

The Local Control Theory of Plant Resource Allocation

Glenn Ledder

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

October 8, 2020

With thanks to coauthors Roger Nisbet, Sabrina Russo, and Erik Muller

Acknowledgment: Funded by a National Institute for Mathematical and Biological Synthesis (NIMBioS) Sabbatical Fellowship and by UNL through a Professional Development Leave and a seed grant from the Department of Mathematics and the School of Biological Sciences.

Things to Watch For

- ▶ Mathematical questions come from biological questions.
- ▶ Mathematical properties of a model can often be inferred from biological principles.
 - **Thinking biologically is important.**
- ▶ There will be a lot of examples of undergraduate mathematics:
 - An existence proof for a 2D algebraic system that uses the intermediate value theorem.
 - A uniqueness proof for a 2D algebraic system based on a constrained optimization problem.
 - A first-order ordinary differential equation that exhibits limit cycles because it is coupled to an algebraic equation with multiple solutions.

1. Resource Allocation Theory

- 1.1 Resource Economy for Animals
- 1.2 Resource Economy for Plants

2. Modeling Resource Allocation in Plants

- 2.1 Obligate Syntrophy
- 2.2 The Local Control Theory
- 2.3 Synthesizing Unit Functions
- 2.4 The Mathematical Model

3. Analysis

- 3.1 The SU System
- 3.2 The Dynamical System
- 3.3 Performance of Local Control

Part 1. Resource Allocation Theory

Life History Theory

Theoretical ecology:

- ▶ Using biological principles to build mathematical models.
- ▶ Using these mechanistic models to address biological questions.

Some life history theory questions:

- ▶ How do organisms grow and reproduce over time?
- ▶ How do different environments shape the specific traits of successful species?
- ▶ How do individual organisms respond to environmental change?

We specifically address questions about how resource allocation to different organs influences plant growth.

Plant Growth Must Be Adaptive



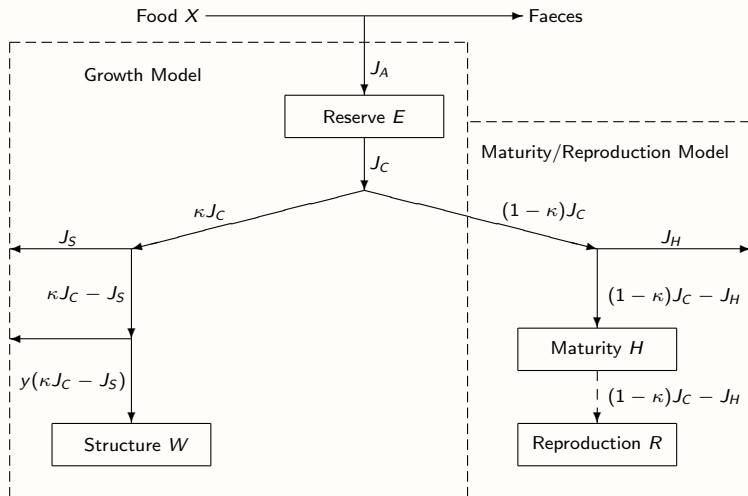
Resource Economy for Animals

- ▶ One resource (usually), carbon or energy.
- ▶ One collection mechanism.

DEB (dynamic energy budget) models

- ▶ A model animal consists of
 - “Structure”: tissues for collecting resources.
 - “Reserves”: stored resources.
 - “Maturation”: “organization” and reproductive organs.
- ▶ New resources go into reserves.
- ▶ Reserves are mobilized according to some balance principle.
- ▶ Set fractions of mobilized reserves are earmarked for structure and maturation/reproduction.

Basic DEB Animal Model



Optimal Growth Theory for Plants (Iwasa et al 1984)

1. Photosynthate production requires light (collected by leaves) and water (collected by roots).
 2. Shoots and roots are made of photosynthate.
 3. The marginal value of an organ is defined as the lifetime photosynthate gain resulting from an increment of organ size at time t .
- ▶ The Pontryagin maximum principle shows that growth is optimal when the marginal values of leaves and roots are equal.
 - ▶ This is biologically equivalent to saying a plant adjusts its shoot:root balance to be equally limited by light and water.

