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Towards a more biologically realistic use of Droop's equations to model growth under multiple nutrient limitation

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Droop's model was originally designed to describe the growth of unicellular phytoplankton species in chemostats but it is now commonly used for a variety of organisms in models of trophic interactions, ecosystem functioning, and evolution. Despite its ubiquitous use, Droop's model is still limited by several simplifying assumptions. For example, the assumption of equal theoretical maximum growth rates for all nutrients is commonly used to describe growth limited by multiple nutrients. This assumption, however, is both biologically unrealistic and potentially misleading. We propose the alternative hypothesis of equal realized maximum growth rates for all nutrients. We support our hypothesis with empirical and theoretical arguments and discuss how it may improve our understanding of the biology of growth, while avoiding some of the pitfalls of the previous assumption.

Ecologists have developed a suite of tools to model the growth of populations, including Lotka–Volterra functions, which describe predation and competition, the logistic equation and Monod's model, which describe the growth of populations, and Droop's model. The latter model was originally derived to describe the growth of a unicellular phytoplankton species with varying nutrient quotas (Droop 1974, 1975, Box 1) but it has also been used to model the growth of macroalgae (Pedersen and Borum 1996), bacteria (Heldal et al. 1996), protists (Grover and Chrzanowski 2006) and terrestrial plants (Ågren 1988, Sterner and Elser 2002). More recently, Droop's model has been used to investigate ecological interactions (Grover 1991, Andersen 1997, Revilla and Weissing 2008), ecosystem functioning (Mongin et al. 2003, Ballantyne et al. 2008, Hall et al. 2008), and phytoplankton physiological evolution (Klausmeier et al. 2004, 2007). The widespread use of Droop's model warrants a thorough investigation of its underlying assumptions, parameter estimations and biological interpretation.

One weakness in the use of Droop's model in complex systems is that some variables and parameters lack clear biological interpretation and can only be derived experimentally (Droop 1973). Several authors have attempted to provide mechanistic explanations of Droop's model (Kooi and Kooijman 1994, Zonneveld 1996, Lemesle and Mailleret 2008) but these theoretical explanations are incongruent and often inaccessible to those who use Droop's model with a more applied focus. What is more, the uncertainty in the biological interpretation of the model has led to misuses and misconceptions (Turpin 1986, Droop 2003, Flynn 2008b).

Here, we address a common usage of the model that we view as unjustified: the assumption of a theoretical maximum growth rate common to all limiting nutrients when the growth of an organism with multiple potential limiting nutrients is modeled. Although several researchers have argued that there is no theoretical basis for this assumption (Terry 1980, Turpin 1986), this assumption is still commonly made in current studies.

We investigate this assumption by first deriving an extended version of Droop's model for growth limited by multiple nutrients. Then, we synthesize previous research that argues against the simplifying assumption of a single theoretical maximum growth rate common to all limiting nutrients and present our main argument against this assumption: the dependence of critical ratios of nutrients on growth rate.

To solve this weakness in Droop's model we propose a hypothesis that meets the simplicity requirements of ecologists who assume equal theoretical maximum growth rates, but that better fits data and has a theoretical basis and a clear biological interpretation, i.e. the realized, not theoretical, maximum growth rates should be equal in most populations limited by multiple nutrients.

Finally, we provide synthetic evidence in support of our proposed solution.

Droop's model applied to multiple-nutrient limitation

The extension of Droop's model from single- to multiple-nutrient limitation is straightforward (Box 2). The only

Box 1

Droop's model equations:
Population dynamics:

$$\frac{dX}{dt} = (\mu - m)X$$

X: population density; μ: growth rate; m: mortality rate.

Growth rate control:

$$\mu = \bar{\mu}\left(1 - \frac{q^{min}}{q}\right)$$

q: internal quota of the limiting resource; q^{min}: minimum quota of the limiting resource; $\bar{\mu}$: theoretical maximum growth rate for $q \rightarrow +\infty$.

Resource internal quota dynamics:

$$\frac{dq}{dt} = \rho(r) - \mu q$$

ρ: specific uptake rate of the limiting resource; r: external concentration of the limiting resource.

complication resides in deciding how multiple resources influence realized growth rates. Generally, Liebig's law of the minimum is used because models in which the growth rate is controlled solely by the most limiting resource often show a better fit to data than do multiplicative models (Droop 1974, Rhee 1978, Kooijman 1998).

According to this model, for a given growth rate μ, the limiting nutrient has a quota q_l equal to:

$$q_1 = \frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu} \tag{1}$$

where $\bar{\mu}_1$ is the theoretical maximum growth rate for the limiting nutrient. In contrast, non-limiting nutrients have a quota q_{nl} satisfying:

$$q_{nl} > \frac{\bar{\mu}_{nl} q_{nl}^{min}}{\bar{\mu}_{nl} - \mu} \tag{2}$$

otherwise they would be limiting resources as well.

Box 2

Droop's model for a multiple-resource limited growth:
Population dynamics:
Same as Box 1.

Growth rate control:

$$\mu = \mathrm{Min}[\mu_i];\ \mu_i = \bar{\mu}_i\left(1 - \frac{q_i^{min}}{q_i}\right)$$

μ_i: potential growth rate if resource i were limiting; q_i: resource i internal quota; q_i^{min} : resource i minimum internal quota; $\bar{\mu}_i$: theoretical maximum growth rate for resource i.

Resource internal quota dynamics:

$$\frac{dq_i}{dt} = \rho_i(r_i) - \mu q_i$$

ρ_i: specific uptake rate of resource i; r_i: resource i external concentration.

Many authors make the additional assumption that:

$$\bar{\mu}_i = \bar{\mu}_j = ... = \bar{\mu}_n$$

for all potentially limiting resources (Legovic and Cruzado 1997, Grover and Chrzanowski 2006, Klausmeier et al. 2007).

