl \( a/C \) of nutrient-replete cells in balanced growth to irradiance can be described by two parameters: the maximum value of chl \( a/C \) in low-light acclimated cells (chl \( a/C_m \)) and the light saturation parameter of the growth rate versus irradiance response curve (\( K_a \)). All species examined show very similar responses (Geider et al. 1997, Kana et al. 1997) (Fig. 10A), with chl \( a/C \) declining to about 60% of its maximum value at a growth rate of about 50% of \( \mu_m \). Earlier reviews (Geider 1987, 1989, Langdon 1988) have also emphasized the similarities in the relationships linking chl \( a/C \), growth rate and irradiance, and additional observations consistent with Figures 9B and 10A have been reported for other diatoms (Rhee and Gotham 1981, Sakshaug et al. 1991, Thompson et al. 1989), a chlorophyte (Geider and Osborne 1986), an euglenophyte (Cook 1963), and a cyanophyte (Foy and Gibson 1982).

**CELL PIGMENT CONTENT: ACCESSORY CHL AND CAROTENOIDs**

Reductions in the cell contents of accessory light-harvesting pigments are commonly observed in response to increasing irradiance. As with reductions in chl \( a \), the decline of accessory pigments is evident at
irradiances well below those at which growth is light saturated (Fig. 9, C and E). The cellular quotas of accessory chl (chl b and chl c) decline by 80%–90%, whereas photosynthetic carotenoids and phycobilins decline by 50%–90% over comparable ranges of irradiance. These declines may parallel the decline in chl a, so that there is limited variability in the accessory pigment:chl a ratio (Dubinsky et al. 1986). Observations for nine species from four algal classes show that the chl b:chl a and chl c:chl a ratios vary little over the range of irradiances under which growth is light limited (Fig. 9, D and F). At higher irradiances, the accessory chl:chl a ratios decline (Fig. 9D). Comparable data have also been reported for cryptophytes (Goericke and Montoya 1998), diatoms (Falkowski et al. 1985, Sakshaug et al. 1991), dinoflagellates (Prézelin 1976, Prézelin and Sweeney 1978, Falkowski et al. 1985, Iglesias-Prieto and Trench 1994), prymnesiophytes (Falkowski et al. 1985), prasinophytes (Buma et al. 1993), and a chlorophyte (Sukenik et al. 1988).

The overall decrease in cellular pigment content with irradiance is due to a decrease in the number of PSI and PSII reaction centers. In addition, there can be declines in the ratio of light-harvesting antennae and/or inner antennae complexes relative to reaction center complexes. Because of differences in the pigment quotas of various pigment–protein complexes (Fig. 8), declines in accessory chl:chl a and photosynthetic carotenoid:chl a ratios may provide insight into changes in specific light-harvesting complexes relative to reaction centers (Yamamoto and Bassi 1996).

The phycobilins of the cyanophytes and the chl b of a prochlorophyte followed similar trends to the eukaryotic accessory chls and photosynthetic carotenoids, declining with irradiance (Fig. 9E). The decline in phycobilin:chl a observed in the cyanobacteria *Microcystis aeruginosa* and *Synechococcus* sp. was much more marked than declines in the photosynthetic carotenoid:chl a ratio in eukaryotic species, except in the case of the prymnesiophyte *Phaeocystis antarctica* (Fig. 9F). This reflects the fact that phycobilisomes lack chl, but other light-harvesting complexes contain it. In the phycobilisome, the principle changes in pigment content during photoacclimation come from changes in