Resource Allocation in Plants

1. Photosynthate production requires light (collected by leaves) and **nutrients** (collected by roots), along with water.
 2. Shoots and roots are made of **a combination of photosynthate** from leaves **and nutrients** from roots.
 3. The marginal value of an organ **is not well defined** because there is no common currency to connect photosynthate and nutrients.
- **Changing conditions alter the relative values of photosynthate and nutrients, which alters the relative values of shoots and roots.**

- └ 1. Resource Allocation Theory
 - └ 1.2 Resource Economy for Plants

Challenges in Modeling Optimal Resource Allocation

Practical Challenges

- ▶ Having two resources means different organ stoichiometries and more allocation parameters.

Theoretical Challenges

- ▶ Optimal growth requires a global strategy that responds to changing conditions, but no mechanism is known.
- ▶ Optimal growth probably does not yield maximum fitness.
 - Surely mortality risk also contributes to fitness.

Part 2. Modeling Resource Allocation in Plants

Obligate Syntrophy

Obligate syntrophy: when two species are mutually dependent on resources produced or assimilated by the other.

Lichens are an example of obligate syntrophy:

- ▶ A fungus collects nutrients from the “soil,” but cannot collect energy or fix carbon.
- ▶ An alga collects energy through photosynthesis and fixes carbon from the atmosphere, but cannot collect nutrients.
- ▶ Each partner obtains its missing resource from the other while sharing only the portion of its own resource that it can't use.
- ▶ The fungus and alga have separate genomes. They have co-adapted, but they do not “cooperate.”

The Local Control Theory

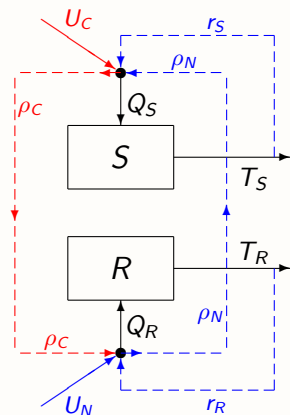
Model the plant shoot-root system as an example of obligate syntrophy, where each component acts selfishly.

- ▶ “Shoots” produce “C” (photosynthate) and “roots” assimilate “N” (critical nutrient, usually inorganic nitrogen).
- ▶ New shoot/root biomass must be assembled from C and N input streams by “synthesizing units,” using stoichiometric ratios $1:\eta_S$ and $1:\eta_R$. (We expect $\eta_S > \eta_R$ for plants.)
- ▶ Each partner controls its local resource but shares what it can't use.

The Local Control Hypothesis

Local control produces “good” results in a changing environment.

Model Schematic



R, S : root and shoot biomasses

Q_R, Q_S : biomass production rates

T_R, T_S : biomass loss rates

• : synthesizing units

U_N, U_C : N and C assimilation rates

r_R, r_S : resorbed N from lost tissue

ρ_N, ρ_C : surplus of local resource

$$X' = Q_X - T_X, \quad T_X = \gamma_X X \quad (X = R, S)$$

$$U_i = \alpha_i X \quad (i = N, C), \quad r_X = \sigma_X \cdot \eta_X T_X$$

$$\rho_C = U_C - Q_S$$

$$\rho_N = U_N + r_R - \eta_R Q_R$$

Biomass Production Rates



- ▶ The C and N input rates to the shoot SU are U_C and $\rho_N + r_S$.
- ▶ The maximum production rates are U_C and $\eta_S^{-1}(\rho_N + r_S)$.

We write the shoot biomass production rate as

$$Q_S = F_S (U_C, \eta_S^{-1}(\rho_N + r_S)),$$

where F_S is a synthesizing unit (SU) function.