In the next section, we present empirical evidence that contradicts this simplifying assumption. Specifically, empirical data show that the critical ratios of nutrients (i.e. the ratios of nutrient quotas when growth is co-limited) depend on the growth rate, contrary to what is expected if the 'theoretical' maximum growth rates are equal.

Critical ratios do not support the assumption of equal theoretical maximum growth rates

The critical ratio corresponds to the unique combination of nutrient quotas that results in growth being co-limited by the various resources. We can calculate this ratio at a given growth rate, μ, by applying Eq. 1 to all the resources that co-limit growth. For two resources, the critical ratio is:

$$q_1 : q_j = \left(\frac{\bar{\mu}_i q_i^{min}}{\bar{\mu}_i - \mu}\right) \Big/ \left(\frac{\bar{\mu}_j q_j^{min}}{\bar{\mu}_j - \mu}\right) \tag{3}$$

By rewriting this equation as

$$q_1 : q_j = \frac{\bar{\mu}_i q_i^{min}}{\bar{\mu}_j q_j^{min}} + \frac{\bar{\mu}_i q_i^{min}}{\bar{\mu}_j q_j^{min}} \frac{\bar{\mu}_j - \bar{\mu}_i}{\bar{\mu}_i - \mu} \ ,$$

we observe that the critical ratio is a hyperbolic function of the growth rate μ, with asymptotes $\mu = \bar{\mu}_i$ and $q_1 : q_j = \frac{\bar{\mu}_i q_i^{min}}{\bar{\mu}_j q_j^{min}}$. When $\bar{\mu}_i = \bar{\mu}_j$, the critical ratio is independent of the growth rate μ and the terms containing μ in Eq. 3 cancel out. In this scenario, the critical ratio is constant and equal to the ratio of minimum quotas $(\frac{q_i^{min}}{q_j^{min}})$. Most empirical studies, however, have demonstrated that μ does affect the critical ratio; there is a hyperbolic relation between the two variables (Terry 1980, Elrifi and Turpin 1985, Terry et al. 1985). Therefore, empirical evidence rejects the assumption of equal theoretical maximum growth rates. This conclusion is not surprising given that the assumption of equal theoretical maximum growth rates is based neither on theoretical considerations nor on empirical data.

In the next section, we develop a hypothesis that is biologically more reasonable and describes maximum growth rates in a simple way.

A more realistic hypothesis: equal realized maximum growth rates

The growth rate for infinitely large quotas of the limiting resource, $\bar{\mu}$, is never reached since cells have a finite retention

Box 3

Derivation of the realized maximum growth rate:
Internal quota dynamics result from the balance between uptake and dilution by growth:

$$\frac{dq}{dt} = \rho(r) - \mu q.$$

Uptake rate is generally a saturating function of the external resource, so that

$\rho(r) \leq \rho^{max}$

We use Droop's equation for growth rate from Box 1 to define the quota value q^{max} and a corresponding growth rate

$$\mu^{max} = \bar{\mu}\left(1 - \frac{q^{min}}{q^{max}}\right) \text{ such that:}$$

$q^{max}\mu^{max} = \rho^{max}$.

Then, for any $q > q^{max}$, we have $q\mu > q^{max}\mu^{max} = \rho^{max} > \rho(r)$.

Consequently,

$$\frac{dq}{dt} = \rho(r) - \mu q < 0.$$

Thus, q decreases until it reaches, at most, the value of q^{max}. This proves that q^{max} and μ^{max} act as upper boundaries for q and μ, respectively.

Box 4

Unicity of the upper boundary on growth rates for multiple-nutrient limitation:
Let us assume that there exist two nutrients i and j, among n available resources, such that $\mu_i^{max} \neq \mu_j^{max}$.

Then, let us first reorder nutrient indices such that the nutrient with the smallest μ^{max} is labeled with the number 1 and so on: $\mu_i^{max} \leq \mu_2^{max} \leq \ldots \leq \mu_n^{max}$.

If there exists a time *t* in the dynamics of the population, for which $\mu > \mu_1^{max}$, then $q_1 > q_1^{max}$, because we have either

$$q_1 = \frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu} \text{ (if resource 1 is the limiting resource) or}$$

$$q_1 > \frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu} \text{ (if resource 1 is not limiting growth).}$$

Since we assumed that $\mu > \mu_1^{max}$, then we have

$$\frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu} > \frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu_1^{max}} . \frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu_1^{max}} \text{ is also equal to } q_1^{max}. \text{ So,}$$

collecting all these inequalities together yields

$$q_1 \geq \frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu} > \frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu_1^{max}} = q_1^{max} \text{ and so, } q_1 > q_1^{max}.$$

Since both $\mu > \mu_1^{max}$ and $q_1 > q_1^{max}$, then $\mu q_1 > \mu_1^{max} q_1^{max}$. On the other hand, we have by definition $\mu_1^{max} q_1^{max} = \rho_1^{max}$ (Box 3).

So, $\mu q_1 > \rho_1^{max}$.

Since $\rho_1(r_1) \leq \rho_1^{max}$, then $\rho_1(r_1) \leq \rho_1^{max} < \mu q_1$.

Thus, we conclude that $\frac{dq_1}{dt} = \rho_1(r_1) - \mu q_1 < 0$.

Then, q_1 will decrease until it becomes the limiting resource and μ is, at most, equal to μ_1^{max}.

capacity for any given resource. However, the maximum value of the growth rate, μ^{max}, and the corresponding maximum quota, q^{max}, do represent a biological reality (see definition in Box 3). We therefore refer to $\bar{\mu}$ as the theoretical maximum growth rate and μ^{max} as the realized maximum growth rate.

