FEATURE ARTICLE: NOTE

Optimal allocation backs Droop's cell-quota model

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ABSTRACT: Droop's cell-quota model is the most successful description of phytoplankton growth in laboratory cultures and is increasingly being introduced into the ecosystem components of biogeochemical models. Although the Droop model's parameters can be easily interpreted in biological terms, it was nevertheless derived empirically and lacks a sound mechanistic foundation. Here we derive Droop's model from a simple optimality condition which maximises net growth rate. Our approach links the maximum cell quota to the cost of nutrient acquisition and suggests that respiration is influenced more strongly by C fixation than by N assimilation.

KEY WORDS: Optimality-based model · Cell quota · Droop model

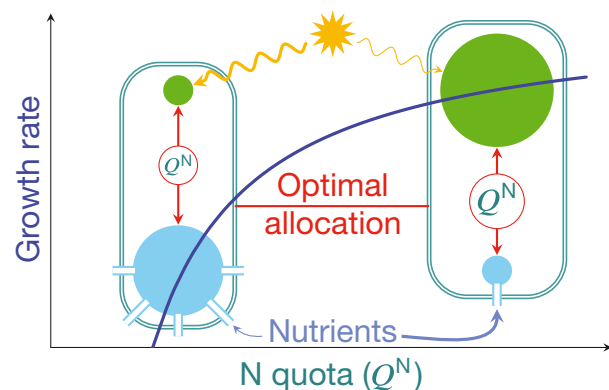Droop's cell-quota model of growth rate as a function of cell quota (dark blue curve) represents optimal allocation of phytoplankton cellular N (Q^N) between light harvesting (green disks) and nutrient acquisition (blue discs with pipes). The optimal allocation responds to the availability (width of light blue and yellow arrows) of both nutrients and light.

Diagram: M. Pahlow

INTRODUCTION

Droop originally derived the cell-quota model as an empirical description of the observed relationship between growth rate and cellular content, or cell quota (of vitamin B12; Droop 1968, 1973):

$$\mu = \hat{\mu}\left(1 - \frac{Q_0}{Q}\right) \tag{1}$$

where μ is relative growth rate, $\hat{\mu}$ is potential growth rate, Q is cell quota and Q_0 is minimum or subsistence quota. Because of the strong correlation between most cellular constituents and biomass in terms of carbon (C), cell quotas are best expressed per unit biomass, as constituent:C ratios (Droop 1983). In this form, it remains the simplest and most successful formulation of phytoplankton growth as a function of

biochemical composition (Flynn 2008), and has been widely used in different variants in 0-, 1- and even 2-dimensional global biogeochemical models (e.g. Moore et al. 2002, Mongin et al. 2003, Wirtz & Pahlow 2010). Similarities to Droop's cell-quota model have even been used to lend support to other modelling approaches. For example, Kooijman (2001) reported that the cell-quota model could, under certain assumptions, be linked to the DEB (dynamic energy budget) theory, and Wirtz & Pahlow (2010) found that their optimality-based adaptive dynamics behaved very similarly to Eq. (1). However, the cell-quota model lacks a sound mechanistic underpinning and fails, e.g., to predict a maximum quota (Flynn 2008). In the following, we present an analytical derivation of Droop's cell-quota

Table 1. Symbol definitions and units. $\hat{\mu}_g^I$, Q_s^N, $\hat{V}^N$ (or $\hat{V}_{max}^N$), ζ^C and ζ^N are parameters, all others are derived quantities