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**Fig. 8.** Diagrammatic representation of the distribution of pigments among the pigment–protein complexes of the photosystems, including the light-harvesting complexes (LHC), peripheral complexes (PC), and reaction center complexes (RC). Data are from Yamamoto and Bassi (1996). Tabulated data are given as ratios of molecules per polypeptide within each complex and are grouped as chl a, photosynthetic accessory chl (Acc. Chl), photosynthetic accessory carotenoids (PSC), photosynthetic carotenoids (PPC), and xanthophylls (Xanth). The area of each square in the diagram is proportional to the abundance of pigments per unit of the pigment–protein complex and shows the ratios both between and within complexes. Note that the relative numbers of each complex also vary. The peripheral complex of PSI comprises the CP29, CP26, and CP24 subunits. The PSII reaction center comprises the D1/D2 heterodimer and CP47 and CP43.
Fig. 9. Growth and pigment quotas as a function of growth irradiance in nutrient-replete microalgae and cyanobacteria. Irradiance is shown in dimensionless form as the ratio of growth irradiance to $K_E$, the saturation parameter of the growth rate vs. irradiance curve (Eq. 3). (A) Relationship between relative growth rate and irradiance. (B) The relationship between cellular quota of chl a and irradiance. (C) The relationship between the cellular quota of accessory chl ($b$ and $c$) and irradiance. (D) The relationship between the accessory chl:chl a ratio and irradiance. (E) The relationship between the cellular quota of photosynthetic carotenoids (PSC) or phycobilins (PB) and irradiance. (F) The relationship between the photosynthetic carotenoid:chl a and phycobilin:chl a ratios and irradiance. (G) The relationship between the cellular quota of photoprotective xanthophylls and irradiance. (H) The relationship between the photoprotective xanthophyll:chl a ratio and irradiance. For B–H, the pigment ratios are normalized to the maximum value obtained.
the length of the phycobilin-containing distal rods rather than in the chl α-containing reaction center (Kana and Gilibert 1987a). A chl b-containing cyanophyte, Prochlorothrix hollandica, also differed from the eukaryotic species in that there was no change in the chl b quota with irradiance (Burger-Wiersma and Post 1989). Because the chl a content did decline, there was a rise in the chl b/chl a ratio with irradiance.

**CELL PIGMENT CONTENT: NONPHOTOSYNTHETIC PIGMENTS**

In eukaryotic species the cellular quota of photoprotective xanthophylls increases with growth irradiance above K_E (Fig. 9G). The simultaneous decline in the chl a quota with increased irradiance results in a pronounced rise in the photoprotective xanthophyll:chl a ratio over the range of growth irradiances (Fig. 9H). Comparable results have been documented in diatoms, a dinoflagellate, a chrysophyte, and a chlorophyte (Demers et al. 1991, Sakshaug et al. 1991, Casper-Lindley and Björkman 1998). The trends in the β-carotene quota were more variable, decreasing with irradiance in diatoms (Willemoës and Monas 1991, Goericke and Welschmeyer 1992b) and increasing in a prymnesiophyte (Moisan et al. 1998). These data may indicate an increase in the abundance of the peripheral complexes relative to the light-harvesting complexes in PSII and/or an increase in the ratio of PSII to PSI photosynthetic units (Yamamoto and Bassi 1996) (Fig. 8).

The photoprotective carotenoids in prokaryotes are either α- or β-carotene, which are in the reaction centers, and zeaxanthin, which is located in the cytoplasmic or outer cell wall membranes in cyanobacteria (Resch and Gibson 1983) and which does not appear to be involved in photosynthesis (Kana et al. 1988). In the prochlorophyte Prochlorococcus marina and the cyanophyte Synechococcus sp., α- and β-carotene covary with chl a (Kana et al. 1988, Moore et al. 1995), so that the ratio is independent of irradiance. In contrast, the zeaxanthin quota, once corrected for changes in cell volume, did not vary with irradiance. (The variability with irradiance in Fig. 9G is due to variability in cell size [cf. Fig. 2Cl.]). The decline in chl a caused an increase in zeaxanthin:chl a ratio (Kana et al. 1988, Moore et al. 1995). The overall trend in the photoprotective carotenoid:chl a ratio (Fig. 9H) therefore depends on the relative abundance of the two pigments.

There are two consequences of the observed changes in the absolute and relative abundances of pigments. The first is that as growth becomes light saturated, the cellular absorption cross-section decreases so that cells absorb a smaller fraction of the light that impinges on them. The second is that as the proportion of photosynthetic pigments declines and the proportion of photoprotective pigments rises with growth irradiance, the ability to dissipate excess absorbed energy increases, although the ratio of all carotenoids to chl a may not change greatly. A consequence of this is that apparent quantum yields determined from light absorption and the initial slope of the PE curve (Eq. 7) will fall even in the absence of any change in the quantum yield of photochemistry.