Contrary to $\bar{\mu}$, which is a fitting parameter that is biologically unfeasible, μ^{max} has a clear biological interpretation. μ^{max} is the growth rate achieved when the availability of the limiting resource is very high. It is the resource uptake machinery, not resource availability per se, that limits growth. The number of active enzymes involved in the uptake process generally sets the maximum resource uptake rate. This number, in turn, depends on the rates of transcription, translation, translocation and activation of the genes involved in the uptake pathway. Ultimately, these rates are controlled by the regulation of the complex network of genes involved in the cell machinery. Hence, μ^{max} is the expression of the cell machinery as it reaches its production limit, and is unrelated to the availability of the various resources. Consequently, we hypothesize that μ^{max} is equal for all nutrients:

$$\mu_i^{max} = \mu_j^{max} = ... = \mu_n^{max}$$

In the following section we provide a formal justification for this intuitive hypothesis.

Arguments for the equality of realized maximum growth rates

(1) Unicity of the realized maximum growth rate
In Box 4, we prove that, if μ^{max} is different for some nutrients, only the smallest μ^{max} can ever be reached effectively and all other μ^{max} are *de facto* theoretical values that are unfeasible. Our proof is a simple extension of the proof that μ^{max} is an upper boundary for a single limiting resource (Box 3). It shows that μ should stay below the smallest μ^{max}, which represents a unique upper boundary for the realized growth rates.

(2) Economical design to match functional demand
Since only μ_1^{max}, the smallest μ^{max}, can ever effectively be reached, for a cell to maintain a $\mu_i^{max} > \mu_1^{max}$ it must invest in the maximum uptake rate of resource *i* without any gain in terms of increased growth rate. We invoke a principle similar to the concept of symmorphosis used in animal physiology to argue against such a possibility: organisms should be designed economically, so that structural design matches functional demand (Weibel et al. 1991). The principle of symmorphosis states that the functional limits of a structure – a tissue or part of a tissue – involved in a physiological function cannot exceed the maximum rate of this function. It is based on the assumption that the larger a structure, the costlier its maintenance for the

organism. It was developed mainly from a careful evaluation of the process of respiration in vertebrates. For example, it is found that total muscle mitochondrial volume and O_2 circulation capacity are proportional to the maximal rate of O_2 consumption (Weibel et al. 1991). The scope and limitations of the symmorphosis principle still remain to be fully investigated, but it should prove more fruitful when applied to dominant physiological functions that involve a sequence of structures, like respiration and growth, which concerns us here. A corollary of this principle is that cells should decrease their investment in the uptake machinery of resources that yield higher realized maximum growth rates than the smallest of them, until all realized maximum growth rates are equal: $\mu_i^{max} = \mu_j^{max} = ... = \mu_n^{max}$.

(3) Empirical evidence from luxury uptake

Luxury uptake is the uptake of a non-limiting resource above the level required for growth. At a given growth rate, it can be described quantitatively by the ratio of the quota of the resource when it is not limiting to the quota when it is limiting:

$$R = \frac{q_{nl}}{q_l} = \frac{q_{nl}}{\dfrac{\bar{\mu}\, q^{min}}{\bar{\mu} - \mu}} \qquad (4)$$

If realized maximum growth rates are equal, all resources are limiting when $\mu \approx \mu^{max}$. Consequently, there should be no luxury uptake at this realized maximum growth rate, and $R \approx 1$ for all resources. Most experiments that measure resource quotas at growth rates close to the realized maximum growth rate show no evidence of luxury uptake (Goldman et al. 1979, Elrifi and Turpin 1985), thus providing circumstantial empirical evidence for the assumption of equal realized maximum growth rates. Figure 3 and 6 in Elrifi and Turpin (1985) and Fig. 3 in Egli (1991) provide striking examples of luxury uptake declining with the dilution rate until it vanishes at μ_{max} for a phytoplankton species and a bacterial strain, respectively. More generally, it is widely known that the elemental and biochemical composition of organisms is more constrained at high than at low growth rates (Herbert 1976, Vrede et al. 2004). This suggests that the uptake machineries of many resources reach their maximum ability simultaneously when growth rates approach their realized maximum, as assumed by the hypothesis of equal realized maximum growth rates for all resources.

Discussion

Several authors have argued against the validity of the assumption of equal theoretical maximum growth rates when applying Droop's model to the growth of an organism with multiple potential limiting resources (Terry et al. 1985, Turpin 1986). Terry et al. (1985) showed that only when the ratios of the minimum to the maximum internal quotas (q^{min}/q^{max}) are equal for all nutrients can this equality hold. Both empirical data and theoretical considerations argue against the equality of the minimum-to-maximum quota ratios as a rule (Ågren 2004, Goldman and Mccarthy 1978). The assumption of equal theoretical maximum growth rates, however, is still commonly made. The reasons for its continuing use probably differ from one study to the other. However, they probably fall into two main categories:

1) *A confusion between the theoretical and realized maximum growth rates*. It is an unfortunate turn of events that the species chosen by Droop for his seminal study (Droop 1973) had similar minimum-to-maximum internal quotas for the two resources chosen, i.e. around 3.5 for phosphorus and 4.5 for silicon, yielding similar theoretical maximum growth rates for the two resources (Droop 1974, 2003, Table 1). Based on these results, Droop himself did not clearly make the difference between the theoretical maximum growth rate of his model and the realized maximum growth rate that can be measured in chemostats or batch cultures. It is only after Burmaster (1979) established mathematically the equivalence between Monod's and Droop's models at steady state that Droop (1983) declared that "the difference is important and the two parameters should not be confused". He even showed how the confusion between the two parameters could weaken the predictive value of his model (Droop 2003).
2) *A search for mathematical and theoretical convenience.* Many authors choose to use a unique, common theoretical maximum growth rates for all resources because it results in simpler calculations and derivations (Legovic and Cruzado 1997). They are probably encouraged to do so because few papers have investigated the consequences of this simplification on model predictions (but see Elrifi and Turpin 1985, Turpin 1986). Most of the other mechanistic investigations of Droop's model either ignore the multiplicity of potential limiting resources (Kooi and Kooijman 1994, Lemesle and Mailleret 2008) or are mainly interested in the study of the relation between non-limiting internal quotas and growth rate (Zonneveld 1996, Flynn 2008a, 2008b). They do not address the specific issue of the relation between maximum growth rates under multiple-nutrient limitation.

