A Carbon Economy Model for Tree Growth

Preliminary Report

Glenn Ledder[1] Sabrina E. Russo[2] Caroline Farrior[3]

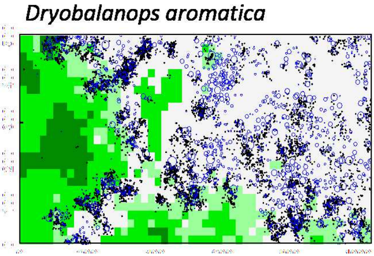
[1]Department of Mathematics
University of Nebraska-Lincoln
gledder@unl.edu

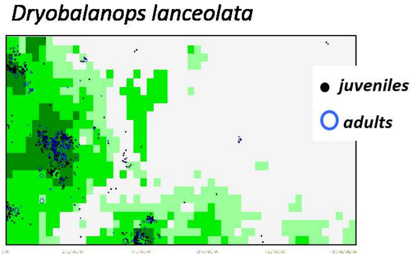
[2]School of Biological Sciences
University of Nebraska-Lincoln

[3]University of Tennessee-Knoxville

January 11, 2015

Soil Associations of *Dryobalanops*





White: sandy soil   Dark green: clay soil

Circles and dots are individual trees

- Small variations in soil type, water availability, and light levels give local advantages to different species.

Biological Background

- 764 different tree species in 130-acres (0.2 square miles) at the Lambir Hills Forest Dynamics Plot in Borneo.
  - 73% are aggregated on a single soil type (of 4).
- **Different species have different leaf characteristics:**
  - Thin and flimsy, with little protection against herbivores.
  - Tough or suffused with noxious chemicals (caffeine, etc).
    - *D. aromatica* contains camphor (an antimicrobial and anesthetic).
- Research Goal:
  Develop a mechanistic model to predict response of **growth rates** and **leaf characteristics** to **environmental conditions**.

Problem Overview

- Environmental Conditions:
  - Light level ϕ_0
  - Nitrogen availability n
  - Herbivory pressure η
- (Optimized) Leaf Characteristics:
  - 'Integrity' to 'productivity' ratio z (responds to ϕ_0, n, η)
  - Thickness (responds to ϕ_0)
  - Display (responds to ϕ_0)
- (Emergent) Leaf Characteristics:
  - Longevity (age when maintenance equals production)

Principal Quantities

- Independent Variables

t	time
x	age of leaf cohort
$\tau = t - x$	time of construction for leaf cohort

- Dependent Variables

$w(x,t)$	'productivity' carbon mass of leaf cohort of age x
$W(t)$	total 'productivity' carbon mass
$B(t) = w(0,t)$	construction rate of 'productivity' tissue
$z(\tau)$	'integrity' per unit 'productivity'

- Functions

$\gamma(z)$	base tissue loss rate
$\phi(x,t)$	light level for leaves of age x
$F(x,t)$	net investment rate function

Overview

1. **Define the broad framework of the model.**
2. Identify and analyze the simplest plausible version of the model.
3. Add realism/complexity and run simulations.

'Productivity' Retention Over Time

- Initial state is 1 unit of 'productivity'.
- Tissue loss is by natural decay with rate $\Gamma(z) = \eta\gamma(z)$.
  - η is environmental hostility factor.
- 'Productivity' carbon in initial cohort:

$$W_0(t) = e^{-\Gamma(z_0)t}$$

- 'Productivity' carbon in cohort of age x:

$$w(x,t) = B(t-x)e^{-x\Gamma(z(t-x))}$$

- Total 'productivity' carbon:

$$W(t) = W_0(t) + \int_0^t w(x,t)\,dx$$

Net Investment Rate Function $F(x, t)$

- Carbon production per unit 'productivity':

$$A(\phi(x, t))$$

- Rate of allocation to leaves from leaves of age x:

$$\kappa A(\phi(x, t))w(x, t)$$

- Rate of photosynthetic respiration from leaves of age x:

$$\rho A(\phi(x, t))w(x, t)$$

- Rate of maintenance respiration from leaves of age x:

