Appendices

A Forcing functions

The time (t) dependent forcing function used in Figures 4, 5 and 6 is defined as

$$f(t) = \sum_{n=N} \frac{\sin(2nt\pi/T)}{n} \tag{A1}$$

In Figure 4 the complex function is achieved by assuming $N = \{1, 5, 6, 7, 8, 9\}$ and $T = 15$ days. In Figures 5 and 6 the sinusoidal forcing functions were achieved by assuming $N = 1$ with T as an independent variable. In both cases, $f(t)$ was linearly rescaled between 0.05 and 0.95.

B Model derivations

Dynamic Quota model:

The Dynamic Quota model is defined following Legović and Cruzado (1997) and Klausmeier et al. (2004).

$$\frac{dR_i}{dt} = \kappa\left(R_i^{supply} - R_i\right) - \rho_i B_C \tag{B1}$$

$$\frac{dB_i}{dt} = \rho_i B_C - \kappa B_i \tag{B2}$$

$$\frac{dB_C}{dt} = B_C(\mu - \kappa) \tag{B3}$$

Parameter symbols are defined in Table 2. We define μ as the carbon-biomass-specific rate of carbon synthesis, limited by the most-limiting nutrient quota and an imposed environmental limitation factor, γ.

$$\mu = \gamma \min\left[\mu_i^{\infty}(1 - \frac{Q_i^{min}}{Q_i})\right]_{i=\{N,P\}} \tag{B4}$$

The nutrient quota is the nutrient biomass to carbon biomass ratio.

$$Q_i = \frac{B_i}{B_C} \tag{B5}$$

The quota-limited Michaelis-Menten nutrient uptake rate, ρ_i, is given by

$$\rho_i = \frac{\rho_i^{max}\alpha_i R_i}{\rho_i^{max} + \alpha_i R_i} \cdot \frac{Q_i^{max} - Q_i}{Q_i^{\Delta}} \tag{B6}$$

Where $Q_i^{\Delta} = Q_i^{max} - Q_i^{min}$.

The Balanced Growth assumption:

We can assume that nutrient uptake and light-limited carbon synthesis are in balance relative to the quota, and that this balance is achieved by instant acclimation of the quota.

$$\tilde{Q}_i = \frac{\rho_i}{\mu} \tag{B7}$$

Substituting in from equation B6, we find

$$\frac{\rho_i^{max} \alpha_i R_i}{\rho_i^{max} + \alpha_i R_i} \cdot \frac{Q_i^{max} - \tilde{Q}_i}{Q_i^{\Delta}} = \mu \tilde{Q}_i \tag{B8}$$

Which we can solve for the instantly acclimated nutrient quota $\tilde{Q}$,

$$\tilde{Q}_i = \frac{\rho_i^{max} \alpha_i R_i Q_i^{max}}{\rho_i^{max} \alpha_i R_i + \mu(\rho_i^{max} + \alpha_i R_i) Q_i^{\Delta}} \tag{B9}$$

Assuming that $i = lim$ (i.e. the most limiting nutrient), the population growth rate, μ, can be found by substituting equation B9 into equation B4, such that

$$\mu = \frac{\gamma \mu_i^{\infty} \rho_i^{max} \alpha_i R_i}{\alpha_i R_i \left(\gamma \mu_i^{\infty} Q_i^{min} + \rho_i^{max} \, Q_i^{max} / Q_i^{\Delta} \right) + \gamma \mu_i^{\infty} \rho_i^{max} Q_i^{min}} \tag{B10}$$

We can look at this solution for μ in two key limits. Firstly, under nutrient-saturated conditions, as $R_i \to \infty$. In this limit, terms in the denominator not containing R_i can be neglected, such that

$$\mu \approx \frac{\gamma \mu_i^{\infty} \rho_i^{max}}{\gamma \mu_i^{\infty} Q_i^{min} + \rho_i^{max} \, Q_i^{max} / Q_i^{\Delta}} \tag{B11}$$

This is effectively the resource-saturated maximum population growth rate (for any given value of γ)

$$\mu_{\gamma,i}^{max} = \frac{\gamma \mu_i^{\infty} \rho_i^{max}}{\gamma \mu_i^{\infty} Q_i^{min} + \rho_i^{max} \, Q_i^{max} / Q_i^{\Delta}} \tag{B12}$$

Note that $\mu_{\gamma,i}^{max}$ is a non-linear function of γ. This is because the resource-saturated growth rate ($\mu_{\gamma,i}^{max}$) may be largely insensitive to γ if it is primarily limited by the maximum rate of nutrient uptake (see Ward et al. 2017).