Thus, the assumption of equal theoretical maximum growth rates is often made out of convenience or confusion and does not bear any biological significance. In some cases, it can even lead to an inaccurate biological interpretation of important growth parameters. For example, this assumption yields critical ratios that are independent of the growth rate and equal to the ratios of minimum quotas. Consequently, some authors have over-interpreted the ecological and evolutionary significance of minimum quotas and their ratios (Rhee and Gotham 1980, Klausmeier et al. 2008): if critical ratios vary with growth rates, minimum quotas do not represent the resources used in structures and machinery and their ratios are not optimal under all growth conditions, as is often assumed.

This inappropriate assumption is particularly likely to generate problems in models of complex interactions between multiple species. Droop's equations are increasingly used to model competition (Grover 1991, Hall et al.

2008, Revilla and Weissing 2008) and trophic interactions (Andersen 1997, Mongin et al. 2003, Kuang et al. 2004). In such models, errors in the predicted growth, limitation and composition of single populations can propagate to affect the dynamics of other populations, which may result in faulty predictions at higher levels. For example, Turpin (1986) demonstrated that the coexistence of competing species critically depends on the order of the theoretical maximum growth rates of the limiting resources. Predictions about food web structure and resource fluxes from ecosystem models based on Droop's equations are also likely to be affected by this simplifying assumption.

Nonetheless, we recognize the need for simple equations that provide a realistic representation of upper limits on growth rate. For this purpose, we used theoretical and empirical evidence to propose a derivation of Droop's equations that assumes that the realized maximum growth rates, instead of the theoretical maximum growth rates, are equal. Experimental manipulations of phytoplankton growth show little or no luxury uptake of resources at the highest growth rates (Droop 1974, Goldman and Peavey 1979, Elrifi and Turpin 1985), therefore supporting the hypothesis of equal realized maximum growth rates. We also used an evolutionary argument based on economical design similar to the symmorphosis principle (Weibel et al.1991) to argue that the maximum capacity of the uptake machinery should not be oversized for a given resource. These arguments advocate for the inclusion of equal realized maximum growth rates in the standard set of equations describing Droop's model under multiple-nutrient limitation.

Consequences for competition

Our assumption of equal realized maximum growth rates can provide new insights into the coexistence of competing species. Under this assumption, the R* values of the various resources are proportional, so that all co-limitation points in the resource plane fall on a straight line as the growth rate changes (see Box 5 and Tilman 1980 for an introduction to R* values, resource planes and resource competition theory in general). Thus, this hypothesis leads to a stronger constraint on species' resource use and competitive ability (compare (A) and (B) in Fig. 1). For example, the measurement of Monod's half saturation constants for the various resources is sufficient to predict the exact position of the co-limitation points of a given species (Fig. 1A). Overall, fewer parameters may be required to predict the outcome of competition for limiting resources.

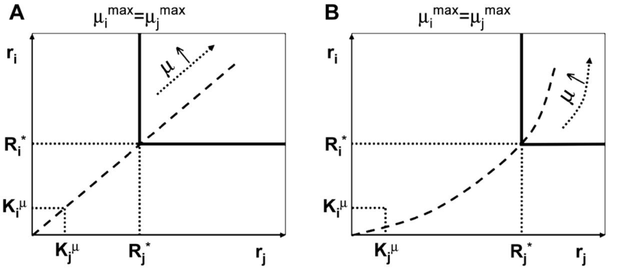

Figure 1. Growth isoclines (plain lines) as a function of growth rate μ. In (A), $\mu_i^{max} = \mu_j^{max}$; co-limitation points are located on a straight line (dashed line) that includes the point (K_i^μ, K_j^μ). In (B) $\mu_i^{max} \neq \mu_j^{max}$; co-limitation points are on a curved line that cannot be determined precisely without knowing the exact values of both μ_i^{max} and μ_j^{max}.

Box 5

Effect of equal realized maximum growth rates on R* values:

At equilibrium, Droop's model with Michaelis-Menten uptake can be rewritten as:

$$\mu = \mathrm{Min}[\mu_i^{max} \frac{r_i}{K_i^\mu + r_i}]; \text{ with } K_i^\mu = \frac{q_i^{min}}{q_i^{max}} K_i$$

K_i: half-saturation constant for resource i uptake rate.

Let us define R_i^* as the external concentration of the limiting resource i at equilibrium:

$$R_i^* = K_i^\mu \frac{\mu_i^{max}}{\mu_i^{max} - \mu}.$$

If we assume that $\mu_i^{max}=\mu_j^{max}=...=\mu^{max}$, it is straightforward to show that: $R_i^*: R_j^*=K_i^*: K_j^*$.