**CELLS DO NOT MAXIMIZE LIGHT-LIMITED PHOTOSYNTHETIC RATES DURING ACCLIMATION TO LOW LIGHT**

The carbon-specific rate of photosynthesis at low irradiance is the product of chl a:C, the chl a-specific light absorption coefficient (α_C), the maximum quantum efficiency of photosynthesis (φ_m), and irradiance (E) (Kiefer and Mitchell 1983, Langdon 1987, Geider et al. 1996).

\[
P^C = \text{chl ~a:C ~} \alpha \_\text{C} \phi_m \text{E} = \alpha \_C E \tag{8}
\]

where P^C is the carbon-specific photosynthetic rate that, like growth rate, has units of inverse time. Variations in light-limited photosynthetic rates due to photoacclimation can be accounted for largely in terms of changes of chl a:C, which varies continuously over the light-limited range for most species (Fig. 10A). Although low-light acclimated cells, with higher chl a:C, have higher carbon-specific photosynthetic rates at any given light-limited irradiance than high-light acclimated cells (Fig. 10B), carbon assimilation is not maximized across all irradiances. To maximize carbon assimilation and hence growth rate at subsaturating irradiances, the pigment content would need to be maintained across all subsaturating growth irradiances, given the condition that under balanced growth, energy inputs (i.e. light absorption) and growth are matched. This is not observed. In fact, chl a:C declines progressively as growth irradiance increases (Fig. 10A), declining to 71 ± 4% (mean ± SE) of the maximum value at K_E, an irradiance at which growth rate has increased to only 63% of the maximum rate.

In the preceding analysis we assumed that cellular light absorption is proportional to cell chl a content. This need not be the case as the efficiency of absorption declines at high chl a:C because of increased pigment packaging. Even so, in those few data sets in which both the pigment quota and the absorption cross-section are reported, the pattern is seen even after correction for pigment packing. The chl a quota, which does not account for changes in the efficiency of light absorption due to pigment packaging, declines well before light saturation of growth rate (Fig. 10C). The absorption cross-section standardized to cell carbon or cell volume, which does account for changes in the efficiency of light absorption, shows the same trend (Fig. 10D), although the decline is less pronounced, reaching on average 76% of the maximum at K_E. (These estimates were derived by fitting both growth rate and chl a:C to irradiance [Table 2].) Thus, photoacclimation does not maximize light absorption and hence carbon assimilation and growth rate at all subsaturating (light-limiting) growth irradiances.
cells do not maximize the light-saturated photosynthetic rate at high light

Under nutrient-replete conditions, control of light-saturated photosynthesis is thought to reside in the dark reactions, specifically at Rubisco (Björkman 1981, Sukenik et al. 1987) or in the process of regenerating the acceptor molecule ribulose 1,5-bisphosphate (reviewed by Geider and MacIntyre 2002), although the slow turnover rate of the cyt b$_6$f complex may also limit the maximum photosynthetic rate (Fleischhacker and Senger 1978, Wilhelm and Wild 1984). Under nutrient-limited conditions, control may shift to PSII (nitrogen limitation) or PSI (iron limitation) (Vassiliev et al. 1995, Berges et al. 1996). Maximum photosynthetic capacity may also be set by the reduced levels of functional PSII under photoinhibiting conditions (Kok 1956) or when reaction center II has been poisoned with 3-[3,4-dichlorophenyl]-1,1-dimethylurea (DCMU) (Behrenfeld et al. 1999).

High-light acclimated cells typically have lower car-
### Table 2. Fit parameters for cultures under nutrient-replete growth.