Secondly, we can consider equation B10 under extreme resource limitation, as $R_i \to 0$. Under this assumption, we can neglect the terms in the denominator that do contain R_i, and this gives

$$\mu \approx \frac{\alpha_i R_i}{Q_i^{min}} \tag{B13}$$

If we define a new composite parameter $\beta_i = \frac{\alpha_i}{Q_i^{min}}$, we find that

$$\mu \approx \beta_i R_i \tag{B14}$$

Here β_i is therefore the resource affinity under balanced growth. We can substitute the composite parameters $\mu_{\gamma,i}^{max}$ and β_i into equation B10 in order to find a simplified expression for the population growth rate

$$\mu = \frac{\mu_{\gamma,i}^{max} \beta_i R_i}{\mu_{\gamma,i}^{max} + \beta_i R_i} \tag{B15}$$

or, more generally, if we drop the assumption that i is the most-limiting nutrient,

$$\mu = \min\left(\frac{\mu_{\gamma,N}^{max} \beta_N R_N}{\mu_{\gamma,N}^{max} + \beta_N R_N}, \frac{\mu_{\gamma,P}^{max} \beta_P R_P}{\mu_{\gamma,P}^{max} + \beta_P R_P}\right) \tag{B16}$$

Finally, the equations outlined above are based on the appearance of μ_i^∞ in Equation B4. This asymptotic growth rate is unobservable, but it can be derived from the equilibrium Elrifi and Turpin (1985) data by rearranging equation B12 (assuming $\gamma = 1$).

$$\mu_i^\infty = \frac{\mu^{max} \rho_i^{max} Q_i^{max}}{\left(\rho_i^{max} - \mu^{max} Q_i^{min}\right) Q_i^\Delta} \tag{B17}$$

C Mass balance in the Instant Acclimation model

The phytoplankton growth models use two potentially limiting nutrients, so we must define different correction factors for the limiting and non-limiting nutrients. This is because, unlike the limiting nutrient quota (Q_{lim}), the non-limiting nutrient quota (Q_{non}) is sensitive to both the limiting and non-limiting nutrients (R_{lim} and R_{non}).

$$\psi_{lim} = \left[\frac{\partial \tilde{Q}_{lim}}{\partial \gamma}\frac{d\gamma}{dt} + \frac{\partial \tilde{Q}_{lim}}{\partial R_{lim}}\frac{dR_{lim}}{dt}\right] B_C \tag{C1}$$

$$\psi_{non} = \left[\frac{\partial \tilde{Q}_{non}}{\partial \gamma}\frac{d\gamma}{dt} + \frac{\partial \tilde{Q}_{non}}{\partial R_{lim}}\frac{dR_{lim}}{dt} + \frac{\partial \tilde{Q}_{non}}{\partial R_{non}}\frac{dR_{non}}{dt}\right] B_C \tag{C2}$$

These terms account for the instantaneous adjustment of the quotas in response to changes in light and temperature limitation (γ) and the limiting and non-limiting nutrients (N and P). Note that the time-derivatives of R_i (Table 1) can be rearranged to avoid the appearance of dR_i/dt in the right-hand-sides (Smith et al. 2016).

$$\frac{dR_{lim}}{dt} = \frac{\kappa\left(R_{lim}^{supply} - R_{lim}\right) - \left[\mu\tilde{Q}_{lim} + \frac{\partial\tilde{Q}_{lim}}{\partial\gamma}\frac{d\gamma}{dt}\right]B_C}{1 + \frac{\partial\tilde{Q}_{lim}}{\partial R_{lim}}B_C} \tag{C3}$$

$$\frac{dR_{non}}{dt} = \frac{\kappa\left(R_{non}^{supply} - R_{non}\right) - \left[\mu\tilde{Q}_{lim} + \frac{\partial\tilde{Q}_{lim}}{\partial\gamma}\frac{d\gamma}{dt} + \frac{\partial\tilde{Q}_{non}}{\partial R_{lim}}\frac{dR_{lim}}{dt}\right]B_C}{1 + \frac{\partial\tilde{Q}_{non}}{\partial R_{non}}B_C} \tag{C4}$$

The derivative of γ with respect to time was calculated numerically. Note that equation C3 must be solved before equation C4, because the latter is dependent on the former. This sequential solution requires the assumption of non-interactive nutrient limitation terms. If nutrient limitation was interactive (e.g. a multiplicative function), equations C3 and C4 would need to be estimated through a potentially costly iterative process. The derivatives of the quotas with respect to R_{lim}, R_{non} and γ were calculated using the Matlab Symbolic Math Toolbox. The results are cumbersome, and are not reproduced here.