Figure 1 shows that the patterns of co-limitation differ between models that assume equal theoretical maximum growth rates and our model that assumes equal realized maximum growth rates. But are these differences significant enough to worry about them? To answer this question, we compared the predictions of the two types of models in the case of two species competing for two essential resources. We used the same set of parameter values to estimate either the theoretical or the realized maximum growth rates in the two models (see Appendix 1 for details). In agreement with Fig. 1, our version of the model results in straight co-limitation lines for the two species (Fig. 2A). The two lines start from the origin of the resource plane, but do not cross elsewhere. In the version of the model with equal theoretical maximum growth rates, the two co-limitation lines are curvilinear (Fig. 2B). We chose the parameter values so that these lines intersect in the positive quadrant. Numerical simulations show that these two different configurations result in a significant difference in the outcome of competition between the two species. In our model version, species 1 excludes the other species for all values of the dilution rate D below the washout rate (Fig. 2C). In the second version, however, there is a dilution rate above which the outcome of competition is reversed, i.e. species 2 competitively excludes species 1 (Fig. 2D). Below this threshold dilution rate, the equilibrium densities of the two species are very similar to those of our model version. This observation highlights the fact that a small difference between two models in part of the parameter space does not preclude significant differences in another part. Since the same set of source parameters were used for both models, this example shows that a slight change in the assumptions underlying the estimation of derived parameters can lead to drastic change in the outcome of a model. Admittedly, we chose the source parameters to highlight the difference between the two models. But our objective here is simply to show that our new assumption of equal realized maximum growth rates can indeed result

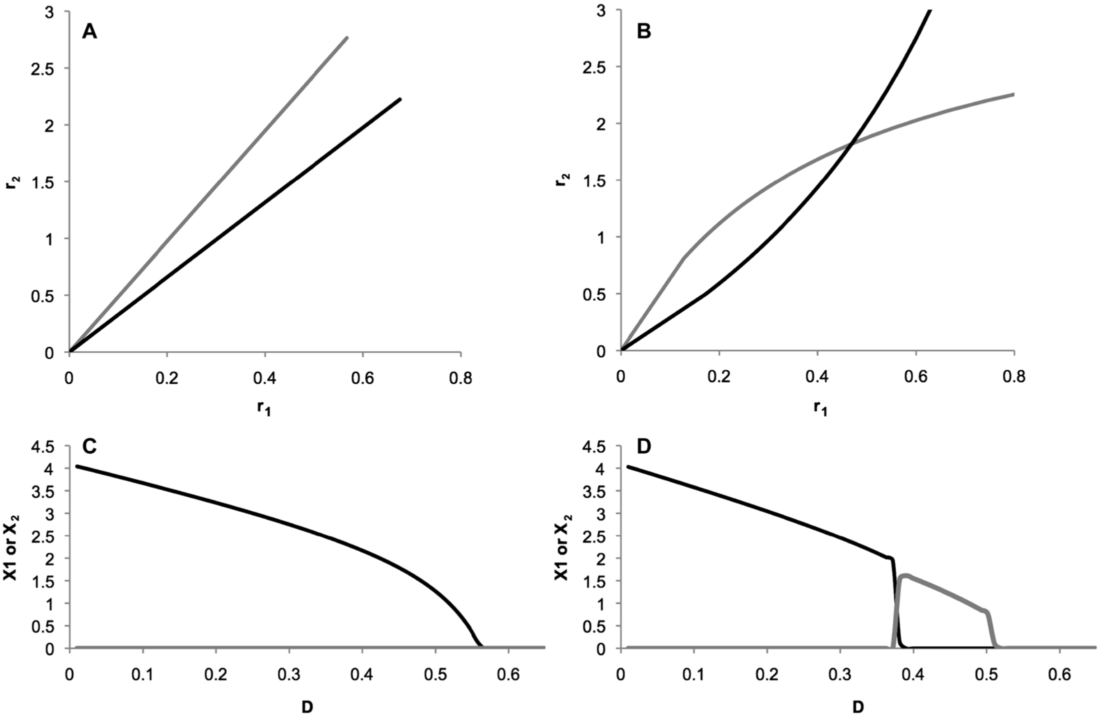

Figure 2. A chemostat model of two species (X_1 and X_2) competing for two resources (r_1 and r_2). (A) and (B) show the co-limitation point in the resource plane as a function of the dilution rate D. (C) and (D) show the equilibrium densities of the two species as a function of the dilution rate D for the two species. In (A) and (C), it is assumed that the *realized* maximum growth rates are equal for the two species. In (B) and (D), it is assumed that the *theoretical* maximum growth rates are equal. Species 1 is in black and species 2 in grey.

in predictions that are significantly different from the usual assumption of equal theoretical maximum growth rates.

Alternative formulations to Droop's model

From the very first attempts to fit Droop's model to empirical data, it became clear that the Michaelis–Menten function was not sufficient to adequately describe the uptake of resources by organisms (Droop 1974, Tilman and Kilham 1976). In particular, it was found early on that the maximum uptake rate of a nutrient is a function of its internal quota (Rhee 1973). Since then, numerous alternative formulations to the Michaelis–Menten function have been used to describe uptake rates (Morel 1987, Thingstad 1987, Aksnes and Egge 1991, Klausmeier et al. 2007, Smith et al. 2009). Can these alternative formulations affect our proofs and arguments? To answer this question, we studied two of the most common uptake rate formulations that include effects from internal quotas, i.e. Morel's (Morel 1987) and Thingstad's (Thingstad 1987). We checked that our proof of the unicity of the realized maximum growth rate (Box 4) still holds under these alternative formulations (Appendix 2). Our arguments based on economical design and empirical evidence for the decrease in luxury uptake with the growth rate do not depend on the precise formulation of the uptake rate. We found that the smallest realized maximum growth rate is also a unique upper boundary on realized growth rates when Morel's or Thingstad's formulations are used for uptake rates (Appendix 2). More generally, a closer look at the logical steps of the proofs in Box 4 and Appendix 2 indicates that only three conditions are required to show that the smallest of all realized maximum growth rates serves as a unique upper boundary for the growth rate under multiple-nutrient limitation:

(1) The uptake rates must be bounded (in mathematical terms, there exists ρ_i^{max} such that $\rho(r_i) \leq \rho_i^{max}$, for all resources r_i).
(2) There must be a one-to-one positive relation between the growth rate and the limiting nutrient internal quota (a condition fulfilled by Droop's equation $\mu = \bar{\mu}\,(1 - \frac{q^{min}}{q}))$.
(3) The resources should be essential (in particular, their effects on growth rate should not be additive).

