

TOWARD A GENERAL DESCRIPTION OF PHYTOPLANKTON GROWTH FOR BIOGEOCHEMICAL MODELS

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1. Introduction

The growth of phytoplankton is fundamentally important to biogeochemical cycling in the sea, and models of this process are essential to describing the fluxes of carbon, nitrogen, and many other elements in the ocean. We address here nitrogen-based models that predict the photosynthesis and growth of phytoplankton for use in basin-scale simulations of marine biogeochemical processes. These models describe light absorption by photosynthetic pigments and biological transformations of carbon and nitrogen, so they must specify, implicitly or explicitly, the cellular chemical composition of phytoplankton (i.e., chlorophyll *a*, C and N) and photosynthesis per unit chlorophyll *a* as a function of irradiance (P^B vs. E).

It is important to recognize that neither the relative proportions of cellular constituents nor the P^B vs. E relationship are constant (Fig. 1): rather, for

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individual species in culture they vary with the growth rate of phytoplankton (μ ; d^{-1}) as influenced by daylength (D), irradiance (E), limiting nutrient (here we discuss dissolved inorganic nitrogen, N), and temperature (T). Our task is to describe how this variation can be predicted and how these predictions can be incorporated into numerical simulations of biogeochemical dynamics in the ocean. Construction and validation of a general model is well beyond the scope of this report. Likewise, a comprehensive review of growth models and supporting experimental studies, though appropriate to the task, is not possible in this context. Instead, we present a general analytical framework and some quantitative relationships that can be examined for consistency with experimental data. It would seem reasonable, and perhaps essential, to compare our predictions explicitly with those of others who have performed thorough reviews and analyses of some aspects of microalgal growth (e.g. Shuter, 1979; Laws & Bannister, 1980; Zevenboom & Mur, 1984; Falkowski et al., 1985; Geider et al., 1986a; Geider, 1987; Langdon, 1988; Laws & Chalup, 1990; Kiefer, this volume), but this is an extremely demanding task that, unfortunately, could not be attempted.

Some members of this working group are uncomfortable even suggesting that a general, physiologically-based model of phytoplankton growth can be used to describe primary production in the sea. First, as we will show, experimental data are insufficient to resolve critical questions. The second complication is taxonomic diversity: there are important, but incompletely resolved, biochemical and physiological differences between groups that are surely important in the sea (Geider, 1992a), but we are a long way from predicting ecological success of different taxa in general models of ocean processes (see Margalef, 1978). Finally, we acknowledge the difficulties in extrapolating results of laboratory studies to the ocean. Not only is it technically demanding to simulate important characteristics of the marine environment (e.g., vertical mixing, intermittent nutrient supply, and interspecies interactions), but it is extremely difficult to validate model predictions because growth rates and chemical composition of natural phytoplankton cannot be measured directly (Eppley, 1980). Clearly, realism must be sacrificed in our modeling efforts.

Acknowledging misgivings expressed by some members of this working group, we suggest how phytoplankton growth might be described in a numerical model of biogeochemical processes in the sea. The foundation is an analytical description of adapted growth and chemical composition as a function of D , E ,