<table>
<thead>
<tr>
<th>Species</th>
<th>L:D</th>
<th>$K_s$ (μmol photons·m$^{-2}$·s$^{-1}$)</th>
<th>$\mu_{max}$ (d$^{-1}$)</th>
<th>Chl a:C$_{m}$ (g·g$^{-1}$)</th>
<th>$P_{m}^C$ (10$^6$ g·C·[mol photons]$^{-1}$·m$^{-2}$·[g chl]$^{-1}$)</th>
<th>$\alpha^{SE}$</th>
<th>$n$</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphidinium carteri</td>
<td>24:0</td>
<td>24 ± 5</td>
<td>0.67 ± 0.03</td>
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<td></td>
<td></td>
<td></td>
<td>Sosik et al. (1989)</td>
</tr>
<tr>
<td>Cryptophyte sp. 169</td>
<td>12:12</td>
<td>9 ± 1</td>
<td>0.45 ± 0.02</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Buma et al. (1993)</td>
</tr>
<tr>
<td>Cryptophyte sp. 169</td>
<td>24:0</td>
<td>8 ± 1</td>
<td>0.59 ± 0.02</td>
<td></td>
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<td></td>
<td></td>
<td>Buma et al. (1993)</td>
</tr>
<tr>
<td>Emiliania huxleyi</td>
<td>18:6</td>
<td>69 ± 11</td>
<td>0.83 ± 0.04</td>
<td>0.036 ± 0.006</td>
<td>3.58 ± 0.16</td>
<td>1.10 ± 0.08</td>
<td></td>
<td>Nielsen (1997)</td>
</tr>
<tr>
<td>Emiliania huxleyi</td>
<td>24:0</td>
<td>69 ± 14</td>
<td>0.83 ± 0.05</td>
<td>0.028 ± 0.002</td>
<td>1.06 ± 0.17</td>
<td>0.93 ± 0.04</td>
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<td>Nielsen (1997)</td>
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<tr>
<td>Emiliania huxleyi</td>
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<td>26 ± 2</td>
<td>0.65 ± 0.02</td>
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<td>Stolte et al. (2000)</td>
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<td>Gymnodinium tamarensis</td>
<td>14:10</td>
<td>168 ± 80</td>
<td>0.61 ± 0.15</td>
<td>0.015 ± 0.004</td>
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<td></td>
<td></td>
<td>Langton (1987)</td>
</tr>
<tr>
<td>Gyrodinium cf. aurantium</td>
<td>12:12</td>
<td>35 ± 6</td>
<td>0.26 ± 0.01</td>
<td>0.032 ± 0.016</td>
<td>1.22 ± 0.27</td>
<td>0.68 ± 0.04</td>
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<td>Garcia and Purdie (1992)</td>
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<td>Hymenomonas carterae</td>
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<td>95 ± 13</td>
<td>1.45 ± 0.08</td>
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<td>83 ± 10</td>
<td>1.23 ± 0.05</td>
<td>0.025 ± 0.001</td>
<td>2.20 ± 0.23</td>
<td>1.30 ± 0.11</td>
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<td>Falkowski et al. (1985)</td>
</tr>
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<td>Micractinys acuta</td>
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<td>78 ± 16</td>
<td>1.79 ± 0.13</td>
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<td>Oscillatoria redei</td>
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<td>25 ± 1</td>
<td>0.27 ± 0.01</td>
<td>0.037 ± 0.001</td>
<td>1.46 ± 0.15</td>
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<td>Oscillatoria redei</td>
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<td>0.031 ± 0.006</td>
<td>2.34 ± 0.57</td>
<td>0.71 ± 0.06</td>
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<td>88 ± 19</td>
<td>0.50 ± 0.02</td>
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<td>Moisan &amp; Mitchell (1999)</td>
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<tr>
