Quantitative phytoplankton physiology: implications for primary production and phytoplankton growth

Richard J. Geider


A review of quantitative information on phytoplankton growth and photosynthesis obtained from studies employing clonal phytoplankton cultures has been undertaken. Where data permit, both chlorophyll-specific and carbon-specific photosynthesis rates have been obtained. This analysis uses as its basis the photosynthesis-light response curve employed within the context of an energy budget for phytoplankton growth. Variability in the chlorophyll-specific light absorption coefficient ($a_{\text{chl}}$), the maximum photon efficiency of photosynthesis ($\phi_m$), and the chlorophyll-specific light-saturated photosynthesis rate ($P_m^\text{chl}$) contribute to variations in photosynthesis rate. Much of the variability in $a_{\text{chl}}$ can be attributed to interspecific variability in $a_{\text{chl}}$, whereas variability in $P_m^\text{chl}$ arises from both genetic and adaptive sources. The maximum quantum efficiency of photosynthesis appears to be largely independent of irradiance, but declines in response to nitrate limitation. Variability in the chlorophyll-a:carbon ratio, and the respiration and excretion rates contribute to uncoupling of growth from gross photosynthesis. Finally, the relationship between the traditional approach to the photosynthesis-irradiance (PI) curve based on the light-saturated photosynthesis rate ($P_m^\text{chl}$) and the light-limited initial slope ($a_{\text{chl}}$), and the biophysical approach based on the photosynthetic unit (PSU) cross-section ($a_{\text{psu}}$), minimum turnover time for photosynthetic electron transfer ($\tau$) and the photosynthetic unit size (chlorophyll: PSU), is summarized.

Richard J. Geider: College of Marine Studies, University of Delaware, 700 Pilottown Rd., Lewes, DE 19958-1298, USA.

Introduction

Oceanographers often wish to estimate phytoplankton productivity from more readily measured variables such as chlorophyll $a$ concentration and irradiance (Ryther and Yentsch, 1957; Cullen, 1990). Use of in vivo fluorometry to monitor chlorophyll $a$ concentration from ships (Lorenzen, 1966) and moorings (Whitlette and Wirick, 1986), and radiometric sensors for estimating chlorophyll $a$ from aircraft and satellites (Gordon and Morel, 1983; Lewis, 1992) have greatly increased the spatial and temporal resolution and coverage with which phytoplankton abundance can be measured. Unfortunately, there has not been a corresponding increase in the ability to measure photosynthesis, although deployment of high resolution $O_2$ sensors (Maccio and Pandol, 1988), and fluorometers to measure flash-induced (Kolber et al., 1990) and passive chlorophyll fluorescence (Kiefer et al., 1989) may allow increases in the spatial and temporal coverage of phytoplankton primary production. In lieu of more widespread applications of these techniques, investigators often rely on empirical algorithms relating primary production and surface chlorophyll $a$ concentration to estimate primary production from satellite data (Eppley et al., 1985; Lohrenz et al., 1988; Balch et al., 1989). Bio-optical models of varying degrees of complexity (Platt, 1986; Cullen, 1990; Platt and Sathyendranath, 1991; Bidigare et al., 1992) attempt to provide a rational basis for estimating phytoplankton photosynthesis from the light and biomass fields.

Essentially all of the biology in bio-optical models of phytoplankton production resides in the response of photosynthesis to irradiance. However, there are at least three different ways of modeling the light dependence of photosynthesis (Table 1). First, gross photosynthesis can be described as a saturating function of irradiance employing two parameters (Equations 1 and 2). Typically, the parameters employed are the light-saturated photosynthesis rate (designated $P_m^\text{chl}$) and the...
Quantitative phytoplankton physiology

Table 1. Alternative mathematical formulations of the photosynthesis–irradiance response curve.

