

TRAIT MODEL EQUATIONS

Megan Sullivan

July 2022

1 Theory: Cell Model Optimization

The optimal strategy balances growth rates limited by photosynthetic rate, biosynthetic rate, and nutrient uptake rate.

The model aims to maximize $\mu = \min\{\mu_L, \mu_E, \mu_P, \mu_N\}$ where

$$\mu_L = \frac{\alpha_I L}{1 + \Phi_S} \quad (1)$$

$$\mu_E = k_{ST} E \quad (2)$$

$$\mu_P = \frac{a_P f_{ProtA}}{r^2 (EP_E + \gamma_S P_S)} \quad (3)$$

$$\mu_N = \frac{a_N}{r^2 (EN_E + LN_L + \gamma_S N_S + \frac{\alpha_S}{2r} (f_{ProtA} N_{Prot} + N_M))} \quad (4)$$

over L, E, r, f_{ProtA}

subject to:

$$L + E + \frac{\alpha_S}{r} + \gamma_S = 1 \quad (5)$$

$$E \geq 0$$

$$L \geq 0$$

$$r \geq 0$$

$$f_{ProtAmin}(r) \leq f_{ProtA} \leq 1$$

where

$$f_{ProtAmin} = \begin{cases} \frac{2A_{min}r}{\alpha_S}, & \text{if } r < \frac{\alpha_S}{2A_{min}} \\ 1, & \text{if } r \geq \frac{\alpha_S}{2A_{min}} \end{cases}$$

We define a radius r_{FullA} above which the cell must dedicate all of the uptake apparatus (defined as half of the surface-associated structure pool) to nutrient uptake proteins. For radii smaller than r_{FullA} , the cell may reduce its allocation to uptake proteins to $f_{ProtAmin}$, which is equivalent to the ratio of r to r_{FullA} .

When the cell radius is less than r_{FullA} , the cell mass dedicated to phosphorus uptake proteins would exceed 5% of the total cell dry mass if we allowed the uptake pool to be entirely filled with uptake proteins.

Because small cells can reduce their allocation to uptake proteins down to the point where the allocation to uptake proteins equals A_{Min} (set to 5% in our model), $2A_{Min}$ (here, 10%) is the maximum allocation to surface-associated structure allowed in the model.

first observe that the the three inequality statements are strict inequalities. We never have $E = 0$ or $L = 0$ because then growth rate would be zero, and we never have $r = 0$ because that would violate $E + L + \frac{\alpha_S}{r} + \gamma_S = 1$. The requirement of $E + L + \frac{\alpha_S}{r} + \gamma_S = 1$ sets a non-zero lower limit on the cell size:

$$r \geq \frac{\alpha_S}{1 - \gamma_S}$$

Now lets consider how the different growth rates depend on E , L , and $1/r$ given the constraint that $E + L + \frac{\alpha_S}{r} + \gamma_S = 1$.

$$\begin{aligned} L : & \begin{cases} \mu_L \text{ is an increasing function of } L \text{ (i.e. } \frac{\partial \mu_L}{\partial L} > 0) \\ \mu_E \text{ and } \mu_P \text{ are independent of } L \\ \mu_N \text{ is a decreasing function of } L \end{cases} \\ E : & \begin{cases} \mu_L \text{ is independent of } E \\ \mu_E \text{ is an increasing function of } E \\ \mu_P \text{ and } \mu_N \text{ are decreasing function of } E \end{cases} \\ \frac{1}{r} : & \begin{cases} \mu_L \text{ and } \mu_E \text{ are independent of } \frac{1}{r} \\ \mu_P \text{ and } \mu_N \text{ are increasing functions of } \frac{1}{r} \end{cases} \end{aligned}$$

Suppose photosynthesis is not the limiting rate (i.e. $\mu_L > \mu$), then we can reduce L until $\mu = \mu_L$ and increase $\frac{1}{r}$, which increases μ_P and μ_N and leaves μ_E unchanged. Similarly, if $\mu_E > \mu$, we can reduce E until $\mu_E = \mu$ and increase $\frac{1}{r}$, which increases μ_P and μ_N and leaves μ_L unchanged. Therefore, we must have that $\mu = \mu_E = \mu_L$.

We use the fact that $\mu = \mu_E = \mu_L$ to eliminate L .

$$\begin{aligned} \mu_L &= \mu_E \\ \frac{\alpha_I L}{1 + \Phi_S} &= k_{ST} E \\ L &= \frac{k_{ST} E (1 + \Phi_S)}{\alpha_I} \end{aligned}$$

the equality constraint (eq. 5) then becomes

$$\underbrace{E \left(1 + \frac{k_{ST}(1 + \Phi_S)}{\alpha_I} \right)}_{c_I} + \frac{\alpha_S}{r} + \gamma_S = 1$$

The portion of the equation in parenthesis will be referred to as c_I for the remainder of this document for simplicity. This value is not a function of any of the pools E , L , S , or the cell size, so it can be treated as a constant here. We can now write r in terms of E .

$$r = \frac{\alpha_S}{1 - \gamma_S - c_I E}$$

Note that increasing E increases L and decreases $\frac{1}{r}$. All three decrease μ_P and μ_N . but μ_E increases with increasing E . Therefore at the optimal solution, we will have either:

$$\begin{aligned}\mu_E &= \mu_P < \mu_N && \text{(P-limited)} \\ \mu_E &= \mu_N < \mu_P && \text{(N-limited)} \\ \mu_E &= \mu_P = \mu_N && \text{(N and P Co-limited)}\end{aligned}$$

So far we have not needed to consider f_{ProtA} , but now it becomes important. Notice that μ_P is an increasing function of f_{ProtA} and the μ_N is a decreasing function of f_{ProtA} . However f_{ProtA} is constrained.

