

Optimal life history strategies accounting for resource and meristem allocation

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Classic models for the evolution of life history strategies in plants assume that selection acts on and optimizes resource allocation to growth versus reproduction.

Plant growth is modular: development proceeds by decisions about what to do with meristems (plant stem cells!). Do meristems remain dormant, branch, or transition to reproduction?

The goal of this project is to extend resource-based models for life history strategies to include development, and to evaluate how this affects optimal life history strategies.

Optimal control applied to life history evolution

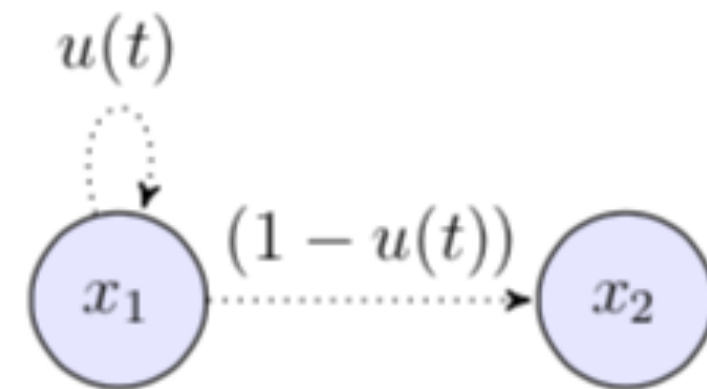
We present a motivating idea of optimal control theory in a classic application from King and Roughgarden [104] on allocation between vegetative and reproductive growth for annual plants. This plant growth model formulated by Cohen [36] divides the plant into two parts: the vegetative part, consisting of leaves, stems, and roots, and the reproductive part. The products of photosynthesis (growth) are partitioned into these parts, and the rate of photosynthesis is assumed to be proportional to the weight of the vegetative part. Let $x_1(t)$ be the weight of the vegetative part at time t and $x_2(t)$ the weight of the reproductive part. Consider the following ordinary differential equation model:

$$\begin{aligned}x_1'(t) &= u(t)x_1(t), \\x_2'(t) &= (1 - u(t))x_2(t), \\0 &\leq u(t) \leq 1, \\x_1(0) &> 0, x_2(0) \geq 0,\end{aligned}$$

where the function $u(t)$ is the fraction of the photosynthate partitioned to vegetative growth. The natural evolution of the plant should encourage maximal growth of the reproductive part in order to ensure effective reproduction. Therefore, the goal is to find a partitioning pattern control $u(t)$ which maximizes the functional

$$\int_0^T \ln(x_2(t)) dt.$$

The maximum season length is the upper bound T on the time interval, and it is assumed that all season lengths from zero to a fixed maximum have equal probability of occurrence. The natural logarithm appears here because it is believed the evolution of the plant favors reproduction in a nonlinear way.



model assumes photosynthesis is proportional to size of vegetative pool; photosynthate is partitioned to the two pools

Step one for me is solving the classic control problem with numerically

Analytical solution: control and adjoint from King and Roughgarden (TPB 1982)