1. **Exponential formulation** (Jassby and Platt, 1976)

\[
P_{\text{chl}} = P_m^{\text{chl}} \left(1 - \exp\left(-\alpha_{\text{chl}} I_0 / P_m^{\text{chl}}\right)\right)
\]

where:
- \(P_{\text{chl}}\) = chlorophyll a specific photosynthesis rate (mol CO₂ g⁻¹ chl a s⁻¹)
- \(P_m^{\text{chl}}\) = light-saturated photosynthesis rate (mol CO₂ g⁻¹ chl a s⁻¹)
- \(\alpha_{\text{chl}}\) = initial slope of the PI curve (mol CO₂ mol⁻¹ photons m²⁻¹ chl a)
- \(I_0\) = irradiance (mol photons m⁻² s⁻¹)

This equation can be reformulated in terms of the light saturation parameter \(I_k\) (mol photons m⁻² s⁻¹) by noting the identity \(I_k = P_m^{\text{chl}} / \alpha_{\text{chl}}\).

\[
P_{\text{chl}} = P_m^{\text{chl}} \left(1 - \exp\left(-I_0 / I_k\right)\right)
\]

II. **Target theory** (Dubinsky et al., 1986)

\[
P_{\text{chl}} = \left(1 - \exp(-\sigma \tau I_0)\right) / (4\pi \tau)
\]

where:
- \(\sigma\) = absorption cross-section of photosystem II (m² mol⁻¹ reaction centers)
- \(\tau\) = the turnover time of photosystem II (s)
- \(\eta\) = "size" of photosystem II (g Chl a PSII⁻¹) determined from O₂ flash yield
- \(4\) = number of electrons transferred by PSII per O₂ evolved or CO₂ fixed

Note that the product \(\sigma \tau I_0\) has units of mol photons mol⁻¹ reaction centers. The dimensions mol mol⁻¹ cancel, even though the comparison is between photons and reaction centers.

III. **Light absorption and photosynthetic efficiency** (Sakshaug et al., 1989)

\[
P_{\text{chl}} = a^{\text{chl}} \Phi_m I_0 \left(1 - \exp\left(-\sigma \tau I_0\right)\right) / (4\pi \tau)
\]

where:
- \(\Phi_m\) = maximum photon efficiency of photosynthesis (mol C mol⁻¹ photons),
- \(a^{\text{chl}}\) = chlorophyll a-specific light adsorption cross-section (m⁻² g⁻¹ chl a).

IV. **Relationships amongst the parameters of the models outlined above**

\[
P_m^{\text{chl}} = 1 / (4\pi \tau) = (a^{\text{chl}} \Phi_m) / (\sigma \tau)
\]

\[
I_k = 1 / (\sigma \tau) = P_m^{\text{chl}} / \alpha_{\text{chl}}
\]

\[
\alpha_{\text{chl}} = \Phi_m a^{\text{chl}} = \sigma / 4\pi
\]

V. **Energy balance for growth** (Geider et al., 1986; Geider, 1990):

\[
\mu + r + e = 12P_m^{\text{chl}} \theta \left[1 - \exp\left(-\alpha_{\text{chl}} I_0 / P_m^{\text{chl}}\right)\right]
\]

where:
- \(\mu\) = growth rate (s⁻¹)
- \(r\) = respiration rate (s⁻¹)
- \(e\) = excretion rate (s⁻¹)
- \(\theta\) = chlorophyll:a carbon ratio (g chl a g⁻¹ C)

The areal primary production is obtained by integrating the photosynthesis irradiance (PI) curve over depth and time (Platt et al., 1990). Recent investigations have considered the importance of the vertical distribution of chlorophyll a, the angular and spectral distributions of the underwater irradiance field, the time dependence of surface irradiance and climatology of \(P_m^{\text{chl}}\) and \(\alpha_{\text{chl}}\) (Platt, 1986; Sathyendranath et al., 1989; Platt et al., 1990; Platt and Sathyendranath, 1991; Morel, 1991). However, a systematic examination of genetic and adaptive variability of the PI curve parameters \(P_m^{\text{chl}}\) and \(\alpha_{\text{chl}}\) has received less attention.