<td>Phaeocystis tricornutum</td>
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<td>52 ± 3</td>
<td>1.52 ± 0.05</td>
<td>0.078 ± 0.005</td>
<td>2.13 ± 0.28</td>
<td>0.71 ± 0.07</td>
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<td>Geider et al. (1985, 1986)</td>
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<td>Phaeocystis tricornutum</td>
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<td>120 ± 14</td>
<td>1.06 ± 0.04</td>
<td>0.067 ± 0.005</td>
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<td>34 ± 3</td>
<td>0.66 ± 0.02</td>
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<td>Procentrum micans</td>
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<td>149 ± 18</td>
<td>0.18 ± 0.01</td>
<td>0.007 ± 0.002</td>
<td>0.27 ± 0.01</td>
<td>1.10 ± 0.11</td>
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<td>16 ± 1</td>
<td>0.50 ± 0.02</td>
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<td>48 ± 6</td>
<td>0.11 ± 0.01</td>
<td>0.008 ± 0.004</td>
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<td>1.73 ± 0.02</td>
<td>0.016 ± 0.003</td>
<td>2.95 ± 0.24</td>
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<td>Thalassiosira pseudonana</td>
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<td>93 ± 12</td>
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<td>0.060 ± 0.004</td>
<td>3.25 ± 0.24</td>
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<td>Geider, unpublished data</td>
</tr>
<tr>
<td>Thalassiosira pseudonana</td>
<td>12:12</td>
<td>115 ± 12</td>
<td>1.70 ± 0.07</td>
<td>0.051 ± 0.010</td>
<td>3.83 ± 0.22</td>
<td>0.76 ± 0.10</td>
<td></td>
<td>Yang, Machnuye, and Cullen (unpublished data)</td>
</tr>
<tr>
<td>Thalassiosira weissflogi</td>
<td>24:0</td>
<td>164 ± 20</td>
<td>1.91 ± 0.09</td>
<td>0.055 ± 0.005</td>
<td>3.01 ± 0.21</td>
<td>0.48 ± 0.05</td>
<td></td>
<td>Falkowski et al. (1985)</td>
</tr>
<tr>
<td>Thalassiosira weissflogi</td>
<td>24:0</td>
<td>37 ± 5</td>
<td>1.14 ± 0.04</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Goericke &amp; Welschmeyer (1992a)</td>
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<tr>
<td>Thalassiosira weissflogi</td>
<td>12:12</td>
<td>78 ± 9</td>
<td>1.15 ± 0.05</td>
<td>0.058 ± 0.002</td>
<td></td>
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<td>Law &amp; Bannister (1980)</td>
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<tr>
<td>Thalassiosira weissflogi</td>
<td>24:0</td>
<td>86 ± 17</td>
<td>2.33 ± 0.16</td>
<td></td>
<td></td>
<td></td>
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<td>Sosik et al. (1989)</td>
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Values are means ± SE, except for $n$. The light-saturation parameter of the growth vs. irradiance curve ($K_s$) and maximum growth rate ($\mu_{max}$) were obtained by fitting Equation 3. The maximum value of the chl a:C ratio (chl a:C$_{m}$) was obtained by fitting the following equation (Geider et al. 1997): chl a:C$_{m}$ = chl a:C$_{m}$ + $m$·$\alpha$, where $m$ is a constant. Values of the carbon-specific light-saturated rate of photosynthesis ($P_{m}^C$) and the chl a-specific initial slope ($\alpha^{SE}$) are means over the range of growth irradiance. L:D is the ratio of light to dark in the photoperiod (24-h period). $n$ is the number of observations.