Similarly,

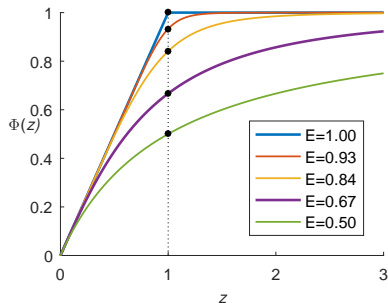
$$Q_R = F_R (\rho_C, \eta_R^{-1}(U_N + r_R)).$$

Synthesizing Unit Functions

We assume a *symmetric, ratio-dependent* SU function F :

$$F(v, w) = v \Phi\left(\frac{w}{v}\right) = w \Phi\left(\frac{v}{w}\right),$$

$$\Phi(0) = 0, \quad \Phi' \geq 0, \quad \Phi'' \leq 0, \quad \Phi(\infty) = 1.$$



- ▶ Efficiency $E = \Phi(1)$ is the fraction of resources that is used when supplied in the stoichiometric ratio.
- ▶ The heavy curves are known mechanistic models.
- ▶ The light curves are from a family of empirical models.

Modeling Strategy

Models consist of parameters as well as variables. This requires that they be viewed at two different organizational levels.

The Narrow level: Parameters are fixed and the model defines the dependent variables as functions of the independent variables.

- ▶ Simulations operate on the narrow level and produce results (equilibria, stability, uniqueness, etc) for a single point in the parameter space.

The Broad level: The model is a map from the space of parameters to a space of outputs.

- ▶ Analysis operates on the broad level and tries to draw conclusions about how the parameters determine the results.

Recasting the Model

The base model has 2 state variables that are unbounded in time and 8 parameters. We can improve the model in several ways:

- ▶ Recast it with [a modified version of] the shoot-root ratio as the dependent variable.
- ▶ Define auxiliary variables (x and y) that represent input ratios to the SUs and use them in place of the production rates Q_S and Q_R .
- ▶ Combine the resorbed N in the root with the assimilated N.
- ▶ Scale everything (nondimensionalize using well-chosen representative values).

Elements of the Mathematical Model

Parameters

- ▶ E : The SU efficiency
- ▶ α : The ratio of C:N assimilation coefficients
 - measures the relative ease of collecting C compared to N
- ▶ β : The stoichiometric ratio (N:C for shoots / N:C for roots)
 - measures the relative importance to each partner of the imported resource
- ▶ Γ : The ratio of N resorption in the shoot to local C input
 - plays a relatively minor role because resorption is a secondary source of N.

State Variable (ratio of C assimilation to N assimilation)

$$u(t) = \alpha \frac{S(t)}{R(t)}$$

The Full Dynamical System

$$\frac{1}{u} \frac{du}{dt} = \alpha \Phi(x) - \Phi(y), \quad (1)$$

where $x(u)$ and $y(u)$ are solutions of the SU system equations

$$\beta u(x - \Gamma) = 1 - \Phi(y), \quad y = u[1 - \Phi(x)]. \quad (2)$$

- ▶ $x(u)$ and $y(u)$ are the ratios of the input rates (imported resource divided by local resource) in the shoot and root SUs, respectively.
- ▶ Φ is the SU function

The SU Problem

- ▶ Analysis of the 1D dynamical system is strongly dependent on the analysis of the two-parameter algebraic SU system.

SU Problem

Given u , as well as the parameters β and Γ , find $x > \Gamma$ and $y > 0$ such that

$$\beta u(x - \Gamma) = \Theta(y), \quad y = u\Theta(x), \quad (2)$$

where $\Theta \equiv 1 - \Phi$.

- ▶ Note that each x pairs with at most a unique y , and vice versa.

Part 3. Analysis

Important Questions

Mathematical Questions

1. For what regions in the parameter space does the SU system have 0/1/multiple solutions?
2. Can the dynamical system have multiple equilibria?
3. What happens if the dynamical system has no stable equilibria?