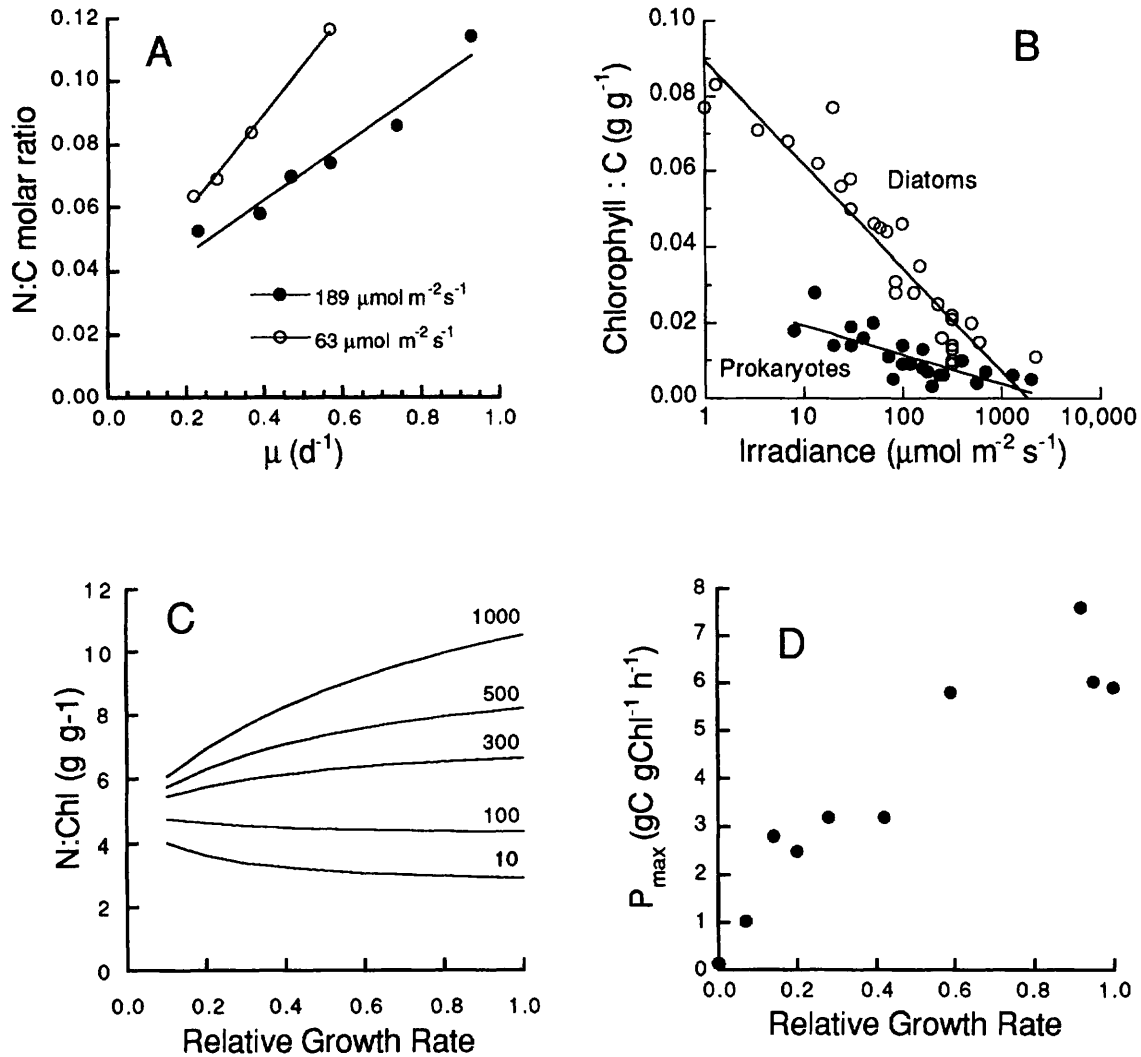


Fig. 1. Chemical and physiological characteristics of phytoplankton in culture. A. The molar N:C ratio of *Pavlova lutheri* as a function of nutrient-limited growth rate (d^{-1}) for two different irradiances, 63 and $189 \mu mol m^{-2} s^{-1}$ (from Chalup & Laws, 1990). B. Chl:C ($g:g$) of cultures as a function of growth irradiance for diatoms and prokaryotes, illustrating substantial taxonomic differences (Geider, 1992a). C. Predictions of N:Chl ($g:g$) as a function of N-limited growth rate for different growth irradiances in $\mu mol m^{-2} s^{-1}$ (Laws & Chalup, 1990). Relative growth rate is μ normalized to the nutrient-saturated growth rate at that irradiance and temperature. D. Maximal rate of normalized photosynthesis, P_{max} ($gC gChl^{-1} h^{-1}$) for the diatom *Chaetoceros gracilis* as a function of N-limited growth rate in continuous culture at $160 \mu mol m^{-2} s^{-1}$ (data from Thomas & Dodson, 1972). Relative growth rate as in C. Some subsequent studies have found a similar pattern, and others have found no relationship between P_{max} and N-limited growth rate (see Cullen *et al.*, 1992).

N , and T . This steady-state model should be developed as a guide for a numerical model that is appropriate for dynamic simulations where steady-state is not achieved. Although our presentation provides few answers, it gives a framework for integrating information on microalgal growth, in order to improve predictions of growth rates and chemical composition for global models. Also, our laboured struggle to find generalizations highlights the pressing need for further research to resolve unanswered questions central to biogeochemical modeling.

2. Analytical Model of Adapted Growth

True to a well-established tradition (cf. Geider *et al.*, 1986 and references therein), the nascent *DENT* (daylength, irradiance, nutrient, temperature) model is an energy budget, based on C. Such models describe the relationships between specific growth rate, the ratio of cellular C to chlorophyll a , and the efficiency of photosynthesis. Because biogeochemical models for the ocean are often based on N, the cellular N:C ratio should also be predicted. This steady-state model would serve as a guide for a dynamic model, which, given enough time under constant conditions, would converge upon the same growth rate and chemical composition as the steady-state model.

The steady-state *DENT* model is based on a simple equality:

$$\mu + r = \frac{P^C}{C}. \quad (1)$$

That is, the gross growth rate (net growth rate, μ , plus respiration, r : d^{-1}) equals the gross photosynthetic rate (P^C , $\text{gC cell}^{-1} \text{d}^{-1}$) normalized to cellular C (gC cell^{-1}). Excretion is implicit in the respiration term. Equation 1 is made meaningful by describing P^C as a function of light absorption and photosynthetic efficiency, in one of many possible representations:

$$\mu + r = D \cdot E \cdot a_{\text{chl}} \cdot \phi \cdot \frac{\text{Chl}}{C} \quad (2a)$$

where D is dimensionless daylength (h/24h), E is mean irradiance during the photoperiod ($\mu\text{mol m}^{-2} \text{s}^{-1}$), a_{chl} is the Chl-specific absorption coefficient ($\text{m}^2 \text{gChl}^{-1}$), ϕ is photosynthetic quantum yield ($\text{mol C (mol photons)}^{-1}$), and Chl is cellular chlorophyll a (gChl cell^{-1}). The product, $D \cdot E \cdot a_{\text{chl}} \cdot \phi \cdot \text{Chl}$ is gross cellular photosynthesis, P^C . Evidence for the applicability of the energy balance comes primarily from an examination of the intraspecific responses of μ , Chl and C (Kiefer & Mitchell, 1983; Sakshaug et al., 1989; Nielsen, 1992), with few independent, direct measurements of all of the variables in eq. 2a.