* Significant increase with growth irradiance ($P < 0.05$, see text for details).
† Significant decrease with growth irradiance ($P < 0.05$, see text for details).
bon-specific rates of photosynthesis ($P_C$) at light-limiting irradiances than low- and moderate-light acclimated cells (Fig. 10B). This is a consequence of reductions in chl $a$C and thus the carbon-specific rate of light absorption (Figs. 7 and 10A). In compensation for this reduced photosynthetic performance at low light, one might expect that additional resources would be allocated to the “dark” reactions of photosynthesis (Shuter 1979), with the result that cells acclimated to high irradiance would possess higher light-saturated photosynthetic rates. However, this is not observed (Fig. 11A). In 11 of the 14 cases shown, there was no significant dependence of $P_{mC}$ on growth irradiance ($P > 0.05$, Bartlett’s type II regression), even though there is a fairly strong probability of $P_{mC}$ varying significantly with irradiance for most eukaryotes (Figs. 7B and 11A), the product of $E_k$ and chl $a$C ratio and growth irradiance for microalgae (B) and cyanobacteria (C). Data are normalized to the mean value across the range of irradiance (Table 2). (D) The relationship between C:N and growth irradiance.

Fig. 11. (A) The relationship between light-saturated carbon-specific photosynthesis, $P_{mC}$, and growth irradiance for nutrient-replete microalgae and cyanobacteria. $P_{mC}$ was normalized to the mean value across growth irradiances (Table 2). Irradiance is shown in dimensionless form as the ratio of growth irradiance to $K_E$, the saturating parameter of the growth rate vs. irradiance curve (Eq. 3). (B and C) The relationship between the product of the saturation parameter of a PE curve, $E_k$, and the chl $a$C ratio and growth irradiance for cyanobacteria (Fig. 11C). One consequence of the invariance in $P_{mC}$ is an inverse relationship between chl $a$C and $E_k$, as previously proposed based on restricted data sets (Bannister 1979, Geider et al. 1997). This follows from the definition of $E_k = P_m/\alpha$ (Talling 1957), where the light-limited and light-saturated rates of photosynthesis are expressed on the same basis. Consequently,

$$E_k = P_{mC}/[\alpha^{chl} a:C]$$

As neither $\alpha^{chl}$ nor $P_{mC}$ vary significantly with irradiance for most eukaryotes (Figs. 7B and 11A), the product of $E_k$ and chl $a$C should be a constant. This is the case for seven of nine cases ($P > 0.05$ for a significant slope, Bartlett’s type II regression, data in Fig. 11B). It did not hold for the cyanobacteria (Fig. 11C), where there was a significant trend in $\alpha^{chl}$ with irradiance (Fig. 7C). This latter result is not surprising be-
cause the dominant change in pigmentation during photoacclimation is in the phycobilins rather than chl a (Fig. 9F).

OVERVIEW OF PHOTOACCLIMATION MODELS

It is not our intention to provide a comprehensive treatment of the various models that have been used to describe photoacclimation. However, we consider selected features of these models within the context of our compilation of data on chl a:C, αchl and Pm:C.

A number of models describe the variability of chl a:C under nutrient-replete and nutrient-limited balanced growth conditions (Shuter 1979, Bannister and Laws 1980, Kiefer and Mitchell 1983, Geider et al. 1996, 1997, 1998). All these models reproduce the features of photoacclimation of chl a:C illustrated in Figure 10A. However, they achieve this end by invoking somewhat different mechanisms and, in their original formulations, very different terminologies. Of these models, only Bannister and Laws (1980) and Geider et al. (1996, 1997, 1998) explicitly treat acclimation of the PE curve and acclimation of chl a:C.

Some features are common to all these models. One essential feature is an energy conservation equation that sets the sum of the growth rate plus respiration rate equal to the photosynthesis rate under conditions of balanced growth. Photosynthesis is in turn treated either explicitly or implicitly as a function of the rate of light absorption and the light-saturated photosynthesis rate. In these models, light absorption is assumed to be linearly related to chl a:C through a constant chl a-specific light absorption coefficient (αchl). This assumption can be relaxed if data permit αchl to be modeled. In the linear low-light initial slope region of the PE curve, the carbon-specific rate of light absorption is converted to a carbon-specific photosynthesis rate by multiplying by a constant quantum efficiency of photosynthesis, designated φm. The assumptions of constant αchl and constant φm imply that αchl is also constant. With the exception of Shuter (1979), photosynthesis is treated as a saturating function of irradiance where the maximum rate is set by a species-specific constant value of Pm:C under nutrient-replete conditions. The models differ in the choice of the function used to describe the PE response curve and the treatment of the mechanism of regulation of chl a:C. Nutrient limitation can be introduced to the models by allowing the PE curve to be modified by reducing Pm:C in line with the reduction in the nutrient supply rate. Now that the similarities among the models have been emphasized, we turn to differences.