Symbol	Unit	Definition
C_c	mol cell^{-1}	Chloroplast C
C_t	mol cell^{-1}	Total cellular C
f_V	–	N fraction devoted to N acquisition
f_V^o	–	Optimal f_V
μ	d^{-1}	Relative growth rate
$\hat{\mu}$	d^{-1}	Potential relative growth rate
$\hat{\mu}^I$	d^{-1}	Potential biomass (C)-normalised C fixation
$\hat{\mu}_g^I$	d^{-1}	Potential biomass-normalised gross C fixation
N_c	mol cell^{-1}	Chloroplast N
N_s	mol cell^{-1}	Cellular N in structural material
N_t	mol cell^{-1}	Total cellular N
Q	mol mol^{-1}	Cell quota (constituent:C_t ratio)
Q_0	mol mol^{-1}	Minimum (subsistence) cell quota
Q^N	mol mol^{-1}	Cellular N:C ratio (N quota)
Q_s^N	mol mol^{-1}	Cellular N_s:C_t ratio
R	d^{-1}	Relative respiration rate
V^N	mol mol^{-1} d^{-1}	Biomass (C)-normalised N acquisition
V_{max}^N	mol mol^{-1} d^{-1}	Maximum biomass-normalised N acquisition
$\hat{V}^N$	mol mol^{-1} d^{-1}	Potential biomass-normalised N acquisition
$\hat{V}_{max}^N$	mol mol^{-1} d^{-1}	Max. potential biomass-normalised N acquisition
ζ^C	–	Respiration cost of C fixation
ζ^N	mol mol^{-1}	Respiration cost of N uptake and assimilation

model (Eq. 1) from a simple optimality condition, which maximises balanced, nitrogen-limited growth and also yields predictions about respiration and the maximum cell quota. Symbol definitions and units are given in Table 1.

OPTIMALITY-BASED DERIVATION OF DROOP'S CELL-QUOTA MODEL

Optimality provides a powerful conceptual basis for the formulation of phytoplankton growth models (Shuter 1979, Smith et al. 2011). Here we derive an optimality condition by balancing respiration and allocation costs against benefits of nutrient acquisition. Respiration (energy) costs of nutrient acquisition are assumed proportional to nutrient acquisition. Allocation costs are formulated as an assumption that a fixed amount of cellular nitrogen (N), represented by the biomass-normalised N cell quota (N:C ratio, Q^N), is bound in structural material and the remainder is allocated between requirements for C and N acquisition (Fig. 1A). Potential C and N acquisition are assumed proportional to the respective relative sizes of the chloroplast (C fixation) and the N acquisition machinery. We define the allocation factor f_V as the fraction of cellular N invested in the N-acquisition machinery (Wirtz & Pahlow 2010). For conceptual simplicity, it is assumed here that N and C are allocated in parallel, implying the same N:C ratio in the
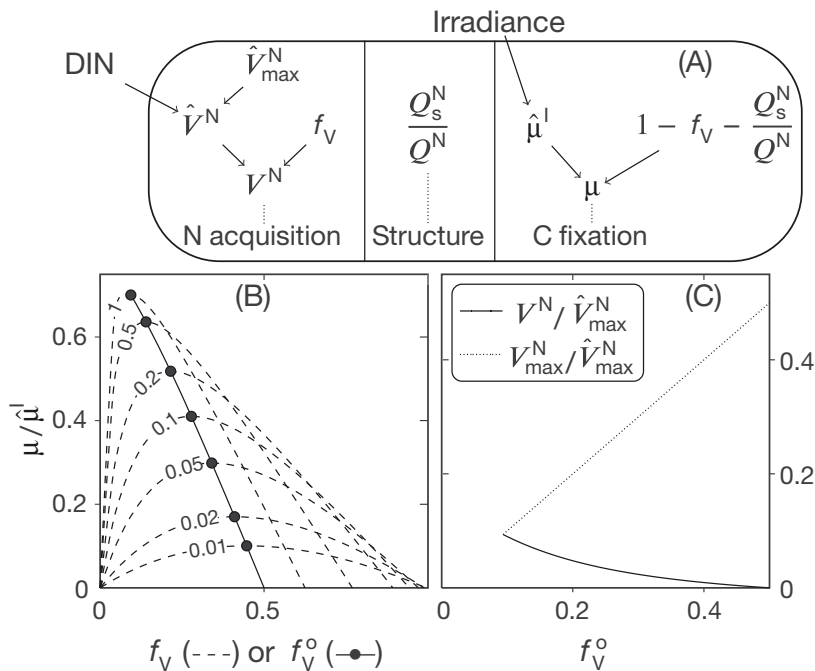