The energy balance (eq. 2a) does not predict growth rate or photosynthesis as functions of D , E , N and T . It is essentially an accountant's ledger, constraining the mathematical relationships among parameters according to a budget for photons and carbon atoms, thereby providing a unified approach for examining genetic and phenotypic adaptation in phytoplankton. A predictive *DENT* model must specify rate processes (i.e., μ and r), chemical composition (i.e., $C:\text{Chl}$), and the photon (ϕ) and light-harvesting (a_{chl}) efficiencies as functions of temperature, irradiance, and nutrient concentrations within the constraint that an energy balance is achieved. The key to a *DENT* model is to describe the functional dependencies between these parameters as functions of D , E , N , and T . Cellular N:C should also be modeled. Many studies have dealt with subsets of this problem (e.g., Bannister, 1979; Shuter, 1979; Dubinsky et al., 1986; Raven & Geider, 1988; Laws & Chalup, 1990; Langdon, 1988), and, in principle, these results can be integrated into a comprehensive description for a species in culture (Kiefer & Cullen, 1992; Kiefer, this volume). Here we suggest a general form for an analytical representation, emphasizing the possible relationships between parameters.

Parameterizing respiration. In order to further constrain the energy balance, it is desirable to specify the relation between respiration and growth. Following Shuter (1979), respiration can be assigned to maintenance respiration (r_0 with units of d^{-1}) which is independent of growth rate, and biosynthesis which is proportional to growth rate:

$$r = r_0 + \beta\mu. \quad (2b)$$

The cost of biosynthesis, β , is dimensionless. The revised energy balance is:

$$\mu(1 + \beta) + r_o = D \cdot E \cdot a_{chl} \cdot \phi \cdot \frac{Chl}{C}. \quad (2c)$$

Hence, by specifying growth rate, we specify the respiration rate as well. We assume that r_o is a physiological “constant” and that the dependence of respiration on D , T , and N can be treated in terms of their effects on μ . The cost of biosynthesis will depend primarily on the rate of protein synthesis, and it may be more appropriate to normalize respiration to protein synthesis rather than growth (this may be particularly important under N- or P- limiting conditions in which phytoplankton typically accumulate carbohydrate and lipid energy reserves). Unfortunately, there is very little evidence which can be employed to determine the values of r_o and β , and it is possible that these parameters depend on taxon and growth condition (for reviews see Geider, 1987; Langdon, 1992).

Although eq. 2b provides an attractive approach to dealing with the problem of parameterizing phytoplankton respiration, it is an approach that is based on inference rather than hard data (see Geider, 1992b). Finally, in parameterizing respiration, we do not explicitly consider the roles of photorespiration (i.e., the reactions initiated by oxygenation of RuBP by the photosynthetic enzyme RUBISCO) and the Mehler reaction (i.e., O_2 photoreduction by components of the photosynthetic electron transport chain) in energy dissipation by phytoplankton. Rather, we assume that these processes can be treated implicitly through their effect on the quantum efficiency of photosynthesis (ϕ) as discussed below.

The temperature function. Analytical representations of *DENT* interactions would be simplified if environmental factors could be nondimensionalized. A temperature function (Fig. 2A) describes the effect of suboptimal temperature on biosynthetic processes:

$$g_T^* = f(T) \quad (3)$$

where g_T^* is a dimensionless factor that scales maximum rate at a given temperature to the maximum rate at optimum temperature. The function could

be used to describe relative growth rate directly, but we will apply it here to temperature-dependent processes that determine growth rate rather than to growth rate *per se*. Nonetheless, we are compelled to use nutrient- and light-saturated growth rate as the best indication of temperature dependence. No analytical representation for $f(T)$ is presented because we are discussing approaches to the modeling effort rather than implementation. Eppley (1972) presented an analytical representation of $f(T)$ for μ that is still being used to predict maximum growth rates of phytoplankton. That equation provides an upper bound for growth rate based on the fastest growing species (i.e., diatoms and chlorophytes) at their optimum temperature (Raven & Geider, 1988). It does not describe the response of individual species to temperature, which is often more pronounced than the Eppley (1972) curve (Li & Morris, 1982), nor is it applicable to all species. In particular, dinoflagellates and large diatoms are characterized by lower growth rates (Raven & Geider, 1988).

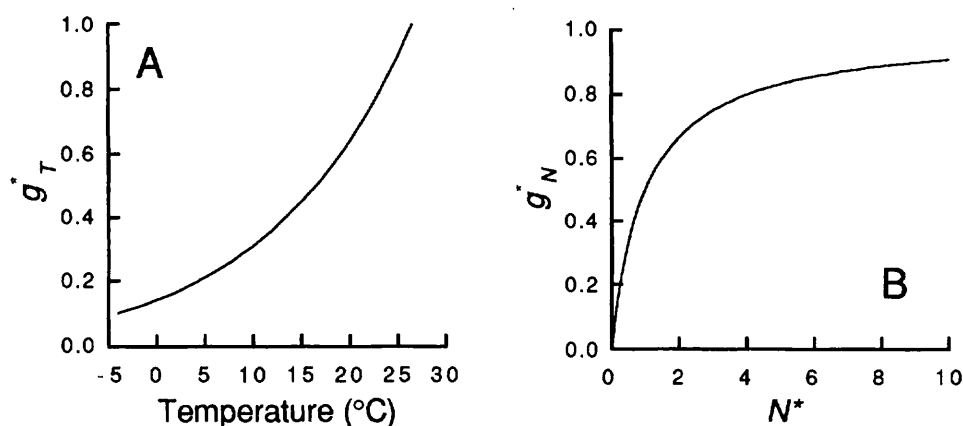


Fig. 2. General features of *DENT* functional relationships. A. The dimensionless temperature function, g_T^* , shown here as an arbitrary Arrhenius function of the form $g_T^* = A \cdot \exp(-B/(T-273))$, where A and B are constants and T is temperature (°C). B. The dimensionless nutrient function, g_N^* (eq. 4), with the concentration of limiting nutrient (N^* , dimensionless) as described in eq. 5.