These three conditions are likely to be met by most, if not all, of the models that realistically describe growth as affected by multiple essential, non-substitutable resources.

Empirical relevance of our model

Numerous empirical measurements confirm, or at least do not contradict our assumption of equal realized maximum growth rates. Droop (Droop 1974) measured the growth limitation of the phytoplankton species *Pavlova*

(*Monochrysis*) *lutheri* by phosphorus and vitamin B_{12}. He found that the realized maximum growth rates for the two resources were reasonably close to each other (Droop 2003, Table 1). Panikov and Pirt (1978) found very similar realized maximum growth rates, around 0.2 day^{-1}, for *Chlorella vulgaris* limited by either N or P. Ahlgren (1985) used the cyanobacteria *Oscillatoria* (*Planktothrix*) *agardhii* and nitrogen and phosphorus as resources. His estimates of the two realized maximum growth rates were also reasonably similar (Droop 2003, Table1). Elrifi and Turpin's (1985) work on *Selenastrum minutum* yielded almost identical realized maximum growth rates for the two limiting resources phosphorus and nitrogen. Borchardt (1994) found similar maximum photosynthetic rates (around 100 mg O_2 g^{-1} dry weight^{-1} h^{-1}) for *Spirogyra fluviatilis* grown under either nitrogen or phosphorus limitation. The realized maximum growth rates of two *Ceratium* species grown with either nitrate or phosphorus limitation were also very close (Baek et al. 2008).

There are, however, a few significant exceptions to this rule. Tilman and Kilham (1976) measured the growth rates of two diatom species under phosphorus and silicon limitation. The results for the first species, *Asterionella formosa*, were in line with our model of equal realized maximum growth rates, with a unique value around 0.9 day^{-1}. However, the second species, *Cyclotella meneghiniana*, had a realized maximum growth rate around 0.8 day^{-1} under phosphorus limitation and 1.3 day^{-1} under silicon limitation. More than twenty years later, for the same species *Cyclotella meneghiniana*, but at a different temperature, Shafik et al. (1997) found realized maximum growth rates of 1.6 day^{-1} and 0.95 day^{-1} for phosphorus- and silicon-limited growth, respectively. A summary table of realized maximum growth rates in Tilman et al. (1982, Table 1) shows that other diatom species present the same pattern of different realized maximum growth rates between P and Si-limited growths measured in the same conditions. These results seem to contradict not only our proposed model of equal realized maximum growth rates but also most of the common, simple models of growth under multiple-nutrient limitation. This suggests that diatoms might require more complicated models. Silicon differ from other essential resources because its metabolic pool in cells is very low. In fact, it is mainly needed as a structural component and can be reclaimed from frustula if needed (Davis et al. 1978).

Our assumption of equal realized maximum growth rates is appropriate for essential, non-substitutable resources. We do not expect this assumption to hold for non-essential, substitutable resources. Two substitutable resources are not necessarily equally efficient nutritionally (e.g. two organic carbon substrates with very different oxidative levels); they do not necessarily follow the same metabolic pathways to assimilation and may thus incur different metabolic costs for the organism ingesting them (e.g. phosphate and dissolved organic phosphorus that require the production of phosphatases). Hence, they are likely to result in different realized maximum growth rates. For example, the work of DeNobel et al. (1997) shows that the realized maximum growth rate of *Aphanizomenon flos-aquae* is much smaller when this species has to fix N_2 instead of taking up ammonium to meet its nitrogen requirements.

Our second argument for the equality of realized maximum growth rates relies on the evolutionary optimization of relative investments in the uptake machineries of different resources. Evolutionary optimization is a process that normally occurs on evolutionary timescales, much longer than the population timescale of the species. Therefore, we do not expect the realized maximum growth rates to be equal if a species is confronted with a new or unfamiliar substrate, or if growth conditions are very different from the conditions under which the species evolved beforehand. As a side note, providing a species with a new substrate and monitoring the changes in the uptake and growth parameters of the other essential resources could be a way to test our theory.

Finally, many microorganisms live in highly variable and complex environments. The optimization of their growth and resource uptake may not necessarily be key to their success. If the maintenance of an oversized uptake machinery for a resource helps them to better survive some harsh selective condition (e.g. freezing or dessication), then a difference in their realized maximum growth rates could be selected for.

In conclusion, we presented theoretical and empirical evidence that the assumption of equal theoretical maximum growth rates in Droop's model under multiple resource limitation is inadequate, and that the assumption of equal realized maximum growth rates is a promising alternative. Our new assumption would result in a more correct and biologically realistic application of Droop's equations to model multiple-nutrient limited growth and avoid some conceptual pitfalls that arise from assuming equal theoretical maximum growth rates. Even though there most probably exist cases where our assumption is not valid, our model should provide a useful conceptual framework to understand the mechanisms responsible for this departure from economical design, and as a starting point to investigate the seemingly vast diversity of growth and uptake patterns that are found in organisms that live on the same essential, elementary resources.

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Appendix 1

Alternate two-species competition models for two essential resources, with equal theoretical maximum growth rates or equal realized maximum growth rates

The two models are similar for the most part. They differ only in the method used to estimate the derived parameters:

Differential equations

Species 1:

$$\frac{dX_1}{dt} = \left(\mu_1\left(q_{11}, q_{12}\right) - D\right)X_1$$

$$\frac{dq_{11}}{dt} = \rho_{11}\left(r_1\right) - \mu_1 q_{11}$$

$$\frac{dq_{12}}{dt} = \rho_{12}\left(r_2\right) - \mu_1 q_{12}$$

Species 2:

$$\frac{dX_2}{dt} = \left(\mu_2\left(q_{21,} q_{22}\right) - D\right)X_2$$

$$\frac{dq_{21}}{dt} = \rho_{21}(r_1) - \mu_2 q_{21}$$

$$\frac{dq_{22}}{dt} = \rho_{22}(r_2) - \mu_2 q_{22}$$

X_i: density of species i; μ_i: growth rate of species i; q_{ij}: species i internal quota of resource j; D: dilution rate of the chemostat; ρ_{ij}: uptake rate of resource j by species i; r_j: external concentration of resource j.