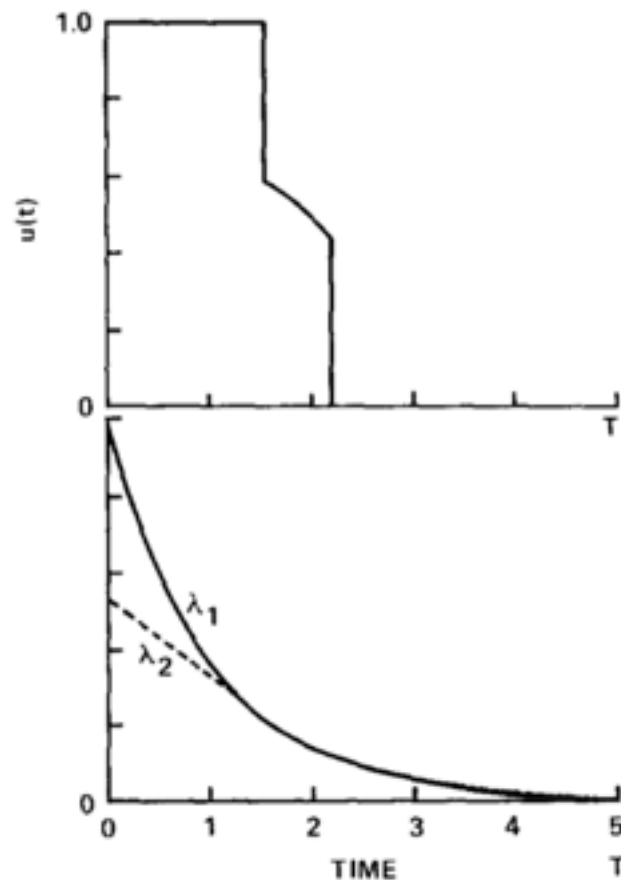
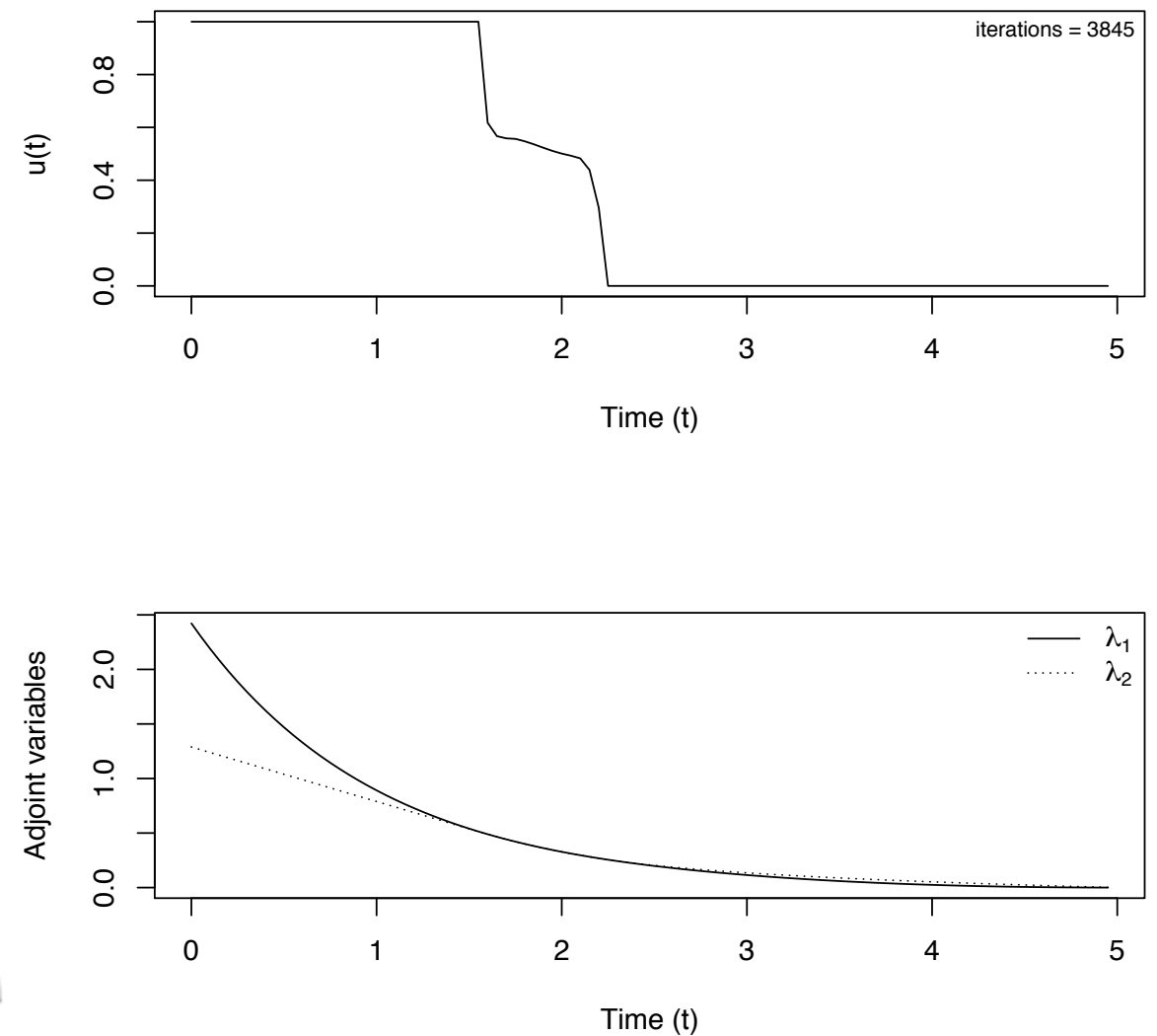


FIG. 4. Adjoint variables and the control maximizing $\int_0^T \log x_2 dt$ when $T=5$ and $x_2(0)/x_1(0) = 2.0$. Initial growth is purely vegetative.

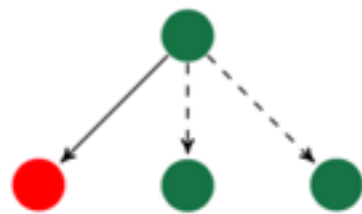
Numerical solution: control and adjoint using forward-backward sweep



Plant growth is modular: my jade agreed to help illustrate this idea



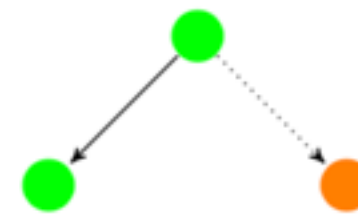
Describe plant development as a set of transitions and productions by meristems



(a) Primary meristem transitioning to one vegetative meristem and generating two primary meristems.



