Ensheng Mathematical Model Framework

RULE

$C_{net_1} > C_{net_2}$

sp. LEAF TRAITS → sp. LEAF CANOPY AREA → sp. CARBON GAIN → competitive outcome

$$\sigma \propto \begin{cases} \lambda \\ n \\ r \\ \tau \end{cases}$$

LMA

$$L = \frac{N_m \lambda}{n}$$

$$C_{net} = \text{Photo} - \text{Resp}$$
$$= f(L)$$

"competition" for light

= light limitation by self shading @ high leaf area

sp_x wins if sp_x $C_{net,x} > C_{net\,i}$ $\forall i \neq x$

$$N_m = \frac{N_{TOT}}{\tau + \lambda}$$

N_{TOT} (environment) total nitrogen

met. environment temp, moisture

competitive outcome changes trait distribution which sets N_m

optimal LMA σ^*

maximizes C_{net} for a given N_m

$$C_{net} = \underbrace{\frac{V}{K}\left(1 - e^{-K\left(\frac{N_m c \sigma}{A + B\sigma}\right)}\right)}_{\text{photosynthesis}} - \underbrace{\left(N_m r c \sigma + \frac{G \sigma N_m}{A + B\sigma}\right)}_{\text{respiration}} = g(N_m, \sigma)$$

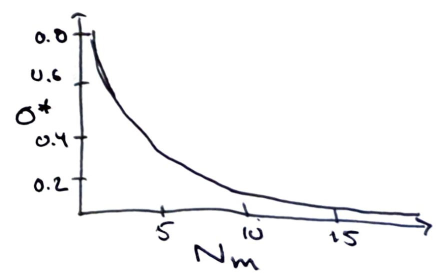
$\frac{dg}{d\sigma} = 0 \Rightarrow$ find optimum value of $\sigma = \sigma^*$ by differentiating

you get IMPLICIT EXPRESSION

$$\boxed{N_m = \frac{A + B\sigma^*}{K c \sigma^*} \ln\left(\frac{V}{(A + B\sigma^*)^2 \frac{r}{A} + \frac{G}{C}}\right)}$$

solve this numerically for σ^* across gradient in N_m (extrinsically set using N_{TOT} assuming no feedback)

$$N_m = \frac{N_{TOT}}{(c+s)\sigma_R} = \frac{A + B\sigma^*}{K c \sigma^*} \ln\left(\frac{V}{(A + B\sigma^*)^2 \frac{r}{A} + \frac{G}{C}}\right) \Rightarrow$$

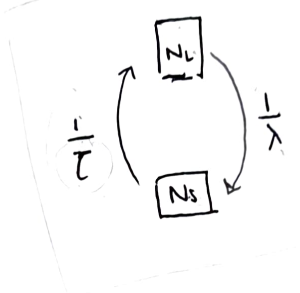


resident or "AVERAGE" extrinsically set

from next page

$$N_{total} = N_{soil} + N_{leaves}$$

$$\frac{dN_s}{dt} = \frac{N_L}{\lambda} - \frac{N_{soil}}{\tau}$$



* assume that system is N limited so uptake is instantaneous — basically N_D to N_B is the rate limiting step

At EQ, $\frac{dN_s}{dt} = 0$

$$\frac{N_L}{\lambda} = \frac{N_s}{\tau} \Rightarrow \frac{N_{TOT} - N_s}{\lambda} = \frac{N_s}{\tau} \Rightarrow \frac{N_s^*}{\tau} = \frac{N_{TOT}}{\lambda + \tau_s}$$

By defn / assumption in this model.

$$N_m = \frac{N_s}{\tau_R} = \frac{N_{TOT}}{\lambda_R + \tau_R} = \frac{N_{TOT}}{(c+s)\sigma_R}$$ ← resident or "AVERAGE of the STAND" e.g. CWM trait

To find optimal σ^*, we then have

$$\frac{N_{TOT}}{(c+s)\sigma_R} = \frac{A + B\sigma^B}{KC\sigma^*} \ln\left(\frac{V}{(A+B)\sigma^* \frac{I}{A} + \frac{G}{G}}\right)$$

ESS LMA σ_{ESS}

When the ESS LMA is the MONODOMINANT RESIDENT, by def$^{\underline{n}}$

$\sigma^{ESS} = \sigma_R = \sigma^*$

↓ s(temp, moisture) sets environmental dependence

$$N_{TOT} = \frac{(A + B\sigma^{ESS})(c+s)}{Kc} \ln(\;\;) \quad \text{as above} \quad (SB5)$$

from differentiating carbon net function + baby N cycle N_m def$^{\underline{n}}$

N_m^{REF} = N mineralization rate for environment {N_{TOT}, temp, soil moisture} with resident sp. w/ minimum LMA $\sigma_{min} = 0.02 \, \frac{kg\,C}{m^2}$

↑

determined by leaf's intrinsic properties
defines integrated environment {N_{TOT}, temp, soil moisture} required for σ_{ESS} to be the evolutionarily stable state

$$N_m^{REF} = \frac{N_{TOT}}{\underbrace{\lambda_{min} + \tau_{min}}_{\text{leaf traits of } \sigma_{min}}}$$