Resource 1:

$$\frac{dr_1}{dt} = D\left(s_1 - r_1\right) - \rho_{11}X_1 - \rho_{21}X_2$$

Resource 2:

$$\frac{dr_2}{dt} = D\left(s_2 - r_2\right) - \rho_{12}X_1 - \rho_{22}X_2$$

s_j: concentration of resource j in supply.

Functions

Growth rate:

$$\mu_i\left(q_{i1}, q_{i2}\right) = \mathrm{Min}\left[\bar{\mu}_{i1}\left(\frac{q_{i1}^{\min}}{q_{i1}}\right), \bar{\mu}_{i2}\left(1 - \frac{q_{i2}^{\min}}{q_{i2}}\right)\right]$$

$q_{ij}^{\min}$: species i minimum quota of resource j; $\bar{\mu}_{ij}$: species i theoretical maximum growth rate on resource j.

Uptake rate:

$$\rho_{ij} = \rho_{ij}^{\max}\frac{r_j}{r_j + K_{ij}}$$

$\rho_{ij}^{\max}$: species i maximum uptake rate of resource j; K_{ij}: species i half-saturation constant for resource j.

Parameters

Source parameters:

Species 1:

$\bar{\mu}_{11} = 1$, $q_{11}^{\max} = 1.5$, $\rho_{11}^{\max} = 2.67$, $K_{11} = 0.47$, $q_{12}^{\min} = 0.98$,
$\rho_{12}^{\max} = 1.24$, $K_{12} = 1.1$

Species 2:

$\bar{\mu}_{22} = 1$, $q_{22}^{\min} = 1.1$, $\rho_{22}^{\max} = 2.28$, $K_{22} = 2.45$, $q_{21}^{\min} = 1.95$,
$\rho_{12}^{\max} = 2.09$, $K_{21} = 0.26$

Resources:

$s_1 = 10$, $s_2 = 4$

Derived parameters:

Version 1 $(\bar{\mu}_{11} = \bar{\mu}_{12}, \bar{\mu}_{21} = \bar{\mu}_{22})$:
Species 1:

$$\bar{\mu}_{12} = \bar{\mu}_{11} = 1,\ \mu_{11}^{\max} = \frac{\rho_{11}^{\max}}{\frac{\rho_{11}^{\max}}{\bar{\mu}_{11}} + q_{11}^{\min}} = 0.64,$$

$$\mu_{12}^{\max} = \frac{\rho_{12}^{\max}}{\frac{\rho_{12}^{\max}}{\bar{\mu}_{12}} + q_{12}^{\min}} = 0.56$$

Species 2:

$$\bar{\mu}_{21} = \bar{\mu}_{22} = 1,\ \mu_{22}^{max} = \frac{\rho_{22}^{max}}{\frac{\rho_{22}^{max}}{\bar{\mu}_{22}} + q_{22}^{min}} = 0.67,$$

$$\mu_{21}^{max} = \frac{\rho_{21}^{max}}{\frac{\rho_{21}^{max}}{\bar{\mu}_{21}} + q_{21}^{min}} = 0.52$$

Version 2 ($\mu_{11}^{max} = \mu_{12}^{max}$, $\mu_{21}^{max} = \mu_{22}^{max}$):

Species 1:

$$\mu_{12}^{max} = \mu_{11}^{max} = \frac{\rho_{11}^{max}}{\frac{\rho_{11}^{max}}{\bar{\mu}_{11}} + q_{11}^{min}} = 0.64,\ \bar{\mu}_{12} = \frac{\rho_{12}^{max}}{\frac{\rho_{12}^{max}}{\mu_{12}^{max}} - q_{12}^{min}} = 1$$

Species 2:

$$\mu_{21}^{max} = \mu_{22}^{max} = \frac{\rho_{22}^{max}}{\frac{\rho_{22}^{max}}{\bar{\mu}_{22}} + q_{22}^{min}} = 0.67,\ \bar{\mu}_{21} = \frac{\rho_{21}^{max}}{\frac{\rho_{21}^{max}}{\mu_{21}^{max}} - q_{21}^{min}} = 1.82$$

Numerical simulations:

Initial conditions:

$X_1(0) = 2$, $q_{11}(0) = 2.75$, $q_{12}(0) = 3$, $X_2(0) = 2$, $q_{21}(0) = 3.75$, $q_{22}(0) = 2.75$, $r_1(0) = 2$, $r_2(0) = 2$

Numerical integration:

Simulations of the two versions of the model (shown in Fig. 2) were run using the simulation software Berkeley Madonna (ver. 8.3.22) using a Runge-Kutta 4 method with a time step of 0.05.

Appendix 2

Droop models with alternative formulations for the uptake rate

Equations for the growth rate, population and internal quota dynamics are not different from the equations presented in Box 2:

$$\frac{dX}{dt} = (\mu - m)X$$

$$\mu = \mathrm{Min}[\mu_i];\ \mu_i = \bar{\mu}_i\left(1 - \frac{q_i^{min}}{q_i}\right)$$

$$\frac{dq_i}{dt} = \rho_i(r_i) - \mu q_i$$

X: population density; μ: growth rate; m: mortality rate; μ_i: potential growth rate if resource i were limiting; q_i: resource i internal quota; q_i^{min} : resource i minimum quota; $\bar{\mu}_i$: theoretical maximum growth rate for resource i; ρ_i: specific uptake rate of resource i; r_i: resource i external concentration.