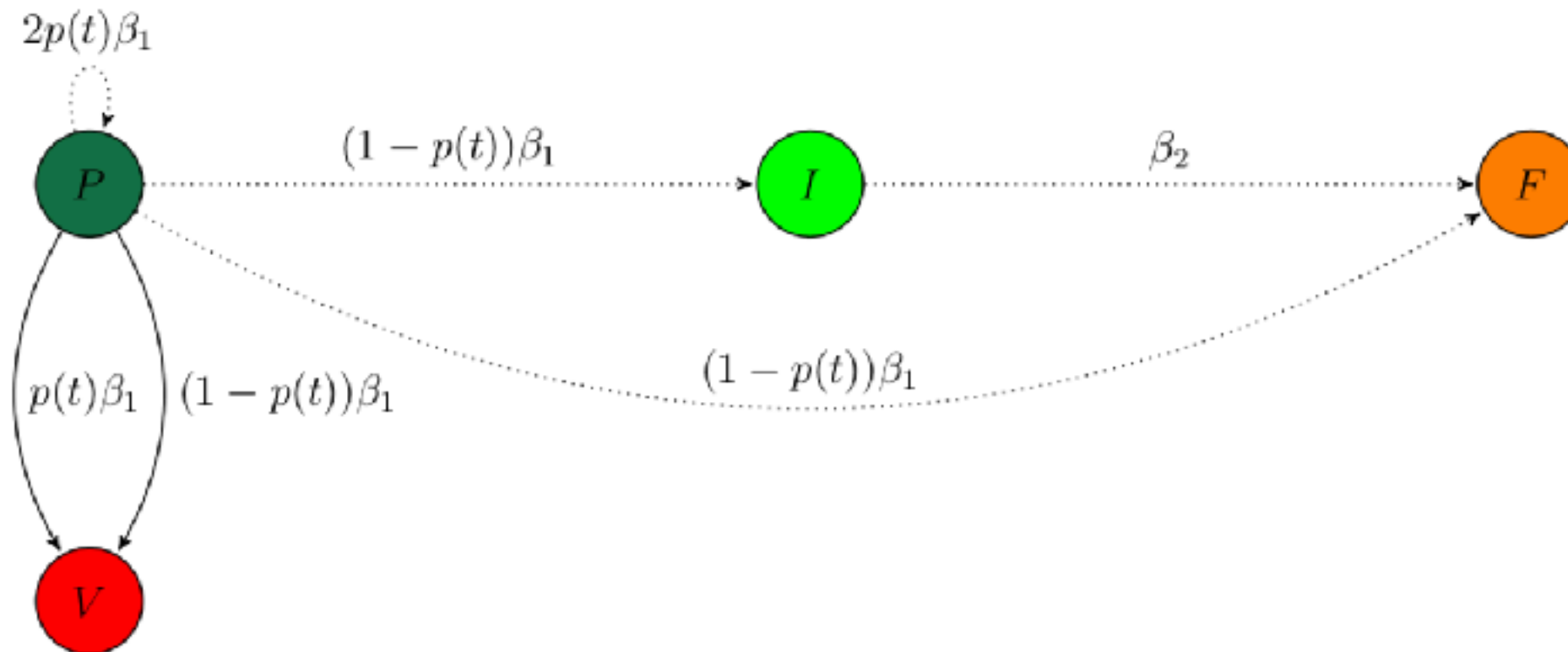
(b) Primary meristem transitioning to one vegetative meristem, and generating inflorescence and floral meristems.



(c) Inflorescence meristem remaining an inflorescence meristem and generating a floral meristem

For example, in (a), a primary/vegetative meristem produces a primary meristem (main branch), a second primary meristem (axillary branch), and a leaf.

Summarize development as system of ODEs and constraints



$$\dot{P} = 2\beta_1 p(t)P - \beta_1 p(t)P - (1-p(t))\beta_1 P$$

$$0 \leq p(t) \leq 1$$

$$\dot{V} = \beta_1 p(t)P + (1-p(t))\beta_1 P$$

$$0 < P$$

$$\dot{I} = \beta_1 (1-p(t))P$$

subject to

$$0 \leq I$$

$$\dot{F} = \beta_1 (1-p(t))P + \beta_2 I$$

$$0 \leq F$$

Some key references

- Cohen, D. 1971. Maximizing final yield when growth is limited by time or by limiting resources. *Journal of Theoretical Biology* 33:299–307.
- Fox, G. A. 1992. Annual plant life histories and the paradigm of resource allocation. *Evolutionary Ecology* 6:482–499.
- Itzkovitz, S., I. C. Blat, T. Jacks, H. Clevers, and A. van Oudenaarden. 2012. Optimality in the Development of Intestinal Crypts. *Cell* 148:608–619.
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- Lenhart, S., and J. T. Workman. 2007. Optimal control applied to biological models. Chapman & Hall/CRC, Boca Raton.