$$\mu w(x, t)$$

- Net rate of investment in leaves from leaves of age x:

$$F(x, t)w(x, t) = [(\kappa - \rho)A(\phi(x, t)) - \mu]w(x, t)$$

Carbon Balance

- Total rate of carbon availability for new leaves:

$$F(t,t)W_0(t) + \int_0^t F(x,t)w(x,t)\,dx.$$

- Total rate of carbon expenditure on new leaves:

$$C(t)B(t), \quad \text{where} \quad C = \beta(1+z)$$

- The carbon balance equation follows from equating the rate of availability with the rate of expenditure.

$$C(t)B(t) = F(t,t)W_0(t) + \int_0^t F(x,t)w(x,t)\,dx$$

Summary of the Model

- The 'productivity' construction rate $B(t)$ is given by

$$C(t)B(t) = F(t,t)e^{-\Gamma(z_0)t} + \int_0^t B(t-x)F(x,t)e^{-x\Gamma(z(t-x))}\,dx$$

where

$$C(t) = \beta(1+z(t)), \qquad \Gamma(z) = \eta\gamma(z) = ?$$

$$F(x,t) = (\kappa - \rho)A(\phi(x,t)) - \mu = ?$$

- The total 'productivity' carbon is then

$$W(t) = e^{-\Gamma(z_0)t} + \int_0^t B(t-x)e^{-x\Gamma(z(t-x))}\,dx$$

- The goal of the analysis is to find z to "maximize" W.

Overview

1. Define the broad framework of the model.
2. **Identify and analyze the simplest plausible version of the model.**
3. Add realism/complexity and run simulations.

The Simplest Plausible Version

- Suppose there is no self-shading. Then the light level ϕ is the same for all leaves. This makes the net investment function F constant.
- With constant investment rate, the optimal 'integrity' investment ratio z and base tissue loss rate $\gamma(z)$ should be constant.
- With $B_0 = F/C$, the model is

$$B(t) = B_0 e^{-\eta\gamma t} + B_0 \int_0^t B(t-x) e^{-\eta\gamma x}\, dx$$

- This equation can be solved with the Laplace transform:

$$B(t) = B_0 e^{(B_0 - \eta\gamma)t}, \quad W(t) = e^{\lambda t}, \qquad \lambda = \frac{F}{C} - \eta\gamma.$$

A Proposed Tissue Loss Model

- Let $X(z) = 1/\gamma(z)$; then X/η is the expected survival time for leaf tissue.
- We get maximum W by maximizing the growth rate

$$\lambda(z) = \frac{F}{\beta(1+z)} - \frac{\eta}{X(z)} > 0$$

- If we think of 'integrity' as a coating on the leaves, additional survival time should be proportional to the thickness of the coating:

$$X(z) = X_0\,(1 + Kz)$$

  Note that X_0/η is the expected survival time when there is no investment in 'integrity'.

Optimal 'Integrity' for the Constant ϕ Model

- Scaling time by X_0/η simplifies the objective function to

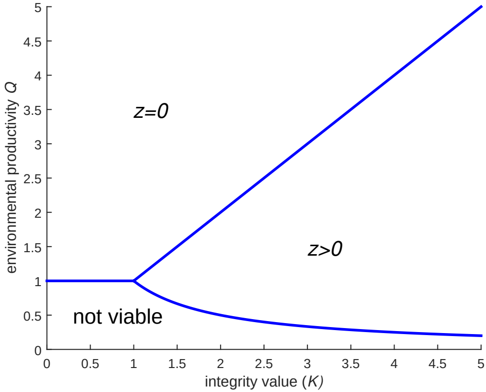
$$r(z) = \frac{Q}{1+z} - \frac{1}{1+Kz}$$

where

$$r = \frac{X_0\lambda}{\eta}, \qquad Q = \frac{FX_0}{\beta\eta}$$

- r is the scaled growth rate
- Q is a lumped parameter representing environmental quality
- $K > 1$ represents the enhanced survival resulting from unit 'integrity'.