The nutrient function. As with the temperature function, it is hoped that the nutrient function will describe the effects of nutrient supply on the processes that determine growth rate, yet the first approximation is an equation relating gross growth rate to nutrient supply. Nutrient-limitation of gross specific growth

rate (the dimensionless factor g_N^*) is described with the Monod equation:

$$g_N^* = \frac{N^*}{1 + N^*}, \quad (4)$$

where N^* is the effective nutrient concentration, defined as $[N]/K_m$, with $[N]$, the nutrient concentration, and K_m , the half-saturation constant for growth, in units of μM . Equation 4 is adequate to describe the nutrient dependence of growth rate when uptake of a non-substitutable limiting nutrient is catalyzed by a single transport mechanism (Morel, 1987). This appears to be the case for P- and Si- limitation of growth. It also applies when growth is limited by either nitrate or ammonium. Tentatively, effective nutrient concentration during growth on both nitrate and ammonium is modeled additively:

$$N^* = \frac{[\text{NH}_4]}{K_{m(\text{NH}_4)}} + \frac{[\text{NO}_3]}{K_{m(\text{NO}_3)}}, \quad (5)$$

with the recognition that nutrient interactions (such as ammonium-inhibition of nitrate uptake), once defined, can be accommodated by treating the saturation constants as variables influenced by the presence of other nutrients.

Unfortunately, the appropriate treatment of growth when nitrate and ammonium are simultaneously present at suboptimal concentrations cannot be specified at present because considerable uncertainty surrounds the interaction of these different nitrogen forms on phytoplankton nitrogen assimilation and growth (Dortch, 1990). Progress in resolving this uncertainty has been hindered by the fact that, until recently, the detection limits (approximately 50 nM) of our techniques for measuring nitrate and ammonium have exceeded the concentrations at which these nutrients limit phytoplankton growth ($K_m < 50$ nM). Although this technical limitation has recently been overcome, the new techniques for measuring nitrate and ammonium at nM concentrations have rarely been employed in ecophysiological investigations (Garside & Glover, 1991). The situation is further complicated by recognition that phytoplankton can assimilate urea and amino acids (Antia et al., 1991). Finally, the role of trace

elements as limiting factors for phytoplankton growth, although the subject of recent investigations, remains uncertain (Bruland et al., 1991; Martin et al., 1991; Morel et al., 1991). In the absence of a mechanistic understanding of the interaction of nitrate, ammonium and other nutrients, we cannot endorse any particular description of nitrate-ammonium interactions. The data required for reaching an informed opinion on this matter are simply not available.

The nutrient function (eq. 4) is assumed to act multiplicatively with the temperature function (eq. 3) with respect to growth rate. Thus, consistent with at least one study (Zevenboom et al., 1980), at any nutrient concentration, the absolute uptake rate (per unit cellular N) scales directly with g_T^* so that the half-saturation constant is independent of temperature.

Quantum yield of photosynthesis. For a model of balanced phytoplankton growth under constant irradiance during the light period, the quantum yield for gross photosynthesis at the growth irradiance is required (designated $\phi(E)$). This is not the same thing as an instantaneous measure of photosynthetic quantum yield versus E for any one growth condition, and few data are available for making the appropriate generalizations. Determination of $\phi(E)$ requires simultaneous measurement of the rates of light absorption, respiration (in the light!) and net photosynthesis at the growth irradiance. Most of our inferences on the light dependence of $\phi(E)$ are in fact based on measurements of the quantum efficiency of growth. The quantum efficiency of growth (not gross photosynthesis at the growth irradiance) has been measured under nutrient-replete (Kok, 1952; Myers, 1980; Pirt et al., 1980; Morel et al., 1987; Osborne & Geider, 1987) and nutrient-limited (Chalup & Laws, 1990) conditions. However, these measurements are fraught with technical difficulties and considerable controversy surrounds the absolute values (Osborne & Geider, 1987).

It is well recognized, nonetheless, that the quantum yield of photosynthesis (ϕ , mol C mol photons⁻¹) declines with increasing irradiance as rate of absorption of photons exceeds the rate at which they can be processed by the photosynthetic apparatus. A relatively simple cumulative one-hit model (Dubinsky et al., 1986; Peterson et al., 1987; Eilers & Peeters, 1988; Falkowski, 1992) describes photosynthetic quantum yield as a function of E during exposures to pulses of light, but that exponential model is not necessarily appropriate for describing steady-state ϕ during acclimated growth. Thus, for nutrient-saturated growth at one temperature, we specify a general function,

$$\phi = \phi_{\max} \cdot f(E/E_k). \quad (6)$$

The maximum quantum yield in low light for that temperature and nutrient concentration is ϕ_{\max} and E is scaled to a saturation irradiance, E_k so that photosynthesis (absorbed irradiance $\cdot \phi$) is a saturating function of irradiance. Because it has been shown that the quantum yield of photosynthesis during growth is a function of instantaneous irradiance rather than cumulative exposure during the day (Sakshaug et al., 1989), daylength is not included in eq. 6. The observations of Chan (1978) for diatoms and dinoflagellates, in which the growth rate was linearly related to the Chl:protein ratio, suggest that light utilization efficiency, hence $\phi(E)$, varies little between species.

