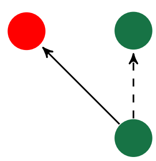
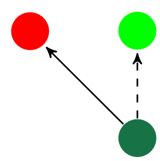
Last updated: May 18, 2021

Unbranched, determinate case

The basic case we consider here is one in which the plant is unbranched and the inflorescence is determinate. Plants with an unbranched structure are defined by primary meristem divisions that generate either a vegetative and primary meristem (Figure 1A) or a vegetative and inflorescence meristem (Figure 1B) but do not branch. A determinate inflorescence is represented in the model as an inflorescence meristem division transitioning to a floral meristem (Figure 1C).



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



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

(c) Inflorescence meristem generating a floral meristem

Figure 1: Meristem transitions in an unbranched plant with a determinate inflorescence.

The table below summarizes the state and control variables in models based on these meristem transitions.

Term	**Description**
P	Primary meristems
V	Vegetative biomass
I	Inflorescence meristems
F	Floral meristems
$u(t)$	The probability that a primary meristem division produces a primary and vegetative meristem (Figure 1A).
$1 - u(t)$	The probability that a primary meristem division produces an inflorescence and a vegetative meristem (Figure 1B).
$\beta_1(t)$	The per-capita rate of division by primary meristems.
$\beta_2(t)$	The per-capita rate of division by inflorescence meristems.

11 Unbranched, determinate case without resource constraint

We are ultimately interested in incorporating resource constraints into our model. However, we start by analyzing a version of the model that does not have resource constraints. The optimal control problem then becomes:

$$\begin{aligned}
&\max_u \int_0^T \log(F(t))\,\mathrm{d}t && \text{Objective function}\\
\text{subject to } &\dot{P} = -[\beta_1(t)][(1-u(t))P] && \text{System of ODEs}\\
&\dot{V} = [\beta_1(t)][u(t)P] + [\beta_1(t)][(1-u(t))P] = \beta_1[P] &&\\
&\dot{I} = [\beta_1(t)][(1-u(t))P] - [\beta_2(t)]I && \qquad (1)\\
&\dot{F} = [\beta_2(t)]I &&\\
&P(0) > 0;\ V(0),\ I(0),\ F(0) \geq 0 && \text{Initial conditions}\\
&0 \leq \beta_1(t), \beta_2(t) \leq M && \text{Meristem constraint}\\
&0 \leq u(t) \leq 1 && \text{Control constraint}
\end{aligned}$$

We write the Hamiltonian as

$$H = \log F + \lambda_1[-\beta_1(1-u)P] + \lambda_2[\beta_1 P] + \lambda_3[\beta_1(1-u)P - \beta_2 I] + \lambda_4[\beta_2 I] \tag{2}$$

To obtain the switching functions, we take the derivative of the Hamiltonian with respect to each control

$$\frac{\partial H}{\partial u} = (\lambda_1 - \lambda_3)\beta_1 P = \Phi_1(t) \text{ at } \beta_1^*, \beta_2^* \tag{3}$$
$$\frac{\partial H}{\partial \beta_1} = (\lambda_3(1-u) - \lambda_1(1-u) + \lambda_2)P = \Phi_2(t) \text{ at } u^*, \beta_2^* \tag{4}$$
$$\frac{\partial H}{\partial \beta_2} = (\lambda_4 - \lambda_3)I = \Phi_3(t) \text{ at } u^*, \beta_1^* \tag{5}$$

The adjoint equations are

$$
\begin{aligned}
-\frac{\partial H}{\partial P} &= \dot{\lambda_1} = \beta_1(\lambda_1(1-u) - \lambda_2 - \lambda_3(1-u)) \\
-\frac{\partial H}{\partial V} &= \dot{\lambda_2} = 0 \\
-\frac{\partial H}{\partial I} &= \dot{\lambda_3} = \beta_2(\lambda_3 - \lambda_4) \\
-\frac{\partial H}{\partial F} &= \dot{\lambda_4} = -\frac{1}{F}
\end{aligned} \tag{6}
$$

The transversality condition is

$$\lambda_1(T) = \lambda_2(T) = \lambda_3(T) = \lambda_4(T) = 0. \tag{7}$$

Without a resource constraint, meristem divisions can occur at the maximum rate (M) at all times. The optimal strategy is $u = 0$ and $\beta_1 = \beta_2 = M$ at all times. In this model, meristems have no value as branches (there is no branching) or as bearers of vegetative, photosynthetic biomass. The optimal strategy is to convert primary meristems to inflorescence meristems ($u = 0$) at the maximum rate ($\beta_1 = M$), and then convert those inflorescence meristems to floral meristems at the maximum rate ($\beta_2 = M$) at all times. We get here by first considering β_2, which we find to be bang-bang. We then consider u and β_1 jointly. I have not been able to analyze this completely but the partial derivatives with respect to the Hamiltonian both suggest that decreases in u and increases β_1 increase H at all times, suggesting that both are bang-bang as well.

Unbranched, determinate case with resource constraint

Including a resource constraint makes this a problem of the kind discussed by Kamien and Schwartz in State Variable Inequality Constraints (p 231) and by Chiang in Optimal Control with Constraints (p 300). We briefly describe the approach suggested by each author.