This communication considers phenotypic and inter-
specific variability of the PI curve. Observations of $P^{ch}_{m}$ and $\alpha^{chl}$ were abstracted from the literature and the results expressed in compatible units of mol C g$^{-1}$ Chl $a$ s$^{-1}$ for $P^{ch}_{m}$ and mol C mol$^{-1}$ photons m$^2$ g$^{-1}$ Chl $a$ for $\alpha^{chl}$. A photosynthetic quotient of unity was assumed for comparison of rates of O$_2$ and CO$_2$ exchange. The theoretical basis for this analysis rests on an energy budget for phytoplankton growth (Equation 6).

Responses to irradiance

Chlorophyll $a$-specific light-saturated photosynthesis ($P^{ch}_{m}$)

In diatoms, the taxon that has been most extensively studied, $P^{ch}_{m}$ of nutrient-sufficient cells varies by about a factor of twenty over the growth irradiance ($I_g$) range $1 \mu$mol m$^{-2}$ s$^{-1} < I_g < 2000 \mu$mol m$^{-2}$ s$^{-1}$, with 75% of the variability in $P^{ch}_{m}$ accounted for by a linear relation to the logarithm of the growth irradiance (Fig. 1A). The considerable scatter in Figure 1A may be due, in part, to variations in analytical techniques for measuring irradiance, photosynthesis and chlorophyll $a$ concentration. Temperature may also be a factor, although for the studies illustrated in Figure 1A, temperature ranged from 18 to 22°C. The investigations of Glover (1980) and Perry et al. (1981) suggest about twofold interspecific variation of $P^{ch}_{m}$ at a given irradiance within diatoms. Thus, $P^{ch}_{m}$ is determined largely by preconditioning environmental conditions, which appear to dominate interspecific variation, in the diatoms. Similarly, $P^{ch}_{m}$ is linearly related to log($I_g$) in most other taxa examined (Fig. 1B). The slope of the relation between $P^{ch}_{m}$ and log ($I_g$) does not vary greatly for the species examined, but the intercept varies widely. Thus, although photoadaptation typically leads to increased $P^{ch}_{m}$ at higher $I_g$, the considerable variability amongst higher taxa (i.e., at the class level) limits utility of $P^{ch}_{m}$ alone as an index of photoadaptation.

Chlorophyll $a$-specific, light-saturated photosynthesis ($P^{ch}_{m}$) shows a variety of responses to nutrient limitation. Although a decrease of $P^{ch}_{m}$ is typically observed as batch cultures enter nutrient-limited stationary phase, $P^{ch}_{m}$ may remain unchanged in continuous cultures maintained at low, but balanced, nutrient-limited growth rates (Cullen et al., 1992). The best that can be said is that the data are variable, with $P^{ch}_{m}$ ranging from $<0.2$ to $1.0 \times 10^{-4}$ mol O$_2$ g$^{-1}$ Chl $a$ s$^{-1}$ at low growth rates ($\mu/\mu m < 0.2$), increasing to values typical of nutrient sufficient cultures as growth rate increases (Fig. 1C).

Initial slope ($\alpha^{chl}$)

In contrast to $P^{ch}_{m}$, $\alpha^{chl}$ often showed little dependence on growth irradiance, varying less than twofold within species in eukaryotes. Typically, $\alpha^{chl}$ remained unchanged or increased with increasing irradiance (Fig. 2A and B). Exceptional are observations for Thalassiosira pseudonana (Cullen and Lewis, 1988) in which $\alpha^{chl}$ decreased about 2.5-fold between $I_g = 20$ and $I_g = 2200 \mu$mol photons m$^{-2}$ s$^{-1}$ (data not shown). The decline may indicate reduced $\phi_{m}$ in cells cultured at 2200 $\mu$mol photons m$^{-2}$ s$^{-1}$, although some of the decline observed by Cullen and Lewis (1988) may be a methodological artifact of short-term $^{14}$C-uptake measurements (Cullen, personal communication). However, $\alpha^{chl}$ showed greater interspecific variability, varying about fivefold (Fig. 2A) within the diatoms. Unlike $P^{ch}_{m}$, $\alpha^{chl}$ is determined by the taxon under investigation rather than by environmental factors in the eukaryotic phytoplankton. In contrast to the pattern observed in the eukaryotes and Prochlorothrix hollandica, $\alpha^{chl}$ decreased with increasing irradiance in the phycobiliprotein containing cyanobacteria (Fig. 2C). The decline is particularly pronounced in the oceanic Synechococcus clone WH7803 (Kana and Gilibert, 1987a, b). It reflects the large decrease in phycobiliprotein:chlorophyll ratio which accompanies adaptation to high irradiances (Foy and Gibson, 1982; Kana and Gilibert, 1987a, b).