Fig. 1. (A) Schematic diagram of N allocation via the allocation factor f_V among N acquisition (protoplast), structure and C fixation (chloroplast). Dissolved inorganic nitrogen (DIN) concentration and maximum potential N uptake ($\hat{V}_{max}^N$) determine potential N uptake ($\hat{V}^N$). N allocation to N acquisition (f_V) then controls actual N uptake (V^N). The fraction of cellular N not allocated to N acquisition and structural material ($1 - f_V - Q_s^N/Q^N$) and the light-dependent potential maximum relative growth rate ($\hat{\mu}^I$) control C fixation, together with the cost of N assimilation (ζ^N, not shown). (B) Relation between relative growth rate (μ, normalised to $\hat{\mu}^I$) and f_V (dashed lines; line labels indicate the saturation of the N uptake apparatus [$\hat{V}^N/\hat{V}_{max}^N$]). Filled circles indicate the maximum of each curve, corresponding to f_V^o; the solid line describes the optimally acclimated behaviour. (C) Relation between f_V^o and actual (V^N) and maximum N uptake (V_{max}^N), both normalised to maximum potential N uptake ($\hat{V}_{max}^N$). V_{max}^N is highest in nutrient-starved cells (high f_V^o), allowing for quick uptake once nutrients become available. Panels B and C are for $\hat{\mu}^I = 1$ d^{-1}, $\hat{V}_{max}^N = 1$ mol mol^{-1} d^{-1}, $Q_s^N = 0.02$ mol mol^{-1} and $\zeta^N = 0.6$ mol mol^{-1}. See Table 1 for full symbol definitions

chloroplast as in the whole cell (Pahlow & Oschlies 2009). The relative size (in terms of biomass) of the chloroplast is then:

$$\frac{N_c}{C_c} = \frac{N_t}{C_t} \Leftrightarrow \frac{C_c}{C_t} = \frac{N_c}{N_t} = \frac{N_t - N_s - f_V N_t}{N_t} = 1 - \frac{Q_s^N}{Q^N} - f_V \quad (2)$$

where the subscripts c, s and t indicate the chloroplast, structural material and whole cell, respectively. Now we define the local, i.e. compartment-specific, biomass-normalised rates of net C and N acquisition as $\hat{\mu}^I$ and $\hat{V}^N$, respectively, where the superscripts refer to external dependencies: $\hat{\mu}^I$ is a function of irradiance and $\hat{V}^N$ is a saturating function of ambient dissolved inorganic nitrogen (DIN) with an inherent maximum, $\hat{V}_{max}^N$ (Fig. 1A). Thus, light dependency is associated with the chloroplast and DIN dependency is associated with the nutrient-acquisition compartment. Then the actual rates of net C and N acquisition, μ^I and V^N, respectively, can be calculated as the products of the local rates and relative sizes of the corresponding compartments:

$$\mu^I = \hat{\mu}^I \left(1 - \frac{Q_s^N}{Q^N} - f_V \right) \quad (3)$$

$$V^N = f_V \hat{V}^N \quad (4)$$

Net relative growth rate (μ) can be defined as the balance of net C fixation by the chloroplast and respiration costs of N acquisition, such that,

$$\mu = \mu^I - \zeta^N V^N = \hat{\mu}^I \left(1 - \frac{Q_s^N}{Q^N} - f_V \right) - \zeta^N f_V \hat{V}^N \quad (5)$$

where ζ^N is the cost of N uptake and assimilation. Note that both local rates may comprise both gain and loss terms, e.g., $\hat{\mu}^I$ represents the balance between gross C fixation and the associated respiration costs within the chloroplast. While the precise forms of the light and DIN functions $\hat{\mu}^I$ and $\hat{V}^N$ do not matter for the present analysis, they must not depend on Q^N or f_V, as we require that Eq. (5) is explicit in these 2 quantities.

In order to find the optimal allocation (f_V^o) between nutrient acquisition and light harvesting, Q^N is eliminated from Eq. (5) with the help of the balanced-growth approximation:

$$\mu Q^N = V^N = f_V \hat{V}^N \Leftrightarrow Q_s^N \frac{\hat{\mu}^I}{\hat{V}^N} + f_V = Q^N \left[\frac{\hat{\mu}^I}{\hat{V}^N}(1 - f_V) - \zeta^N f_V \right] \quad (6)$$

whence the optimality condition for the optimal allocation factor (f_V^o; Fig. 1B) can be defined for balanced growth as:

$$\frac{d\mu}{df_V} \overset{!}{=} 0 \Leftrightarrow f_V^{o2} + 2f_V^o Q_s^N \frac{\hat{\mu}^I}{\hat{V}^N} - \frac{Q_s^N}{\frac{\hat{V}^N}{\hat{\mu}^I} \left(1 + \zeta^N \frac{\hat{V}^N}{\hat{\mu}^I} \right)} = 0 \quad (7)$$