In the simplest view, temperature is expected to affect the rate at which photons can be processed (Li & Morris, 1982; Raven & Geider, 1988), but not their rate of absorption, so E_k should be a function of g_T^* . Thus, to account for T , we replace E_k in eq. 6 with $E_k \cdot g_T^*$. At this stage of the modeling effort, we defer responding to indications that ϕ_{\max} is depressed at very low temperatures (Tilzer et al., 1986; Raven & Geider, 1988) or other suggestions that photosynthetic efficiency is enhanced at lower temperatures (Davison, 1991). Clearly, these types of responses would further complicate efforts at generalization.

The effect of nutrient limitation on $\phi(E)$ is much more difficult to describe because data are scarce: measurements of photosynthetic characteristics have been made during nutrient-limited growth, but ϕ_{\max} and E_k for growth, as in eq. 6, are not the same as ϕ_{\max} and E_k estimated from short-term measurements of photosynthesis (Myers, 1970; Cullen, 1990) or by fluorescence-based probes of photosynthesis (Falkowski, 1992). Even short-term measurements present a confusing picture. Published data for the maximum normalized rate of photosynthesis during nutrient-limited growth are not consistent (Cullen et al., 1992).

The weight of available evidence suggests that ϕ_{\max} is a nonlinear function of nutrient-limited growth rate in continuous culture (Herzig & Falkowski, 1989; Chalup & Laws, 1990; Falkowski, 1992), so ϕ_{\max} should be a function of g_N^* in an equation describing variability of ϕ :

$$\phi_{\max} = \phi_{\text{opt}} \cdot f_1(g_N^*), \quad (7a)$$

where $f_1(g_N^*)$ approaches 1.0 (i.e., ϕ_{\max} approaches the theoretical maximum, ϕ_{opt}) as g_N^* approaches 1.

It is not at all clear how nutrient limitation influences E_k , the saturation parameter for photosynthesis at growth irradiance, so an unspecified function of nutrient limitation is included in an extremely general equation for variation of quantum yield as a function of E , N , and T :

$$\phi = \phi_{\text{opt}} \cdot f_1(g_N^*) \cdot f\left(\frac{E \cdot f_2(g_N^*)}{E_k \cdot g_T^*}\right). \quad (7b)$$

Here, f_1 and f_2 are potentially, but not necessarily, different functions of g_N^* . It is possible (and it would be very convenient) if both $f_1(g_N^*)$ and $f_2(g_N^*)$ were the

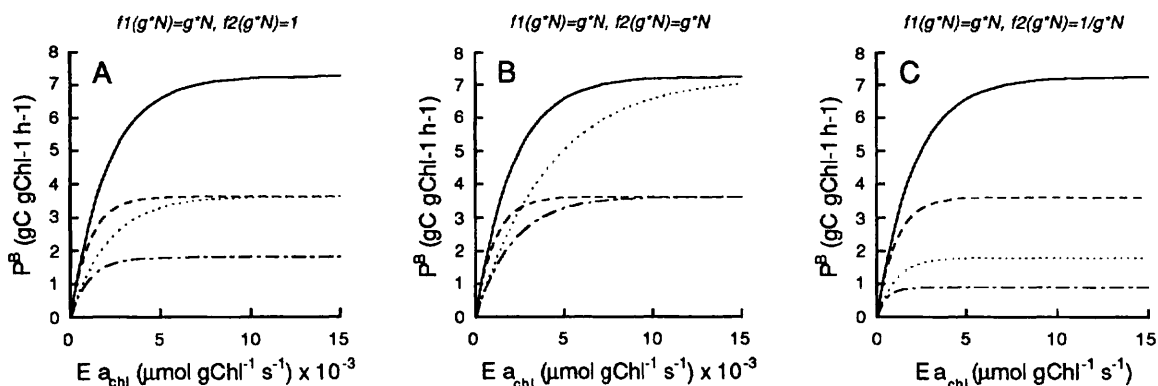


Fig. 3. The relationship between normalized photosynthesis at growth irradiance, P^B ($\text{gC gChl}^{-1} \text{h}^{-1}$) and absorbed irradiance, $E \cdot a_{\text{chl}}$ ($\mu\text{mol photons mg Chl}^{-1} \text{s}^{-1}$) as predicted by different variants of eq. 7b. (—) Nutrient-saturated growth at optimal temperature: $g_N^* = g_T^* = 1.0$; (···) nutrient-limited growth at optimal temperature: $g_N^* = 0.5, g_T^* = 1.0$; (---) nutrient-saturated growth at suboptimal temperature: $g_N^* = 1.0, g_T^* = 0.5$; (- · -) nutrient-limited growth at suboptimal temperature: $g_N^* = 0.5, g_T^* = 0.5$. A. Results from assuming that nutrient-limitation has no effect on the scaling of E_k (i.e., both light-saturated and light-limited $\phi(E)$ are affected the same). B. Nutrient-limitation increases E_k as if the efficiency of electron transport were reduced but capacity per unit chlorophyll a is unaffected by nutrition. C. Nutrient-limitation decreases E_k as if capacity were more sensitive to nutrient limitation than efficiency. These different predictions can be tested with measurements of μ , C:Chl , and a_{chl} on continuous cultures.

same, but that has yet to be resolved. Contrasting predictions of eq. 7b can be examined by plotting normalized photosynthesis, P^B ($\text{gC gChl}^{-1} \text{h}^{-1}$) vs. absorbed irradiance using different nutrient-limitation functions, f_1 and f_2 (Fig. 3). These predictions can be compared to results from laboratory experiments to resolve which functional relationships apply. The variation of the specific absorption coefficient for chlorophyll a (a_{chl}), which also influences P^B , is discussed below.