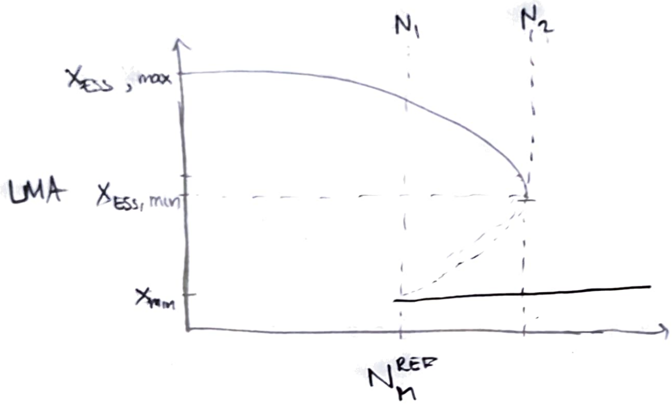
N_m^{REF} is INDEX of N availability that integrates the influence of environmental factors (temp + moisture → τ_{min}) and determines σ_{ESS}

↓ substitute S35 ↓

$$N_m^{REF} = \frac{(A + B\sigma_{ESS})}{Kc\,\sigma_{min}} \ln\left(\frac{V}{(A + B\sigma_{ESS})^2 \frac{r}{A} + \frac{G}{c}}\right)$$

N_m^{REF} INDEPENDENT of ENV and set by σ_{ESS} leaf traits given def$^{\underline{n}}$ of N_{TOT} above (SB5)

ESS LMA σ_{ESS} cont.



1. N_1: $x_{ESS} = x_{min} \Rightarrow$

$$N_1 = N_m^{REF} = \frac{A + B x_{min}}{x_{min} K C} \ln\left(\frac{V}{(A+Bx_{min})^2 \frac{r}{A} + \frac{G}{C}} \right)$$

2. N_2

Find value of $x_{ESS,min}$ → plug into eqn for N_m^{REF} → N_2

3. $x_{ESS,min}$

differentiate expression for N_{TOT} (S35) wrt x, e.g. flip fig 3 on side, find optimum (assume $\frac{G}{C} = 0$) $\Rightarrow$

$x_{ESS,min} \approx$ (stuff)

4. $x_{ESS,max}$: $N_{TOT} = 0$ in S35, solve for x_{ESS}

Invasions: Adaptive dynamics

assume invaders are rare, i.e. do not impact N_m

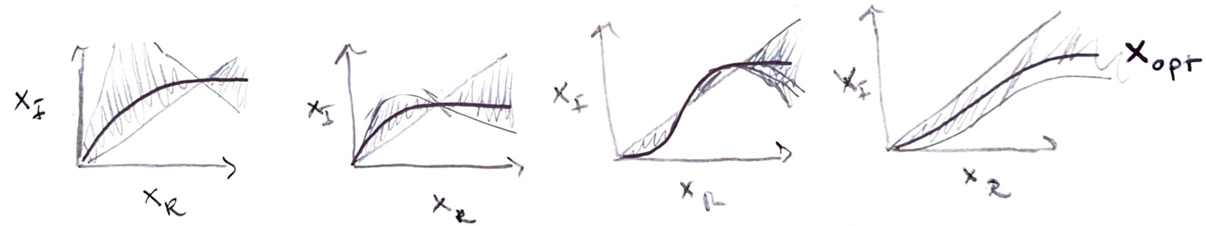
$$C_{net}(x_I \mid x_R) = \left[\frac{V}{k}\left(1 - e^{-k \frac{N_m(x_R) c x_I}{A + B x_I}}\right) - N_m(x_R)\, r c x_I - \frac{G x_I N_m(x_R)}{A + B x_I} \right]$$

$N_m(x_R) = N_m$ when sp. R is the monodominant resident

use simulation to test all combinations of x_I and x_R from $\{0.0005, 0.5\}$

successful invasion iff

$$C_{net}(x_I \mid x_R) > C_{net}(x_R \mid x_R)$$



$N_{TOT} = 50 \frac{gN}{m^2}$ $N_{TOT} = 100 \frac{gN}{m^2}$ $N_{TOT} = 150 \frac{gN}{m^2}$ $N_{TOT} = 200 \frac{gN}{m^2}$

outcome: for a given N_m^{ret} $\left\{ \begin{matrix} N_{TOT} \\ \text{temp} \\ \text{moisture} \end{matrix} \right\}$ environment, I can tell you the "winningest" strategy (X_{ESS}) of LMA. As the environment changes, I can tell you how the competitive outcome (carbon gain) changes.

What this does not tell me is:

- Can sp. with different LMA ever coexist?
  What happens after successful invasion?

- What are the dynamics of the system?
  → When you change environmental conditions from some initial community composition, what happens?
  → Who wins?

- Shifting resource limitation
  Model ASSUMES N-limitation ($L = \frac{N_{max}}{u}$) in expression for leaf area and EQ conditions (e.g. EQ leaf canopy area is INSTANTANEOUSLY created) — there is no rate of plant uptake/competition for nutrient uptake based on trait variation or root allocation

- There's no feedback between plant carbon gain and population (biomass) growth.