The above quadratic equation is readily solved for the optimal allocation factor f_V^o as a function of prescribed model parameters (ζ^N and Q_s^N) and external conditions entering the C and N acquisition terms ($\hat{\mu}^I$ and $\hat{V}^N$). In order to relate our optimality-based concept to Droop's model (Eq. 1), Eq. (6) is rearranged to yield an expression for $\hat{\mu}^I/\hat{V}^N$, which is substituted in Eq. (7) to obtain:

$$\left[f_V^o - \left(1 + \zeta^N Q_s^N \right) \right] \left[f_V^o - \frac{Q_s^N}{Q^N} + \zeta^N \left(Q^N - 2Q_s^N \right) \right] = 0 \quad (8)$$

With the obvious condition $0 < f_V^o < 1$, the second term has to be zero, i.e.

$$f_V^o = \frac{Q_s^N}{Q^N} - \zeta^N \left(Q^N - 2Q_s^N \right) \quad (9)$$

f_V^o is highest for nutrient-starved cells, i.e. V_{max}^N approaches its maximum as $V^N \to 0$ (Fig. 1C), thus providing the means for efficient uptake once nutrient concentrations rise. Substituting Eq. (9) into Eq. (6) yields Q^N as:

$$Q^N = Q_s^N \left[1 + \sqrt{1 + \frac{1}{Q_s^N \left(\frac{\hat{\mu}^I}{\hat{V}^N} + \zeta^N \right)}} \right] \quad (10)$$

which allows analysis of the limit behaviour of the optimal allocation model: maximal Q^N occurs under extreme light limitation, i.e. as $\hat{\mu}^I/\hat{V}^N \to 0$, and Q^N approaches $2Q_s^N$ as $\hat{V}^N \to 0$. Substituting $2Q_s^N$ as the lower limit for Q^N in Eq. (9) yields the upper limit of f_V^o as 0.5 (Fig. 1B). Thus, while the respiration cost (ζ^N) of N acquisition strongly affects the lower limit of f_V^o, this does not apply to the upper limit because the respiration term ($\zeta^N V^N$) in Eq. (5) vanishes as $V^N \to 0$.

After eliminating $\hat{V}^N$ from Eq. (5) with the help of Eq. (6) and substituting f_V^o from Eq. (9) for f_V, Eq. (5) reduces to Droop's cell-quota model for balanced, N-(co-)limited growth under constant irradiance (for which $\hat{\mu}^I$ is constant):

$$\mu = \hat{\mu}^I \left(1 - 2\frac{Q_s^N}{Q^N} \right) \quad (11)$$

which is of the same form as Eq. (1), with $\hat{\mu} \equiv \hat{\mu}^I$, $Q \equiv Q^N$ and $Q_0 \equiv 2Q_s^N$. This derivation shows that Droop's cell-quota model can be understood as a manifestation of optimal growth.