Carbon:chlorophyll ratio. The C:Chl of phytoplankton, θ , is a sensitive indicator of physiological state (Geider, 1987). The cellular content of Chl, relative to C, decreases when nutrients limit growth, thereby reducing the absorption of light, and bringing the rate of light absorption more-or-less into balance with the rate of energy demand. At a given irradiance, θ is inversely proportional to temperature, reflecting cellular regulation that allows more light to be absorbed when higher temperatures permit higher rates of synthesis per unit protein and a greater demand for energy. Chlorophyll content increases when light limits growth, partially compensating for lower photon flux with higher cellular absorption. A fundamental limitation to this compensating cellular regulation is θ_{min} , the minimum C:Chl (i.e., maximum Chl content; Geider, 1987; Langdon, 1988). Along the lines of Kiefer (this volume), the interactions of D , E , N , and T in determining θ are tentatively described as:

$$\theta = f(\theta_{\text{min}}, \frac{D \cdot E \cdot a_{\text{chl}}}{g_T^*}) \cdot \frac{1}{g_N^*}. \quad (8)$$

That is, with respect to temperature, θ is a function of absorbed irradiance relative to g_T^* , constrained by a maximum Chl relative to C (Fig. 4A). As will be shown below, a_{chl} covaries with θ , so eq. 8 might be simplified by altering the function to include the effect of varying a_{chl} implicitly. Nutrient limitation is modeled as having a direct linear relationship with Chl relative to C (e.g. Laws & Bannister, 1980). That is, nutrient limitation is expressed as an increase of θ until the C-specific growth rate matches the growth rate allowed by the nutrient supply (Bannister & Laws, 1980). In eq. 8, this representation violates an energy balance to the extent that $\phi(E)$ changes with g_N^* (see eq. 7b).

A value for θ_{\min} can be estimated in three different ways. First, we can draw on investigations of the macromolecular composition of the photosynthetic apparatus (Geider, 1987). Second, we can rearrange the energy balance (eq. 2) to calculate θ from E and a_{chl} at the compensation irradiance where $\mu=0$ and $r=r_0$. Third, we can empirically measure θ in cells grown at high temperature and low irradiance (Geider, 1987). Minimum values for θ of 7 to 10 gC gChl^{-1} have been observed in chlorophytes and diatoms at temperatures near 25°C (see also Langdon, 1988). However, dinoflagellates and cyanobacteria are characterized by higher values of θ (Chan, 1978; Geider, 1992a). In the dinoflagellates, high θ is associated with low growth rate, whereas in the cyanobacteria high θ arises