One essential feature of Shuter’s (1979) model is the assumption that there is a trade-off between the sizes of the photosynthetic apparatus and the biosynthetic apparatus under nutrient-replete balanced growth. The model assumes that photosynthesis is linearly dependent on the rate of light absorption (i.e. the quantum efficiency of photosynthesis is a constant). Thus, under balanced growth photosynthesis will always be in the initial slope region of the PE curve. This is achieved in part by declines of chl a:C with increasing irradiance and in part by increases in the size of the biosynthetic apparatus. The model also assumes that biosynthesis is proportional to the RNA content. As photosynthesis increases with increased irradiance, the size of the biosynthetic apparatus must increase as well. Thus, Shuter’s model requires that RNA:C increase with increasing growth irradiance to maximize growth rate. At light-limiting irradiances, the increase of RNA:C means that chl a:C must decline because there is a strict trade-off between the proportions of carbon allocated to the biosynthetic and photosynthetic apparatus. Another essential feature of Shuter’s model is the assumption that the biosynthetic apparatus has a maximum size. Thus, Shuter assumes that there is a maximum RNA:C ratio for each species that determines the resource-saturated maximum growth rate. Once RNA:C reaches this level, the model requires that growth becomes light saturated, and further declines of chl a:C at progressively higher irradiances are accompanied by increases of an energy-storage pool of lipids or carbohydrates. The continuing decline of chl a:C with increases of irradiance at light-saturated growth conditions maintains photosynthesis just at the point of light saturation. Shuter’s model provides a good fit to chl a:C ratios of nutrient-replete phytoplankton. However, it does not provide a good description of RNA:C, which is independent of growth irradiance in a number of species (Laws et al. 1983, Thomas and Carr 1985). (These data on RNA:C were not available when Shuter formulated his model.) One consequence of the assumptions described above is that Shuter’s model requires Pm:C to vary in parallel with growth rate under light-limiting conditions. Contrary to this requirement of the model, the data (Fig. 11A) shows that Pm:C is independent of growth irradiance. Furthermore, there is a large excess in the capacity for light-saturated photosynthesis, Pm:C, relative to the achieved growth rates (1.25–5.5×Pm:C; Table 2), as noted previously (Kana and Glibert 1987b). Thus, the trade-off between the sizes of the photosynthetic apparatus and biosynthetic apparatus invoked by Shuter (1979) is not a general feature of algal acclimation and such a trade-off cannot be evoked to explain the decline of chl a:C in the light-limited region of the growth curve.

The Shuter (1979) model assumes that photoacclimation is a zero sum game with reallocation from light harvesting to the dark reactions necessary to increase growth rate. If such reallocation occurs, it is not evident in either RNA:C or Pm:C. Nor is it evident as an increase in lipid or carbohydrate contents because C:N is largely independent of irradiance (Fig. 11D): there was no significant trend (P>0.05) in C:N with irradiance in 13 of 14 data sets reported, the exception being for Phaeodactylum tricornutum. Nonetheless, there is reallocation of carbon from the pigments and associated proteins. One might speculate that this is associated with catalysts involved in protection from photooxidative stress.
Kiefer and Mitchell’s (1983) treatment is somewhat simpler than Shuter’s (1979) model, because they dispense with the explicit treatment of photosynthetic, biosynthetic, and energy-reserve pools. Rather, Kiefer and Mitchell’s model is expressed directly in terms of chl $a/C$. Like Shuter, they equate the sum of growth and respiration rates to the product of light absorption and the quantum efficiency of photosynthesis. However, one major difference between the models is that Kiefer and Mitchell (1983) allow photosynthesis to depart from a linear dependence on the rate of light absorption. They do this through a light-dependent decline in the quantum efficiency of photosynthesis ($\phi$). The model can also be written in terms of the parameters of the PE curve, where the decline of $\phi$ is associated with the approach to, or attainment of, light saturation (Geider 1990).

Like Kiefer and Mitchell (1983), Bannister and Laws (1980) provided a model of photoacclimation that has chl $a/C$ as a central physiological variable. However, rather than treating $\phi$ as a declining function of $E$, they include a fuller treatment of the PE curve. Bannister and Laws (1980) assumed that photoacclimation proceeded such that the product $P^c_{m}/(a^{chl}E)$, where chl $a/C$ was constant. Thus, Bannister and Laws assumed that photoacclimation occurs such that declines of $E_k$ are accompanied by increases of chl $a/C$. (note the similarity to Eq. 9 above).

Geider et al. (1996) developed a model that relaxes the restriction that growth should be balanced. It describes changes of growth rate and chl $a/C$ during transients of irradiance as well as under conditions of constant irradiance. The model was subsequently expanded to include nutrient limitation (Geider et al. 1997) and variable C:N (Geider et al. 1998). Like Bannister and Laws (1980) and Kiefer and Mitchell (1983), Geider et al. (1996) assumed that $P^c_{m}$ was independent of the growth irradiance and that the rate of light absorption was proportional to chl $a/C$. A key feature of the Geider et al. (1996) model is treatment of the regulation of the rate of chl $a$ synthesis by the ratio $P^c_{m}/(a^{chl} \cdot chl \cdot a/C \cdot E)$, which is an energy balance equation (Kana et al. 1997). The dynamic model of Geider et al. (1996) reduces to a very similar model to those described by Bannister and Laws (1980) and Kiefer and Mitchell (1983) for conditions of balanced growth.