Optimal Strategy for a Model Tree



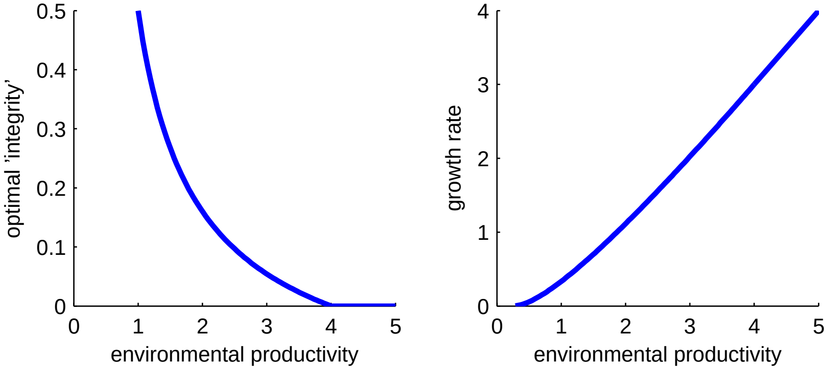
Optimal strategy, given value of ‘integrity’ K and environmental quality Q

Optimal 'Integrity' for the Constant ϕ Model

$$r(z) = \frac{Q}{1+z} - \frac{1}{1+Kz}$$

1. $Q \leq 1/K < 1$
   - Tree is not viable (maximum growth rate is negative)
2. $Q \geq K > 1$
   - Optimal 'integrity' is $z = 0$
3. $1/K < Q < K$
   - Optimal 'integrity' is $z = \dfrac{\sqrt{K} - \sqrt{Q}}{K\sqrt{Q} - \sqrt{K}}$

Optimal Performance of a Model Tree



Optimal 'integrity' and growth rate for the simplest model, with $K = 4$

Overview

1. Define the broad framework of the model.
2. Identify and analyze the simplest plausible version of the model.
3. **Add realism/complexity and run simulations.**

Photosynthesis and Light Attenuation

- We still need models for
  - Photosynthesis $A(\phi)$ for a given light level
  - Light level $\phi(x, t)$ for a given cohort
- Simplified photosynthesis model:

$$A(\phi) = \min(A_m\phi, V)$$

- Beer's Law:

$$\phi(x, t) = \phi_0 e^{-k\ell(x,t)}$$

  - $\ell(x, t)$ is the number of leaf layers younger than x

Newer Leaf Layers

- Let
  - $C(\tau)$ be the area of each leaf cohort
  - $\sigma(\tau)$ be the area per unit mass for each leaf cohort
- Biomass of each leaf cohort:

$$[1 + z(t - x)]\, w(x, t)$$

- Leaf layers for each cohort:

$$\sigma(t - x)\, \frac{1 + z(t - x)}{C(t - x)}\, w(x, t)$$

- Total number of layers above a cohort:

$$\ell(x, t) = \int_x^t \sigma(t - \xi)\, \frac{1 + z(t - \xi)}{C(t - \xi)}\, w(\xi, t)\, d\xi.$$

Summary (given constant z, σ, C, and scaling)

- Find $B(\bar{t})$ from

$$\bar{\beta}(1+z)B(\bar{t}) = \bar{F}(\bar{t},\bar{t})e^{-\bar{t}/(1+Kz)} + \int_0^{\bar{t}} B(\bar{t}-x)\bar{F}(x,\bar{t})e^{-x/(1+Kz)}\,dx$$

where

$$\bar{F}(\bar{x},\bar{t}) = \min\left(e^{-\bar{k}\bar{\ell}(\bar{x},\bar{t})},\bar{V}\right) - \bar{\mu}$$

and

$$\bar{\ell}(\bar{x},\bar{t}) = (1+z)\int_0^{\bar{x}} B(\bar{t}-\xi)\exp\left(-\frac{\xi}{1+Kz}\right)d\xi$$

- Solve numerically at each time step by the Nystrom method (approximate integrals with quadrature formulas).