Biological Questions

1. How does the model plant respond to changes in resource availability?
2. How does local control perform relative to hypothetical global control?

The SU Problem as a Mapping

$$\beta u(x - \Gamma) = \Theta(y), \quad y = u\Theta(x), \quad (2)$$

- Recast as a single algebraic equation for x (given Γ and u):

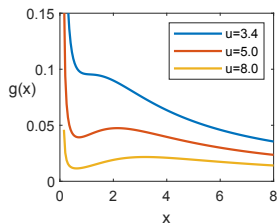
$$\beta = \frac{\Theta(y)}{u(x - \Gamma)} = \frac{\Theta(u\Theta(x))}{u(x - \Gamma)} \equiv g(x; u, \Gamma) \quad (3)$$

Mathematical statement of the SU problem:

Given $\Gamma \in [0, 1)$, $\beta > 0$, and $u > 0$, find x such that $g(x) = \beta$.

Existence of an SU Solution

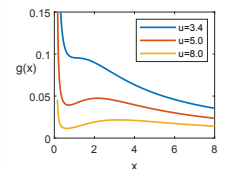
$$g(x; u, \Gamma) = \frac{\Theta(u\Theta(x))}{u(x - \Gamma)}, \quad \Theta(0) = 1, \quad \Theta' \leq 0, \quad \Theta(\infty) = 0.$$



► $g(\Gamma) = \infty$ and $g(\infty) = 0$.

Result 1: $g(x) = \beta > 0$ always has at least one solution in $\Gamma < x < \infty$.

Preliminary Uniqueness Result and Crucial Question



- ▶ If $E \leq 1/2$, then $g' \leq 0$ for all $(x; u, \Gamma)$.

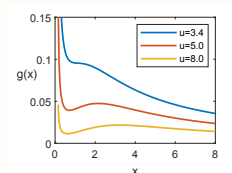
Result 2: Solutions are unique if $E \leq 0.5$.

(We expect $E \geq 2/3$ for biological systems.)

Crucial Question

Given large enough efficiency and $\Gamma \in [0, 1)$, for what range of β does the SU system $g(x(u)) = \beta$ admit multiple solutions for some value of u ?

Uniqueness

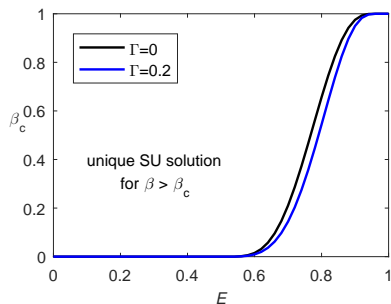


- ▶ As u decreases, g becomes monotone.

Result 3: There is a critical value $\beta_c \leq 1$ such that the SU solution is unique when $\beta \geq \beta_c$, but might not be if $\beta < \beta_c$.

- ▶ β_c is the maximum value that can be achieved by $g(x; u)$ at a point where $g' = 0$.
- ▶ The problem for β_c can be recast as a constrained optimization problem for a function $\psi(x, y)$.

Summary of SU Results



- ▶ Low efficiency guarantees uniqueness.
 - Probably never happens.
 - ▶ $\beta \geq \beta_c$ guarantees uniqueness.
 - ▶ $\Gamma > 0$ slightly increases the tendency for uniqueness.
 - Γ is usually small in nature.
- ▶ **Plants naturally have $\beta > 1$ because carbon fixation requires an enzyme (high in nitrogen).**
- It is less clear when the limiting resource is not nitrogen.

Assimilation Ratio Equilibria

The equilibrium assimilation ratio (x^*, y^*) must satisfy

$$0 = u^{-1} u' = \alpha \Phi(x^*) - \Phi(y^*). \quad (1)$$

and the SU equations

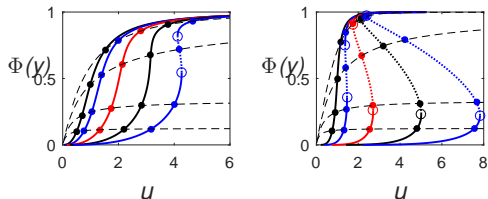
$$\beta u^*(x^* - \Gamma) = 1 - \Phi(y^*), \quad y^* = u^* [1 - \Phi(x^*)]. \quad (2)$$

► (2) defines $y^*(x^*)$ and $u^*(x^*)$; then (1) defines $x^*(\alpha)$.