RESPIRATION

Furthermore, Eq. (5) explicitly links growth to respiration as a corollary of balancing C fixation gains against respiratory costs of N acquisition. The fact
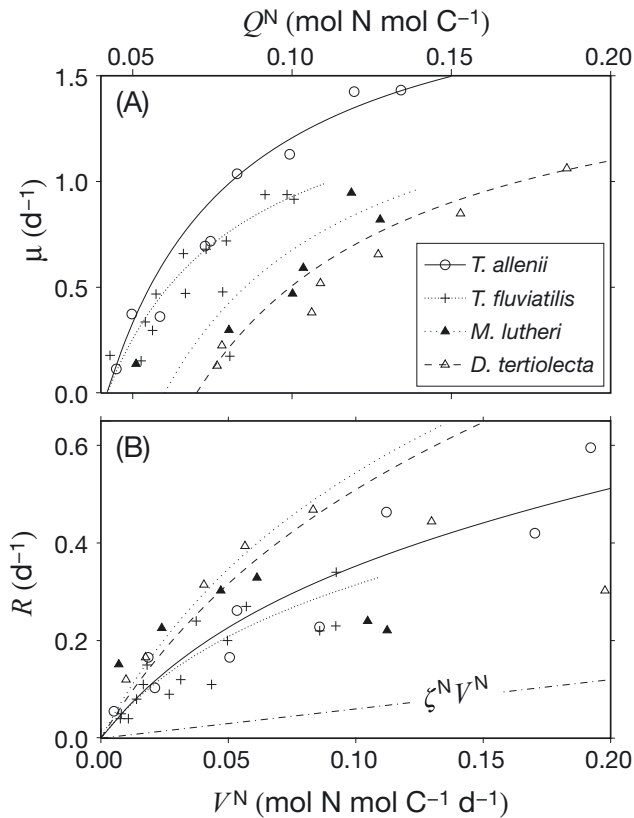
Fig. 2. (A) Growth rate (μ) as a function of N cell quota (N:C ratio) and (B) respiration (R) as a function of nutrient uptake rate ($V^N = \mu Q^N$). Symbols are observations from Laws & Bannister (1980) for *Thalassiosira fluviatilis*, and from Laws & Wong (1978) for *Thalassiosira allenii*, *Monochrysis lutheri* and *Dunaliella tertiolecta*. Lines are model predictions, with $\hat{\mu}_g^I = 2.6$ d^{-1} (except $\hat{\mu}_g^I = 2$ d^{-1} for *T. fluviatilis*), $\zeta^N = 0.6$ mol C mol^{-1} N for all 4 species, $Q_s^N = 0.021, 0.021, 0.03$ and 0.035 mol N mol^{-1} C, and $\zeta^C = 0.2, 0.2, 0.35$ and 0.35, respectively. The dash-dotted line in Panel B indicates the cost of nitrogen acquisition ($\zeta^N V^N$)

that neither $\hat{V}^N$ nor ζ^N appear in Eq. (11) might explain the universality of this relation. However, it also means that observations of growth rate as a function of cell quota alone contain no information about the kinetics and associated costs of nutrient acquisition, which must hence be determined by other means. Laws & Bannister (1980) presented cell-quota observations with Q^N varying between 0.04 ($\rightarrow Q_s^N = 0.02$) and 0.2 mol N mol^{-1} C, likely encompassing close to the full range for *Thalassiosira fluviatilis*, as their cultures comprised both strong nutrient and strong light limitation. We use this range to obtain a rough estimate for ζ^N from Eq. (10), giving about 0.6 mol C mol^{-1} N. This is much lower than previous estimates of around 2 mol C mol^{-1} N, based on some of the data in Fig. 2B (Geider et al. 1998) or theoretical considerations (Pahlow 2005), which

implies that a significant fraction of dark respiration cannot be attributed directly to nutrient acquisition. A relatively simple way to reconcile observed respiration rates with our optimal allocation model is to consider the contribution of the cost of photosynthesis, implicitly contained in $\hat{\mu}^I$, to total respiration. The cost of photosynthesis here represents dark-respiration costs related to all metabolic activities, e.g., protein turnover (Quigg & Beardall 2003), other than nutrient acquisition. We define ζ^C as the fraction of respiration losses within the chloroplast, $\hat{\mu}^I = \hat{\mu}_g^I (1 - \zeta^C)$, so that respiration ($R$) can be written as:

$$R = \zeta^C \hat{\mu}_g^I \left(1 - \frac{Q_s^N}{Q^N} - f_V^o\right) + \zeta^N V^N \qquad (12)$$

where $\hat{\mu}_g^I$ is gross C fixation with respect to the chloroplast. Model predictions from Eqs. (11) & (12) are shown in Fig. 2. The cost of photosynthesis actually dominates R, whereas the cost of N acquisition ($\zeta^N V^N$) contributes only roughly 5 to 25 % (dash-dotted line in Fig. 2B). While a linear dependence of R on V^N (e.g. Shuter 1979, Geider et al. 1998) would fit the observations in Fig. 2B similarly well, this would result in an unrealistically high maintenance respiration (y-intercept) of about 0.1 d^{-1} (not shown). Our optimal allocation model does not suffer from this problem.

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