Variations in $\alpha^{chl}$ can be partitioned into effects associated with changes in the maximum quantum efficiency of photosynthesis ($\phi_{m}$) and the chlorophyll $a$-specific light absorption coefficient ($a^{chl}$). Welschmeyer and Lorenzen (1981) found that interspecific variability in $\alpha^{chl}$ under nutrient-replete conditions mirrored changes in the chlorophyll $a$-specific light absorption coefficient ($a^{chl}$) with the maximum quantum efficiency of photosynthesis ($\phi_{m}$) unchanged. Senger and Fleischhacker (1978) found constant $\phi_{m}$ independent of irradiance, although Dubinsky et al. (1986) reported small declines of $\phi_{m}$ at high growth irradiance ($I_g > 500$ $\mu$mol photons m$^{-2}$ s$^{-1}$), and Geider et al. (1986) reported small declines at low growth irradiances ($I_g < 5 \mu$mol photons m$^{-2}$ s$^{-1}$). The ratio of variable to maximum fluorescence ($Fv/Fm$), as assessed with a pump and probe fluorometer or through selective use of the inhibitor DCMU, is thought to provide a quantitative index of the efficiency of photochemistry in photosystem II (Krause and Weis, 1991). Fluorescence determinations of changes in the maximum quantum efficiency ($Fv/Fm$) of photosystem II (PSII) photochemistry indicate that $\phi_{m}$ is largely independent of growth irradiance ($I_g$) over the range $10 \mu$mol photons m$^{-2}$ s$^{-1} < I_g < 1000 \mu$mol photons m$^{-2}$ s$^{-1}$ (Kolber et al., 1988). Variations of $a^{chl}$ reflect differences in the ratio of accessory pigment to chlorophyll $a$ and of intracellular self-shading (Bricaud et al., 1988). Figure 3 illustrates the dependencies of $\phi_{m}$ on the product of cell diameter and chlorophyll $a$ content, and $\alpha^{chl}$ on the product of chlorophyll $a$:carbon ratio ($\theta$) and the cube root of cell carbon...
Figure 1. A. Relation between $P_m^{\text{chl}}$ and log$I_g$ for the diatoms *Thalassiosira pseudonana* (●) (Cullen and Lewis, 1988; R. Geider, unpubl.); *Thalassiosira weisflogii* (■) (Dubinsky et al., 1986); *Phaeodactylum tricornutum* (▲) (Geider et al., 1985, 1986); six diatom species examined by Glover (1980) (○); two diatoms examined by Chan (1980) (□); and six diatoms examined by Perry et al. (1981) (△). One observation from Perry et al. (1981) for *Skeletonema costatum* at 300 μmol photons m$^{-2}$ s$^{-1}$ was omitted because both $P_m^{\text{chl}}$ and $\alpha^{\text{chl}}$ were exceptionally low, suggesting photoinhibition. The data can be described by $P_m^{\text{chl}} = a + b \log(I_g)$, where $a = 0.055 \pm 0.23$ and $b = 0.471 \pm 0.046$ when $P_m^{\text{chl}}$ is the light-saturated photosynthesis rate in units of $10^{-4}$ mol O$_2$ g$^{-1}$ Chl a s$^{-1}$ and $I_g$ is the growth irradiance expressed in units of μmol photons m$^{-2}$ s$^{-1}$. A photosynthetic quotient of unity is assumed to allow conversion of O$_2$ and CO$_2$ based rates. No attempt has been made to adjust for differences in temperature.