The difference resides in the formulation of the uptake rate function ρ_i.

Morel's function (Morel 1987)

In this model, the maximum uptake rate ρ_i^{max} is a linearly decreasing function of the internal quota q_i. Thus, it varies between an upper boundary $\rho_i^{max,high}$ (when $q_i = q_i^{min}$) and a lower boundary $\rho_i^{max,low}$ (when $q_i = q_i^{max}$) in such a fashion:

$$\rho_i^{max} = \rho_i^{max,high} - \left(\rho_i^{max,high} - \rho_i^{max,low}\right)\frac{q_i - q_i^{min}}{q_i^{max} - q_i^{min}}$$

$$\text{So, } \rho_i(r_i) = \left(\rho_i^{max,high} - \left(\rho_i^{max,high} - \rho_i^{max,low}\right)\frac{q_i - q_i^{min}}{q_i^{max} - q_i^{min}}\right)\frac{r_i}{r_i + K_i}$$

Using this formulation, we aim to prove that, if some resources have different μ_i^{max}, only the smallest μ_i^{max} can ever effectively be reached and all the other μ_i^{max} s are de facto theoretical values that are unfeasible:

Let us first reorder the resource indices such that the resource with the smallest μ_i^{max} is labeled with the number 1: $\mu_1^{max} \le \mu_2^{max} \le \ldots \le \mu_n^{max}$.

If there exists a time t in the dynamics of the population, for which $\mu > \mu_1^{max}$, then $q_1 > q_1^{max}$, because we have either $q_1 = \frac{\bar{\mu} q_1^{min}}{\bar{\mu}_1 - \mu}$ (if resource 1 is the limiting resource) or $q_1 > \frac{\bar{\mu} q_1^{min}}{\bar{\mu}_1 - \mu}$ (if resource 1 is not the limiting resource). Since we assumed that $\mu > \mu_1^{max}$, then $\frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu} > \frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu^{max}}$.

But we also have $\frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu^{max}} = q_1^{max}$. So, collecting all these inequalities together: $q_1 \ge \frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu} > \frac{\bar{\mu}_1 q_1^{min}}{\bar{\mu}_1 - \mu_1^{max}} = q_1^{m}$ or, more simply $q_1 > q_1^{max}$.

Since both $\mu > \mu_1^{max}$ and $q_1 > q_1^{max}$, then $\mu q_1 > \mu_1^{max} q_1^{max}$.

On the other hand, we have $\mu_1^{max} q_1^{max} = \rho_1^{max,low}$ (See Morel 1987 for an explanation).

So, $\mu q_1 > \rho_1^{max,low}$.

Now, because of the negative linear monotonic relation between the maximum uptake rate ρ_i^{max} and the internal quota q_i, $q_1 > q_1^{max}$ means that $\rho_i^{max} < \rho_1^{max,low}$. Obviously, we also have $\rho_1(r_1) \le \rho_1^{max}$.

Thus, collecting these inequalities together yields:

$\rho_1(r_1) \le \rho_1^{max} < \mu q$

So, we conclude that $\frac{dq_1}{dt}\rho(r_1) - \mu q < 0$.

Then, q_1 will decrease until r_1 becomes the limiting resource and μ is, at most, equal to μ_1^{max}.

Hence, given realistic initial conditions (i.e. $\mu < \mu_1^{max}$), μ should stay below μ_1^{max} , and μ_1^{max} represents a unique upper boundary for the realized growth rate.

Thingstad's function (Thingstad 1987)

$$\rho_i(r_i) = \left(\rho_i^{max,high}\frac{q_i^{max} - q_i}{q_i^{max} - q_i^{min}}\right)\frac{r_i}{r_i + K_i}$$

In fact, this formulation is simply a special case of Morel's function in which $\rho_i^{max,low} = 0$.

Although it is only a special case of Morel's, the demonstration of the unicity of the upper boundary for growth rates is slightly different from the previous demonstration:

The main difference lies in that at $q_i = q_i^{max}$, $\rho_i^{max} = 0$. There is thus no uptake possible at q_i^{max}. Then, q_i^{max} and its associated growth rate μ_i^{max} become theoretical, non-reachable values, similarly to $\bar{\mu}_i$.

There still exists an upper boundary on growth rates limited by a resource that can be found by setting $\rho_i^{max} = \mu_i q_i$.

By replacing ρ_i^{max} with its expression $\rho_i^{max,high}\frac{q_i^{max}-q_i}{q_i^{max}-q_i^{min}}$ and μ_i with its expression $\mu_i = \bar{\mu}_i\left(1-\frac{q_i^{min}}{q_i}\right)$ and solving for the equation, one gets explicit expressions for these boundary parameters:

$$\tilde{q}_i^{max} = q_i^{max}\frac{\rho_i^{max,high}+\mu_i^{max}q_i^{min}}{\rho_i^{max,high}+\mu_i^{max}q_i^{max}}$$

$$\tilde{\mu}_i^{max} = \mu_i^{max}\frac{\rho_i^{max,high}}{\rho_i^{max,high}+\mu_i^{max}q_i^{min}}$$

$$\tilde{\rho}_i^{max} = \rho_i^{max,high}\frac{\mu_i^{max}q_i^{max}}{\rho_i^{max,high}+\mu_i^{max}q_i^{min}}$$

Once these new boundary parameters are defined, the same demonstration as with Morel's function can be made, but using $\tilde{q}_i^{max}$, $\tilde{\mu}_i^{max}$, $\tilde{\rho}_i^{max}$ instead of q_i^{max}, μ_i^{max} and $\rho_i^{max,low}$.