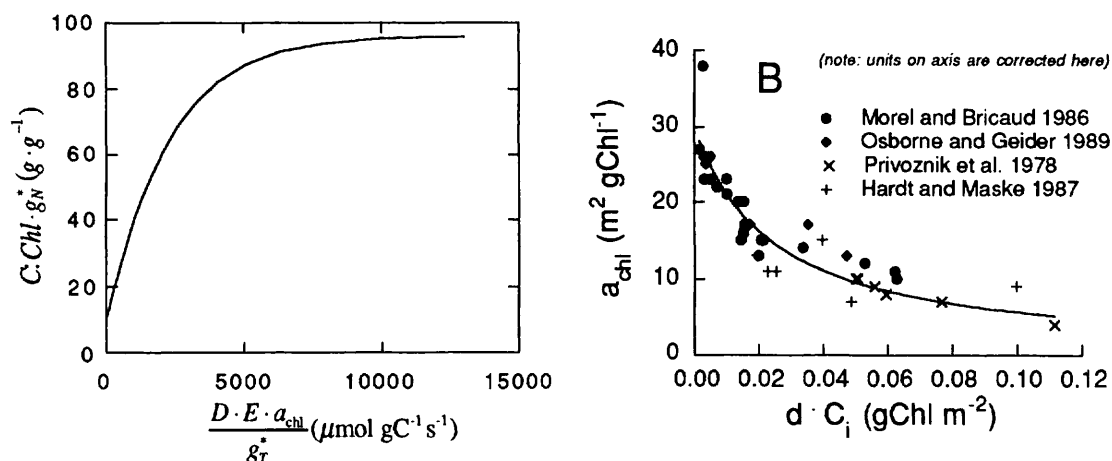


Fig. 4. Variation of θ and a_{chl} . A. The product of C:Chl (g:g) and the nutrient-limitation function g_N^* , as a function of absorbed irradiance over the day, scaled by the temperature function. In this illustration, the θ vs. E relationship has the same form as the photosynthesis ($\phi(E) \cdot E$) vs. E relationship so that during nutrient-sufficient growth, light-limitation of gross growth rate is compensated by increased Chl relative to C. The constraint is that maximum Chl content is limited by θ_{\min} . The predicted relationships between θ , μ , and E are roughly consistent with less general functions presented by Geider (1987) and Langdon (1988). Here, nutrient limitation (g_N^*) is related directly to the amount of Chl relative to C rather than to the efficiency of light utilization. This assumption should be modified when the effects of nutrition on $\phi(E)$ are understood (see text). B. The specific absorption coefficient for Chl, a_{chl} ($\text{m}^2 \text{gChl}^{-1}$), as a function of $d \cdot C_i$, the product of cellular diameter (d , m) and intracellular chlorophyll concentration (C_i , gChl m^{-3}). Symbols represent results from different studies, compiled by Geider (1992a), the source for this comparison. The line is the best fit to the equation, $a_{\text{chl}} = a_{\text{sol}} \cdot (1/(k \cdot d \cdot C_i) + 1)$: $a_{\text{sol}} = 30.3 \text{ m}^2 \text{gChl}^{-1}$, k (an arbitrary coefficient) = 43.4 gChl m^{-2} , $R^2 = 0.84$. More rigorous analytical descriptions of this relationship are presented by Morel and Bricaud (1981). It should be possible to describe a_{chl} as a function of d and θ by relating C_i to θ with an empirical function.

because light harvesting is primarily by phycobiliproteins rather than by chlorophyll-carotenoid protein complexes. There is insufficient data available for characterizing θ_{\min} and the irradiance dependence of θ for other phytoplankton taxa such as the coccolithophorids.

Absorption coefficient for chlorophyll. Normalized photosynthesis, P^B , is frequently measured in the field and predicted in models of biogeochemical cycling. For most studies of phytoplankton growth, P^B can be estimated from measurements of C, Chl and μ (Laws & Bannister, 1980). However, for a general model of phytoplankton growth, it is prudent to describe P^B as a function of light absorption and quantum yield,

$$P^B = \phi \cdot E \cdot a_{\text{chl}}, \quad (9)$$

where a_{chl} ($\text{m}^2 \text{gChl}^{-1}$) is the specific absorption coefficient for chlorophyll a . Differences between patterns of P^B and ϕ are attributable to changes in a_{chl} . Unfortunately, a_{chl} has not been measured as frequently as P^B , so validation of quantum-yield based *DENT* models is difficult although some success has been reported (Marra et al., 1992). It is possible to estimate a_{chl} from optical principles or from empirical relationships, however. A recent example (Geider, 1992) provides us with the basis for proposing that

$$a_{\text{chl}} = f(d, \theta), \quad (10)$$

where d is cell diameter (Fig. 4B). A maximum value for a_{chl} of about $30 \text{ m}^2 \text{gChl}^{-1}$ is approached for small cells and high θ . Basically, self-shading decreases a_{chl} as the internal Chl concentration increases, with the effect being greater for larger cells (Morel & Bricaud, 1981; Kirk, 1983). The influence of variable accessory pigmentation (Bidigare et al., 1992) is not explicitly described here, but, as mentioned above, it can be important, particularly for cyanobacteria.

The *DENT* equation. The details of the functional relationships between parameters (eqs. 3-8, 10) must be examined carefully for consistency with available data from cultures. As anyone who has tried it can attest, comparing measurements from different growth conditions can be extremely difficult. We

feel that the exercise can be facilitated by scaling the independent variables with the dimensionless parameters g_T^* and g_N^* . For example, the similarities between acclimation to lower temperature and to brighter light (Davison, 1991) are qualitatively reconciled when irradiance is scaled to g_T^* , as in eq. 7b. This analytical simplification is based on the concept of relative growth rate as described by Goldman (1980). It is conceptually awkward to use relative growth rate to scale parameters that predict relative growth rate (a problem of circularity that plagues this pursuit), but we have to start somewhere.

Our efforts are directed toward a predictive representation of eq. 2:

$$\mu = \frac{E \cdot D \cdot \text{Chl} \cdot a_{\text{chl}} \cdot \phi}{C} - r = f(D, E, N, T), \quad (11)$$

as well as prediction of P^B through substitution in eq. 9. Although several models have described various aspects of the functional relationships, sometimes in ample detail, the ultimate goal has not yet been achieved, and some of us don't think that we are very close. The principal problems are the apparent complexity of the interactions of environmental factors, and the scarcity of data (sets of growth experiments during which μ , Chl, C and a_{chl} were measured). A great number of growth studies have been performed, however, and indications are that the observations can be incorporated into general descriptions if the appropriate scaling factors are applied. The important thing, we think, is the structure for expressing the relationships:

- 1) maximum rates are a function of temperature (g_T^*);
- 2) nutrient-limitation of growth g_N^* can be expressed as a function of ammonium and nitrate concentrations, scaled to their half-saturation constants;
- 3) C:Chl is a function of absorbed irradiance scaled to g_T^* , and also g_N^* ;
- 4) a_{chl} is a function of Chl and cell diameter; and
- 5) quantum yield (i.e., $\phi(E)$) is a function of g_T^* and probably g_N^* .

Whatever the real patterns are, we hope to see them using this analytical context.

Practical advice. Equations 3 to 8 and 10 can be substituted into a

predictive *DENT* model, but the result is horrendously complex and not particularly instructive, even if the unspecified functions are replaced with analytical representations. Nonetheless, even a complex equation could be used to make predictions for a biogeochemical model of phytoplankton growth. Experience has shown, however, that simplicity is the key for interdisciplinary acceptance of a phytoplankton model. How can the *DENT* model be simplified for use in numerical simulations?