B. Relation between $P_m^{\text{chl}}$ and log$I_g$ for *Thalassiosira weisflogii* (Dubinsky et al., 1986) (■) repeated from Fig 1A; the haptophyte *Isochrysis galbana* (Dubinsky et al., 1986) (▲); the dinoflagellate *Prorocentrum micans* (Dubinsky et al., 1986) (□); the cyanobacterium *Synechococcus* clone WH7803 (Kana and Glibert, 1987a,b) (○); and the cyanobacterium *Oscillatoria redekei* (Foy and Gibson, 1982) (●). Linear regression of $P_m^{\text{chl}}$ on log$I_g$ typically accounted for more than 90% of the variance within species. C. Relation between $P_m^{\text{chl}}$ and growth rate ($\mu$) in nitrate-limited cultures of *Chaetoceros gracilis* (Thomas and Dodson, 1972) (+); *Phaeodactylum tricornutum* (Osborne and Geider, 1986) (□); and Glover (1980) (△); *Thalassiosira pseudonana* (R. Geider, unpubl.) (○); *Isochrysis galbana* (Herzig and Falkowski, 1989) (○); and the chrysophyte *Pavlova lutheri* (Chalup and Laws, 1990) (●).

The cube root of carbon content was used as a measure of the linear dimensions of the cell under the assumption that cell volume was proportional to cell carbon content. This assumption is subject to considerable uncertainty. Unfortunately, there are few simultaneous observations of cell linear dimensions, cell chlorophyll content, cell optical properties, and light-limited photosynthesis.
increased with decreasing growth rate. In these investigations, the decrease of $\phi_m$ in nitrate-limited cultures was more than offset by an increase of $\alpha_{\text{chl}}$ due to a lessening of the package effect and accumulation of carotenoids relative to chlorophyll $a$. Chalup and Laws (1990) and Geider (R. Geider, unpubl.) found that $\alpha_{\text{chl}}$ decreased as the nutrient-limited growth rate declined, indicating marked reductions in $\phi_m$. Finally, Cullen et al. (1992) found that $\alpha_{\text{chl}}$ was independent of the nutrient-limited growth.

Although it appears that $\phi_m$ declines at low nitrate-limited growth rates, the extent of that decline is contentious. Available data from gas exchange and pump and probe fluorescence ($F_v/F_m$) measurements indicate that $\phi_m$ remains near the maximum value at relative growth rates ($\mu/\mu_m > 0.5$) but that decreases of about 50% are observed at $\mu/\mu_m = 0.1$ (Fig. 4). However, the observation of Cullen et al. (1992) that the ratio of DCMU enhanced to in vivo fluorescence of dark-adapted cells is independent of the nitrate-limited growth rate in the diatom *Thalassiosira pseudonana* suggests that $\phi_m$ is unaffected by nitrate limitation in this alga under the culture conditions (i.e., irradiance, duration of light period and temperature) employed.
Chlorophyll a:carbon ratio (\(\theta\))

Chlorosis is commonly observed in response to increases in irradiance or decreases in nutrient supply (Laws and Bannister, 1980). In nutrient-sufficient diatoms, the chlorophyll a:carbon ratio (\(\theta\)) varied by a factor of ten and was found to be inversely related to \(\log(I_g)\) (Fig. 5A). An inverse relation to \(\log(I_g)\) was also observed in the haptophyte *Isochrysis galbana*, and the dinoflagellate *Prorocentrum micans* (Falkowski et al., 1985).

Although \(\theta\) is also inversely related to \(I_g\) in the cyanobacteria and chloroxybacteria (Fig. 5A), the absolute values of \(\theta\) at a given growth irradiance are much lower in the procaryotes than in the diatoms. Data for other classes of nutrient-sufficient phytoplankton appear to fall between the diatom and procaryote trends. Under nitrate-limited conditions, \(\theta\) was linearly related to growth rate (Fig. 5B), as demonstrated previously (Laws and Bannister, 1980). The slope of the relation between \(\theta\) and \(\mu\) increased at low irradiance, indicating that adaptation to irradiance occurs in nutrient-limited phytoplankton in balanced growth.

