FEATURE ARTICLE: NOTE

Optimal allocation backs Droop's cell-quota model

Markus Pahlow*, Andreas Oschlies
GEOMAR Helmholtz Centre for Ocean Research Kiel, Düsternbrooker Weg 20, 24105 Kiel, Germany

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

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):

\[ \mu = \hat{\mu} \left(1 - \frac{Q_b}{Q}\right) \]  

where \( \mu \) is relative growth rate, \( \hat{\mu} \) is potential growth rate, \( Q \) is cell quota and \( Q_b \) 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. \( \ddot{\mu}_I \), \( Q^N \), \( \dot{V}^N \) (or \( \dot{V}^N_{\text{max}} \)), \( \zeta^C \) and \( \zeta^N \) are parameters, all others are derived quantities.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Unit</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>( C_c )</td>
<td>mol cell(^{-1} )</td>
<td>Chloroplast C</td>
</tr>
<tr>
<td>( C_{t} )</td>
<td>mol cell(^{-1} )</td>
<td>Total cellular C</td>
</tr>
<tr>
<td>( f_V )</td>
<td>–</td>
<td>N fraction devoted to N acquisition</td>
</tr>
<tr>
<td>( f_O )</td>
<td>–</td>
<td>Optimal ( f_V )</td>
</tr>
<tr>
<td>( \mu )</td>
<td>d(^{-1} )</td>
<td>Relative growth rate</td>
</tr>
<tr>
<td>( \hat{\mu} )</td>
<td>d(^{-1} )</td>
<td>Potential relative growth rate</td>
</tr>
<tr>
<td>( \hat{\mu}_I )</td>
<td>d(^{-1} )</td>
<td>Potential biomass-normalised C fixation</td>
</tr>
<tr>
<td>( \ddot{\mu}_I )</td>
<td>d(^{-1} )</td>
<td>Potential biomass-normalised gross C fixation</td>
</tr>
<tr>
<td>( N_c )</td>
<td>mol cell(^{-1} )</td>
<td>Chloroplast N</td>
</tr>
<tr>
<td>( N_s )</td>
<td>mol cell(^{-1} )</td>
<td>Cellular N in structural material</td>
</tr>
<tr>
<td>( N_t )</td>
<td>mol cell(^{-1} )</td>
<td>Total cellular N</td>
</tr>
<tr>
<td>( Q )</td>
<td>mol mol(^{-1} )</td>
<td>Cell quota (constituent:C ratio)</td>
</tr>
<tr>
<td>( Q_0 )</td>
<td>mol mol(^{-1} )</td>
<td>Minimum (subsistence) cell quota</td>
</tr>
<tr>
<td>( Q^N )</td>
<td>mol mol(^{-1} )</td>
<td>Cellular N:C ratio (N quota)</td>
</tr>
<tr>
<td>( Q^N_{\text{max}} )</td>
<td>mol mol(^{-1} )</td>
<td>Cellular N:C ratio</td>
</tr>
<tr>
<td>( R )</td>
<td>d(^{-1} )</td>
<td>Relative respiration rate</td>
</tr>
<tr>
<td>( V^N )</td>
<td>mol mol(^{-1} ) d(^{-1} )</td>
<td>Biomass (C)-normalised N acquisition</td>
</tr>
<tr>
<td>( V^N_{\text{max}} )</td>
<td>mol mol(^{-1} ) d(^{-1} )</td>
<td>Maximum biomass-normalised N acquisition</td>
</tr>
<tr>
<td>( \dot{V}^N )</td>
<td>mol mol(^{-1} ) d(^{-1} )</td>
<td>Potential biomass-normalised N acquisition</td>
</tr>
<tr>
<td>( \dot{V}^N_{\text{max}} )</td>
<td>mol mol(^{-1} ) d(^{-1} )</td>
<td>Max. potential biomass-normalised N acquisition</td>
</tr>
<tr>
<td>( \zeta^C )</td>
<td>–</td>
<td>Respiration cost of C fixation</td>
</tr>
<tr>
<td>( \zeta^N )</td>
<td>mol mol(^{-1} )</td>
<td>Respiration cost of N uptake and assimilation</td>
</tr>
</tbody>
</table>

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

\[
\frac{N_c}{C_c} = \frac{N_s}{C_s} = \frac{N_t}{C_t} = \frac{N_c - f_o N_c}{N_t} = 1 - \frac{Q^N}{Q^N} - f_v
\]

(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: \( \hat{\mu} \) is a function of irradiance and \( \hat{V}^N \) is a saturating function of ambient dissolved inorganic nitrogen (DIN) with an inherent maximum, \( \hat{V}_{max}^N \).