Result 4: There is a unique equilibrium assimilation ratio whenever $\alpha\Phi(\Gamma) < 1$ (true in nature, since $\Phi(\Gamma) \ll 1$).

Assimilation Ratio Equilibria

Equilibria are intersections on a graph of root growth vs system state.

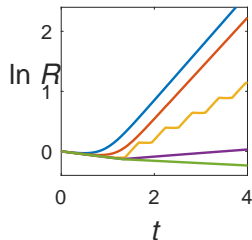
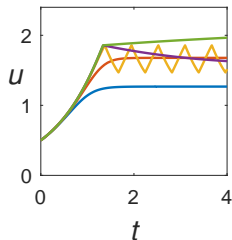
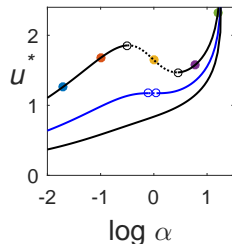


► $E = 0.67$ (left) and $E = 0.84$; β decreases to the right.

Result 5: The equilibrium assimilation ratio is unstable if and only if the plot of root growth vs assimilation ratio has a negative slope at the equilibrium point.

Equilibrium Assimilation Ratio Stability

Result 6: u^* is unstable if and only if the plot of u^* versus α has a negative slope at the equilibrium point.



- Larger α makes $u = \alpha S/R$ larger. But it also means that N is harder to collect, and the plant adjusts by growing more roots. Instability happens when the plant overcompensates with a larger relative change in R than the relative change in α .

Optimal Long-term Growth Rate

Can global control improve the long-term growth rate?

Assume a global control mechanism that can choose the fractions κ_C and κ_N of resources that are shunted directly to the partner (local control means $\kappa_C = \kappa_N = 0$).

- ▶ There will be a long-term equilibrium assimilation ratio $u^*(\kappa_C, \kappa_N)$ and a corresponding growth rate

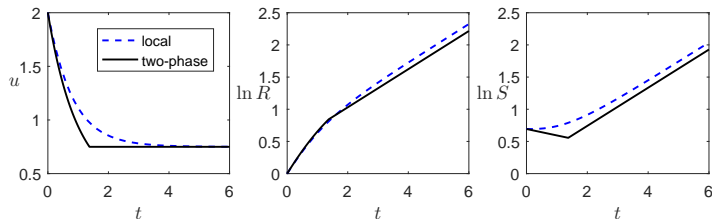
$$G(\kappa_C, \kappa_N) = \frac{R'}{R} = \frac{S'}{S}.$$

Result 7: The best growth rate $G(\kappa_C, \kappa_N)$ is for the local control choices $\kappa_C = \kappa_N = 0$.

Optimal Approach to Steady-State

Can global control do better than local control when there is an imbalance to redress?

- ▶ Start with a shortage of roots.
- ▶ Try $\kappa_C = 1$ until $u = u^*(0, 0)$ and then $\kappa_C = 0$ (bang-bang).



Result 8: The local control strategy is better for redressing imbalance than a bang-bang strategy.

Key Conclusions

- ▶ Obligate syntrophy is stable when each partner has a relatively greater need for the imported resource than its partner has (shoots need a higher proportion of N than roots do). Local allocation yields optimal growth.
 - Obligate syntrophy *can* be unstable and suboptimal when each partner's need for its local resource is sufficiently greater than its need for its imported resource.
- ▶ Modeling supports the conjecture that plants do not require active coordination between roots and shoots.
- ▶ “Obligate Syntrophy” would be a great name for a rock band!