Carbon-specific, light-saturated photosynthesis (\(P^c_{\text{m}}\))

Carbon-specific photosynthesis rates (\(P^c_{\text{m}}\)) are rarely reported in the oceanographic literature because it is difficult to obtain unambiguous measurements of phytoplankton carbon content *in situ*. However, it is instructive to examine variations of \(P^c_{\text{m}}\) in axenic phytoplankton cultures. At light-saturation, \(P^c_{\text{m}}\) is linearly related to the species-specific maximum growth rate, \(\mu_{\text{m}}\), when observations for all available taxa are considered (Fig. 6A). In contrast, \(P^c_{\text{m}}\) is largely independent of \(\mu_{\text{m}}\) (data not shown), as would be expected given the variability illustrated in Figure 1B. These results suggest that, at light saturation, the maximum photosynthesis rate is regulated by growth processes. Similarly, under nitrate-limited conditions, \(P^c_{\text{m}}\) varies linearly with growth rate, \(\mu\) (Fig. 6B). The data suggest that the slope of the
relation between $P_{m1}$ and $\mu$ depends on growth irradiance rather than taxon. A higher slope is found when nutrient-limited cells are cultured at lower irradiance, indicating that phenotypic responses to irradiance persist under nutrient-limited conditions (Bannister and Laws, 1980).

Under nutrient replete conditions, $P_{m1}$ is greatest under mild light-limitation of growth. Phenotypically, $P_{m1}$ of nutrient sufficient phytoplankton appears to show about a threefold range in response to irradiance, although there does not appear to be a great diminution in $P_{m1}$ except at very low, light-limited growth rates.

Interspecific variability of $P_{m1}^{chl}$

By definition $P_{m1}^{chl} = P_{m1}/\theta$. Given the evidence for limited interspecific variability of $\theta$ in diatoms cultured at a fixed $I_g$ (Chan, 1987, 1980; Blasco et al., 1982; Hitchcock, 1982) as illustrated in Figure 5A, it follows that (at a given $I_g$) $P_{m1}^{chl}$ should be correlated with $P_{m1}$. Furthermore, given the relation between $P_{m1}$ and $\mu_m$ (Fig. 6A), it also follows that $P_{m1}^{chl}$ should be correlated with $\mu_m$. Finally, because much of the variability of $\mu_m$ in diatoms can be accounted for by cell size (Banse, 1982; Blasco et al., 1982), it is anticipated that $P_{m1}^{chl}$ will also vary with cell size. Specifically, at comparable growth irradiances, large diatoms should have lower $P_{m1}^{chl}$ than small diatoms, and the extent of variability of $P_{m1}^{chl}$ should be set by the range of $\mu_m$. The few studies of the size dependence of diatom growth and photosynthesis support this assertion. Taguchi (1976) found that $P_{m1}^{chl}$ decreased by about an order of magnitude as diatom cell size increased by five orders of magnitude. However, Taguchi (1976) did not measure growth rate and it appears that balanced growth was not consistently attained in his experiments. Blasco et al. (1982) found that chlorophyll-specific photosynthesis rates measured at the growth irradiance decreased with increasing size in six diatom species examined, and that $P_{m1}^{chl}$ was linearly related to $\mu_m$ with $r^2 = 0.49$ (Fig. 7). Unfortunately, Blasco et al. (1982) did not measure complete PI curves and uncertainty is associated with the assumption that $P_{m1}^{chl}$ is proportional to $P_{m1}^{chl}$. Linear regression of $P_{m1}^{chl}/\theta$ on $\mu_m$ increased the $r^2$ to 0.72, indicating that about 20% of the variance of $P_{m1}^{chl}$ in the data of Blasco et al. (1982) was associated with variations in $\theta$. Differences in respiration, excretion, and measurement errors presumably accounted for the remaining 28% of variance which was not accounted for by $\mu_m$ and $\theta$. In experiments conducted by Glover (1980) on four planktonic diatoms which were not necessarily in balanced growth, 86% of the variance in $P_{m1}^{chl}$ was accounted for by a linear dependence on growth rate (Fig. 7). However, two benthic species were characterized by significantly higher $P_{m1}^{chl}$ at comparable growth rates (Glover, 1980). Taking the data for all six species together, 40% of the variance in $P_{m1}^{chl}$ was accounted for by $\mu_m$. There is insufficient data to examine putative relations amongst $\theta_m$, $\theta$ and $P_{m1}^{chl}$ in other taxa. However, Chan’s (1978) data for diatoms and dinoflagellates suggest that much of the variability in $\mu$ can be accounted for by $\theta$ and $I_g$. 