We close this section by emphasizing that a common feature of many of the photoacclimation models developed to date is that $a^{chl}$ and $P^c_{m}$ are assumed to be independent of growth irradiance. These assumptions are largely consistent with our compilation of data from laboratory cultures for eukaryotes (Figs. 7B and 11A) but not for prokaryotes, where chl $a$ is not a good proxy for light absorption.

CONCLUSIONS

The PE response curve, derived from short-term measurements, reflects a quasi-stable condition of the photosynthetic apparatus and yields significant insight into the regulation of energy and material balance of the cell. The plasticity of the PE response on acclimation time scales (hours to days) can be better understood when photosynthesis is parameterized as a carbon- (or mass-) specific flux. This was done by Myers more than 50 years ago, but most of the subsequent empirical studies lost sight of the constraining relationships between photosynthesis, growth, and carbon- (or mass-) specific fluxes in growing photosynthetic cells.

The patterns of photosynthetic pigment regulation identified in Figure 10A and of $P^c_{m}$ identified in Figure 11A were already evident in data of Myers (1946a,b, 1970, Myers and Graham 1971) and more recent data (Foy and Gibson 1982, Geider et al. 1985, Kana and Glibert 1987a,b). These observations indicate that maximizing the rate of photosynthetic carbon assimilation is not the only criterion governing photoacclimation. Our analysis indicates the need to examine other criteria (Raven 1980) that may affect the contribution of photoacclimation of photosynthetic pigment content to fitness. These include the costs of photoinhibition and repair (Raven and Samuelsson 1986) and costs associated with photooxidative stress or protection from such stress.

In this review, we emphasize the importance of interpreting PE curves in the context of carbon turnover, carbon-specific light absorption properties, and regulation of light-saturated photosynthesis, the combination of which provides a coherent and general understanding of the regulation of photosynthetic pigmentation. We have shown elsewhere that the same underlying processes can account for pigmentation changes arising from acclimation to nitrogen supply and temperature (Geider et al. 1997, 1998, Kana et al. 1997). Despite a general pattern in changes in pigmentation, there are physiological differences between taxa that contribute to their ecological success. For example, maximum growth rate and the maximum pigment biomass ratio can vary by an order of magnitude, and cell size can vary by three orders of magnitude. Other differences include energy and material (N, C) costs of synthesis of light-harvesting pigments (Raven 1984, 1990), the catalytic efficiency and susceptibility to photorespiration of the carboxylating enzyme RUBISCO (Reid and Tabita 1994), mechanisms of excitation energy dissipation (Yamamoto and Bassi 1996), and the extent of oxygen cycling (Kana 1992).

A general pattern in acclimation of photosynthesis to irradiance becomes readily evident when the photosynthetic responses of diverse taxa are related to growth irradiance normalized to the light-saturation parameter for growth ($K_E$). Normalizing growth irradiance in this way results in a “hinge point” that depends on both the species-specific maximum growth rate and the species-specific maximum rate of light absorption. This ratio provides a consistent scaling of “energy pressure” on the photosynthetic apparatus (sensu Maxwell et al. 1996). Recent information from diverse sources points to excitation pressure (ex-
pressed through the redox state of an intersystem component of the photosynthetic electron transfer chain) as a key signal in the regulation of photosynthetic proteins (Durnford and Falkowski 1997). Thus, scaling photoacclimation variables to irradiance alone is insufficient in comparative studies because of species-specific variation in $\Phi_E$.

In the steady state, microalgae and cyanobacteria do not maximize photosynthesis throughout the light-limited region for growth. The reason for down-regulation of light harvesting and therefore potential photosynthetic gain at moderately limiting irradiances is as yet unknown. It may be a consequence of a sensitive redox regulator or response to low levels of phototoxic stress. Considerable work is yet to be done to understand how the “set point” is determined for steady-state pigment concentrations. This is one of the key problems to understanding the biological constraints to maximizing light-harvesting under light limitation and the general selective advantage of photoacclimation to low irradiance.

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