One way to simplify the energy balance is to combine terms. For example, even though both ϕ_{\max} and a_{chl} are functions of nutrient-limited growth rate at a given irradiance and temperature, it is possible that their product (see eq. 9) is acceptably constant (Kiefer & Mitchell, 1983), allowing us to express the energy balance as a function of the P^B vs. E relationship and the C:Chl ratio (see Geider, 1990). One form for such a model could be

$$\mu + r = \frac{\text{Chl}}{C} \cdot D \cdot P_{\max}^B (1 - e^{-E/E_k}), \quad (12)$$

(Cullen, 1990) where both P_{\max}^B (gC gChl⁻¹ h⁻¹; the maximum adapted rate of normalized photosynthesis) and E_k are functions of g_T^* and possibly g_N^* . Given that the left-hand side of the equation can be specified by g_T^* and g_N^* , C:Chl is algebraically constrained. Equation 12 is practical because it has three essential parameters for biogeochemical modeling: growth rate, chemical composition and P^B vs. E . However, the simplification of modeling P^B rather than $\phi \cdot a_{\text{chl}}$ compromises its utility as a physiological description of growth and chemical composition of phytoplankton, leaving us with a problem of describing empirically how P^B vs. E and μ vs. E are influenced by D , E , N , and T . That may be the best we can do.

Equation 12 may fail to hold, even as an approximation. For example, Laws and Chalup (1990) concluded that the product of the quantum yield coefficient (ϕ) and specific absorption coefficient (a_{chl}) was hyperbolically related to nutrient limited growth rate. Thus, detailed growth models can uncover relationships that might be used to modify the oversimplified relationship in eq. 12.

Predicting the ratio of N:C. Cellular nitrogen can be included explicitly in growth models (Shuter, 1979; Laws & Chalup, 1990), and its variation can be

biogeochemical models presently in use. However, a steady-state model cannot describe the photosynthesis, growth, and chemical composition of phytoplankton in variable environments because environmental conditions change too rapidly for steady-state to be assumed. In theory, this type of prediction can be accomplished with a dynamic model of photosynthesis, nutrient uptake, and allocation of cellular carbon on the cellular level (Lancelot et al., 1991a; Lancelot et al., 1991b; Fig. 5). The dynamic model also obviates the problem of assuming constant E during the photoperiod in the steady-state model. We hoped to describe the dynamic model in some detail and to suggest modifications, but this was not possible in the time available. For example, future models could incorporate recently-developed descriptions of P^B vs. E under variable irradiance (Baumert & Uhlmann, 1983; Denman & Marra, 1986; Pahl-Wostl & Imboden, 1990; Janowitz & Kamykowski, 1991). It is clear to us that further development of dynamic models is warranted, with one objective being agreement between the dynamic and steady-state *DENT* model for constant conditions.

4. Other considerations

Our working group considered many aspects of modeling phytoplankton growth for biogeochemical models, but we concentrated on a *DENT* model, trying to tell numerical modelers how one might be constructed. This goal proved to be elusive. Even the most general approaches were hampered by lack of information and insufficient time to assimilate and apply the huge amounts of experimental data that are available. Other considerations, which are important to any modeling effort, further complicate our work, but should be kept in mind as models are developed:

- 1) The size of phytoplankton has important physiological, optical, trophodynamic, and biogeochemical consequences. Phytoplankton should be modeled as at least two classes (big and small), with different functional responses. For example, it could be assumed that diatoms dominate the large size class. That is, only the big cells require Si, and sinking is important only in the large size class — faster when nutrients are depleted (Steele & Yentsch, 1960; see also Waite et al., 1992).

- 2) Limitation of phytoplankton growth by CO₂ is a special case (Raven & Johnston, 1991), which we consider to be unimportant at this stage of model development.
- 3) We cannot suggest *DENT* models for limitation of phytoplankton growth by iron or other trace elements (Morel et al., 1991). It would probably be best to omit iron from models and identify its possible influence from aberrant model behavior.
- 4) It should be recognized that, under certain conditions, respiration can be an extremely important component of energy flow (Geider, 1992b) and that simplified treatments of *r* can lead to poor predictions under those circumstances.

Although numerous other recommendations can be listed, we stop here because the situation as presented is sufficiently intimidating.

5. Caveats

Our generalized descriptions of phytoplankton growth are quite idealistic, yet still vague and incomplete. If appropriate *DENT* models are developed and validated, they are likely to apply initially to only a few species of phytoplankton in culture. It should be clearly recognized that other factors (e.g., taxonomy and environmental variability) will have an influence on predictions. We have no quantitative approach for predicting species composition for natural phytoplankton, thus we expect problems with general models. With time, taxon-specific predictions can be developed and compared with nature. Unfortunately, validation of predictions (i.e. μ , C:Chl and C:N) is complicated by the contribution of detritus to measurements of particulate C and N: we cannot measure directly the growth rate or chemical composition of phytoplankton (Eppley, 1980).

6. Conclusions

Models of global biogeochemical processes in the sea require information on the effects of daylength, irradiance, temperature and nutrients on the biochemical and physiological properties of phytoplankton. Although much has been achieved in describing important interactions, construction of a general descriptive model has proven very difficult. This is a task that requires time, a great deal of study, additional lab work, clear focus, and collaboration. Progress may accelerate if large research programmes recognize explicitly the need to develop models of phytoplankton growth, channeling resources accordingly. The obstacles to formulating good, general models of phytoplankton are daunting indeed, but the need for progress cannot be ignored. The alternative is to use inadequate approximations of C:Chl and P^B vs. E in basin-scale biogeochemical models.

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