Figure 5. A. Relationship between the chlorophyll $a$:carbon ratio and log($I_g$) in diatoms (○) (Chan, 1980; Geider et al., 1985, 1986; Falkowski et al., 1985) and prokaryotes (●) (Raps et al., 1983; Kana and Glibert, 1987a,b; Burger-Wiersma and Post, 1989). The chlorophyll $a$:carbon ratio appears to decline linearly with log($I_g$) in most species examined, although the slope and intercept of the relationship vary widely. Data for other taxa typically fall between the extremes indicated in the figure. B. Relationship between the chlorophyll $a$:carbon ratio and the nutrient-limited growth rate. Data for Thalassiosira pseudonana (R. Geider, unpubl.) cultured at 500 µmol photons m$^{-2}$s$^{-1}$ (●), Phaeodactylum tricornutum (Osborne and Geider, 1986), Isochrysis galbana (Herzig and Falkowski, 1989), and Pavlova lutheri (Chalup and Laws, 1990) cultured at 160-190 µmol photons m$^{-2}$s$^{-1}$ (○); Pavlova lutheri (Chalup and Laws, 1990) cultured at 63 µmol photons m$^{-2}$s$^{-1}$ (■).
Figure 6. A. Relation between $P_m^\text{n}$ and $\mu_m$ in various taxa. Data for *Phaeodactylum tricornutum* (Geider et al., 1985; Li and Morris, 1982), *Isochrysis galbana*, *Thalassiosira weisflogii*, and *Prorocentrum micans* (Falkowski et al., 1985; Dubinsky et al., 1986); *Thalassiosira pseudonana* (R. Geider, unpubl.); *Synechococcus* strain WH7803 (Kana and Glibert, 1987a,b); *Mucocystis aeruginosa* (Raps et al., 1983); *Prochlorothrix hollandica* (Burger-Wiersma and Post, 1989); *Chlorella pyrenoidosa* (Myers and Graham, 1971). Least squares linear regression of $P_m^\text{n}$ on $\mu_m$ yielded an intercept of 0.223 and a slope of 1.273 with $r^2 = 0.942$ for $n = 13$. B. Relation between $P_m^\text{n}$ and $\mu$ in nitrate limited cultures of *Thalassiosira pseudonana* (R. Geider, unpubl.), *Phaeodactylum tricornutum* (Terry, 1982) and *Thalassiosira weisflogii* (Terry, 1982) all cultured at 500 μmol photons m$^{-2}$ s$^{-1}$ (●); *Phaeodactylum tricornutum* (Osborne and Geider, 1986), *Isochrysis galbana* (Herzig and Falkowski, 1989), and *Pavlova lutheri* (Chalup and Laws, 1990), all cultured at 160–190 μmol photons m$^{-2}$ s$^{-1}$ (○); and *Pavlova lutheri* (Chalup and Laws, 1990) cultured at 63 μmol photons m$^{-2}$ s$^{-1}$ (■). Least squares linear regression of $P_m^\text{n}$ on $\mu$ yielded: $P_m^\text{n} = 0.067 + 1.12 \mu$ with $r^2 = 0.942$ for $I_0 = 500 \text{μmol photons m}^{-2} \text{s}^{-1}$ (●); $P_m^\text{n} = 0.0137 + 1.75 \mu$ with $r^2 = 0.944$ for $I_0 = 160–190 \text{μmol photons m}^{-2} \text{s}^{-1}$ (○); $P_m^\text{n} = 0.152 + 3.88 \mu$ with $r^2 = 0.989$ for $I_0 = 63 \text{μmol photons m}^{-2} \text{s}^{-1}$ (■). C. Relation between $P_m^\text{n}$ and $\mu$ for nutrient-sufficient and light-limited cultures of *Phaeodactylum tricornutum* (Geider et al., 1985, 1986) (▲); *Thalassiosira weisflogii* (Dubinsky et al., 1986) (■); *Isochrysis galbana* (Dubinsky et al., 1986) (□); *Synechococcus* strain WH7803 (Kana and Glibert, 1987a,b) (○); and *Thalassiosira pseudonana* (R. Geider, unpubl.) (●).