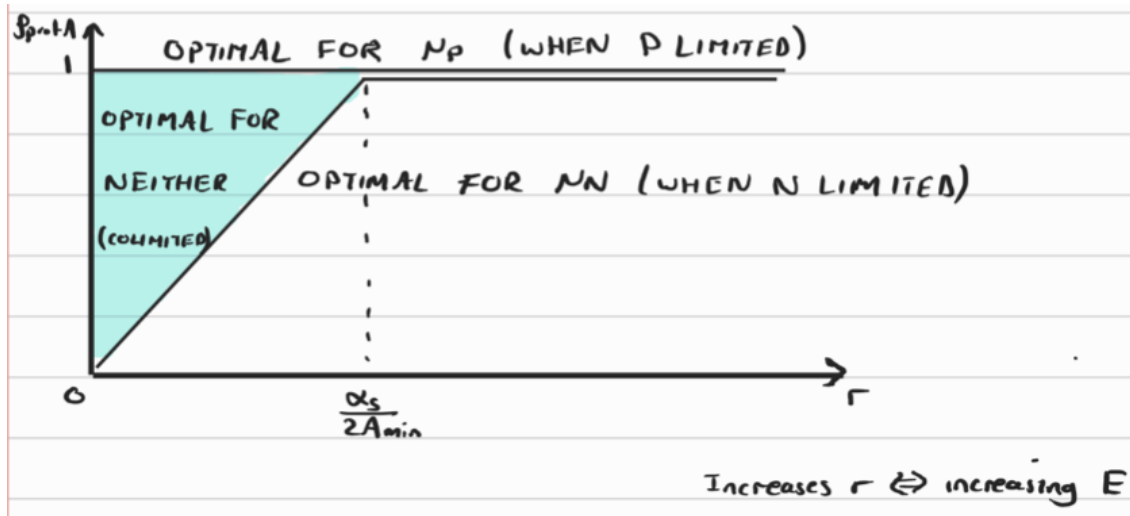


Figure 1: constraint on f_{ProtA} sketch

Now we can plot μ_E and μ_P and μ_N as a function of E (figure 2).

1.1 Model Algorithm Summary

First we solve for μ_P and μ_N under the optimal value of f_{ProtA} . That is we solve for where the blue solid line crosses the black line. ($\mu_E = \mu_P$ with $f_{ProtA} = 1$) and where the red dashed line crosses the black line ($\mu_E = \mu_N$ with $f_{ProtA} = f_{ProtAmin}$).

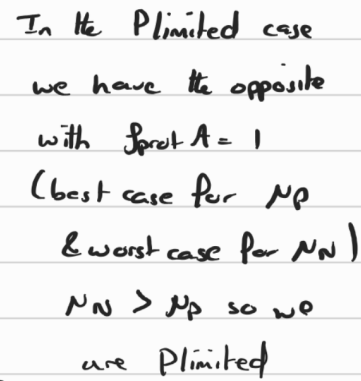
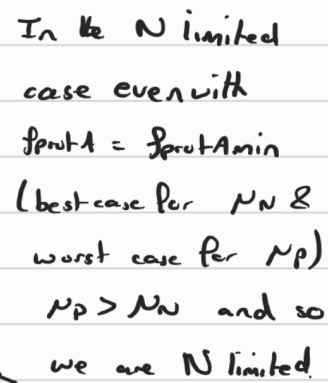
Then we compare the two growth rates and disregard the larger as it is never optimal.

For example, suppose that $\mu_P|_{f_{ProtA}=1} > \mu_N|_{f_{ProtA}=f_{ProtAmin}}$, then we know we are not P-limited. so we are either N-limited or Co-limited.

Then we take the E and f_{ProtA} value for the smaller growth rate and evaluate the other growth rate at this point.

In our example we evaluate μ_P at the calculated E and $f_{ProtA} = f_{ProtAmin}$ (vertical black lines in sketch).

If this new growth rate is smaller, then we are co-limited and we must solve $\mu_E(E) = \mu_N(E, f_{ProtA}) = \mu_P(E, f_{ProtA})$ to find the optimal growth rate. If the new growth rate is larger, then we are done and the old growth rate is optimal.



In the colimited case the regions of permitted N_p & N_w overlap.

The optimal growth rate is found at some intermediate ρ .