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, \( \mu^i \) and \( V^N \), respectively, can be calculated as the products of the local rates and relative sizes of the corresponding compartments:

\[
\mu^i = \hat{\mu}^i \left(1 - \frac{Q^N}{Q^N} - f_v\right)
\]

(3)

\[
V^N = f_v \hat{V}^N
\]

(4)

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

\[
\mu = \mu^i - \zeta^N \hat{V}^N = \hat{\mu}^i \left(1 - \frac{Q^N}{Q^N} - f_v\right) - \zeta^N f_v \hat{V}^N
\]

(5)

where \( \zeta^N \) 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:

\[
\mu Q^N = V^N = f_v \hat{V}^N \Leftrightarrow Q^N = f_v \frac{\hat{\mu}^i}{\hat{V}^N} (1 - f_v) = \hat{\mu}^i (1 - f_v) \hat{V}^N
\]

(6)

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

\[
\frac{d\mu}{df_v} = 0 \Leftrightarrow f_v^o = 2f_v^o Q^N \frac{\hat{\mu}^i}{\hat{V}^N} - \frac{Q^N}{\hat{V}^N} = 0
\]

(7)

The above quadratic equation is readily solved for the optimal allocation factor \( f_v^o \) as a function of prescribed model parameters \( (\hat{\mu}^i, \hat{V}^N) \) and external conditions entering the C and N acquisition terms \( (\zeta^C, \zeta^N) \). 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:

\[
\left[ f_v^o - \left(1 + \zeta^N Q^N\right)\right] f_v^o - \frac{Q^N}{Q^N} + \zeta^N (Q^N - 2Q^N) = 0
\]

(8)

With the obvious condition \( 0 < f_v^o < 1 \), the second term has to be zero, i.e.

\[
f_v^o = \frac{Q^N}{Q^N} - \zeta^N (Q^N - 2Q^N)
\]

(9)

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

\[
Q^N = Q^N_o \left[1 + \frac{1}{Q^N_o^o} \left(\frac{\hat{\mu}^i}{\hat{V}^N} + \zeta^N\right)\right]
\]

(10)

which allows analysis of the limit behaviour of the optimal allocation model: maximal \( Q^N \) occurs under extreme light limitation, i.e. as \( \hat{\mu}^i/\hat{V}^N \rightarrow 0 \), and \( Q^N \) approaches \( 2Q^N_o \) as \( \hat{V}^N \rightarrow 0 \). Substituting \( 2Q^N_o \) 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 \( (\zeta^N) \) of N acquisition strongly affects the lower limit of \( f_v^o \), this does not apply to the upper limit because the respiration term \( (\zeta^C V^N) \) in Eq. (5) vanishes as \( V^N \rightarrow 0 \).

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):

\[
\mu = \hat{\mu}^i \left(1 - \frac{2Q^N}{Q^N_o}\right)
\]

(11)

which is of the same form as Eq. (1), with \( \hat{\mu} = \hat{\mu}^i, Q = Q^N \) and \( Q_o = 2Q^N_o \). 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
that neither $\hat{V}^N$ nor $\zeta^N$ 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 ($\rightarrow Q^N = 0.02$) 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 $\zeta^N$ 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 $\hat{\mu}$, 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 $\zeta^C$ as the fraction of respiration losses within the chloroplast, $\hat{\mu} = \hat{\mu}^g_1$ (1 − $\zeta^C$), so that respiration (R) can be written as:

$$ R = \zeta^C \hat{\mu}^g_1 \left( 1 - \frac{Q^N}{Q^N - f^N_{\mu}} \right) + \zeta^NV^N \quad (12) $$

where $\hat{\mu}^g_1$ 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 ($\zeta^C V^N$) 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 ($\gamma$-intercept) of about 0.1 d$^{-1}$ (not shown). Our optimal allocation model does not suffer from this problem.

**Acknowledgements.** This work is a contribution of the Sonderforschungsbereich 754 ‘Climate-Biogeochemistry Interactions in the Tropical Ocean’ (www.sfb754.de), which is funded by the German Science Foundation (DFG). This article benefitted from the input of 3 anonymous reviewers.

**LITERATURE CITED**


Editorial responsibility: Katherine Richardson, Copenhagen, Denmark

Submitted: June 25, 2012; Accepted: November 14, 2012
Proofs received from author(s): January 4, 2013