Conclusions

This analysis suggests several dominant patterns of phenotypic response of photosynthesis to light and nutrient limitation, building on patterns previously identified (see Shuter (1979) and Richardson et al. (1983) for reviews). Specifically, provided that photoinhibition of growth is avoided, within a species: (1) $P_m^\text{n}$ increases and $\theta$ decreases with increasing irradiance under nutrient-sufficient conditions. (2) $P_m^\text{n}$ varies linearly with $\mu$ under nutrient-limited conditions at both saturating and limiting irradiances. (3) under nutrient-saturated conditions, $P_m^\text{n}$ is maximal under a modest degree of light limitation, decreasing dramatically only as growth rate approaches zero. (4) $\phi_m$ is largely independent of irradiance under nutrient-sufficient con-
ditions, and \( \varphi_{\text{chl}} \) varies largely in response to changes in the light adsorption coefficient \( (a^*_{\text{chl}}) \), (5) variation of \( \varphi_m \) under nutrient-limited conditions has not been adequately resolved, but available evidence indicates approximately twofold reductions at low nitrate-limited relative growth rates.

The pronounced adaptation of phytoplankton photosynthesis outlined above complicates attempts to assess genetic variability of phytoplankton photosynthesis. However, several patterns appear to emerge: (1) \( P_n' \) increases with \( \mu_m \) under nutrient-sufficient, light-saturated conditions, (2) under light- and nutrient-saturated conditions, \( P_n'_{\text{chl}} \) appears to be correlated with \( \mu_m \) in diatoms, the only taxon for which appropriate data are available.

The applicability of this analysis to estimating phytoplankton production in nature is constrained by the limitations of the available data. The laboratory investigations cited are dominated by a few "weed" species, with many oceanic taxa including nano- and picophytoplankton poorly represented. In addition, most of the observations were obtained from cultures maintained under the highly controlled conditions of continuous illumination at fixed irradiance and temperature, under nutrient-sufficient or nutrient-limited balanced growth. Many important questions cannot be adequately reviewed because of the lack of appropriate data. These include (1) the impact of selection pressures during isolation and maintenance of phytoplankton clones in the laboratory (Lynch et al., 1991), (2) the contribution of diel variations in photosynthetic performance to growth (Harding et al., 1981; Gerath and Chisholm, 1989), (3) the variability in response times of photosynthetic performance and pigment content during transients in irradiance, nutrient availability and/or temperature (Post et al., 1984, 1985), (4) responses to spectral quality (Morel et al., 1987), and (5) the responses of pico- and nanoplanckton species typical of the open ocean.

Acknowledgements

My understanding of environmental regulation of photosynthesis in phytoplankton has benefited greatly from discussions with Paul Falkowski, Julie LaRoche, Bruce Osborne, Trevor Platt, and John Raven. Support for this work was provided by the University of Delaware. I thank Hugh MacIntyre for constructive comments on an early version of this manuscript and John Cullen for reviewing the final draft. I thank Peggy Conlon for assistance in preparing the manuscript.

References


Kana, T. M., and Gilbert, P. M. 1987b. Effect of irradiances up to 2000 μE m−2 s−1 on marine Synechococcus WH7803. II.