Kamien and Schwartz formulate problems with state variable inequality constraints in the general form

$$\max \int_{t_0}^{t_1} f(t,x,u)\mathrm{d}t + \phi(x(t_1)) \qquad \text{Objective function}$$

$$\text{subject to } \dot{x} = g(t,x,u),\ x(t_0) = x_0 \qquad \text{System of ODEs, initial conditions}$$

$$k(t,x) \geq 0 \qquad \text{State variable inequality constraint}$$

The optimal control problem we seek to solve does not include a terminal payoff ($\phi(x(t_1))$) so we do not consider that component here. To solve the problem, Kamien and Schwartz associate a multiplier λ with the system of ODEs and a multiplier η with the state variable constraint. The Hamiltonian is then written as

$$H = f(t,x,u) + \lambda g(t,x,u) + \eta k(t,x)$$

Necessary conditions for optimality include satisfying the system of ODEs, the state variable constraint, and the following equations

$$\begin{aligned}
&\frac{\partial H}{\partial u} = \frac{\partial f}{\partial u} + \lambda\frac{\partial g}{\partial u} = 0 && \text{Optimality conditions}\\
&\frac{\partial H}{\partial x} = -\dot{\lambda} = \frac{\partial f}{\partial x} + \lambda\frac{\partial g}{\partial x} + \eta\frac{\partial k}{\partial x} && \text{Adjoint equations}\\
&\lambda(t_1) = \frac{\partial \phi}{\partial x}(x(t_1)) && \text{Transversality condition/payoff}\\
&\eta \geq 0, \eta k(t,x) = 0 && \text{Complementary slackness conditions}
\end{aligned} \tag{8}$$

The optimality conditions, adjoint equations, and transversality conditions are the same as for problems without state variable inequality constraints. The novel component is the complementary slackness condition, which represent the effect of the state variable inequality constraints on the system. When $k(t,x)$ is off the constraint such that $k(t,x) > 0$, the constraint multiplier $\eta = 0$. When $k(t,x)$ is on the constraint such that $k(t,x) = 0$, the constraint multiplier $\eta > 0$. The constraint multiplier η represents the cost of the constraint:

when the constraint is not active there is no cost to it; when the constraint is active the cost is defined by the state of the system.

Chiang takes the following approach:

We rewrite the optimal control problem to include a state variable inequality constraint, which here is the resource constraint

$$
\begin{aligned}
&\max_u \int_0^T \log(F(t))\mathrm{d}t && \text{Objective function} \\
\text{subject to } &\dot{P} = \gamma[\beta_1(t)][(u(t))P] - [\beta_1(t)][(1-u(t))P] && \text{System of ODEs} \\
&\dot{V} = [\beta_1(t)][u(t)P] + [\beta_1(t)][(1-u(t))P] = \beta_1[P] \\
&\dot{I} = [\beta_1(t)][(1-u(t))P] - [\beta_2(t)]I \\
&\dot{F} = [\beta_2(t)]I \\
&P(0) > 0;\ V(0),\ I(0),\ F(0) \geq 0 && \text{Initial conditions} \\
&0 \leq \beta_1(t), \beta_2(t) \leq M && \text{Meristem constraint} \\
&0 \leq \beta_1(t)P + \beta_2(t)I \leq \alpha V && \text{Resource constraint} \\
&0 \leq u(t) \leq 1 && \text{Control constraint}
\end{aligned} \tag{9}
$$

We write the Hamiltonian as

$$
H = \log F + \lambda_1[-\beta_1(1-u)P] + \lambda_2[\beta_1 P] + \lambda_3[\beta_1(1-u)P - \beta_2 I] + \lambda_4[\beta_2 I] + \eta[V - (\beta_1 P + \beta_2 I)] \tag{10}
$$

To obtain the switching functions, we take the derivative of the Hamiltonian with respect to each control

$$
\frac{\partial H}{\partial u} = (\lambda_1 - \lambda_3)\beta_1 P = 0 \text{ at } \beta_1^*, \beta_2^* \tag{11}
$$

$$
\frac{\partial H}{\partial \beta_1} = (\lambda_3(1-u) - \lambda_1(1-u) + \lambda_2 - \eta)P = 0 \text{ at } u^*, \beta_2^* \tag{12}
$$

$$
\frac{\partial H}{\partial \beta_2} = (\lambda_4 - \lambda_3 - \eta)I = 0 \text{ at } u^*, \beta_1^* \tag{13}
$$

The adjoint equations are

$$\begin{aligned}
-\frac{\partial H}{\partial P} &= \dot{\lambda_1} = \beta_1(\lambda_1(1-u) - \lambda_2 - \lambda_3(1-u) + \eta\beta_1) \\
-\frac{\partial H}{\partial V} &= \dot{\lambda_2} = -\eta \\
-\frac{\partial H}{\partial I} &= \dot{\lambda_3} = \beta_2(\eta + \lambda_3 - \lambda_4) \\
-\frac{\partial H}{\partial F} &= \dot{\lambda_4} = -\frac{1}{F}
\end{aligned} \tag{14}$$

The transversality condition is

$$\lambda_1(T) = \lambda_2(T) = \lambda_3(T) = \lambda_4(T) = 0. \tag{15}$$

The complementary slackness condition is

$$\eta \geq 0,\ \eta[V - (\beta_1 P + \beta_2 I)] = 0 \tag{16}$$

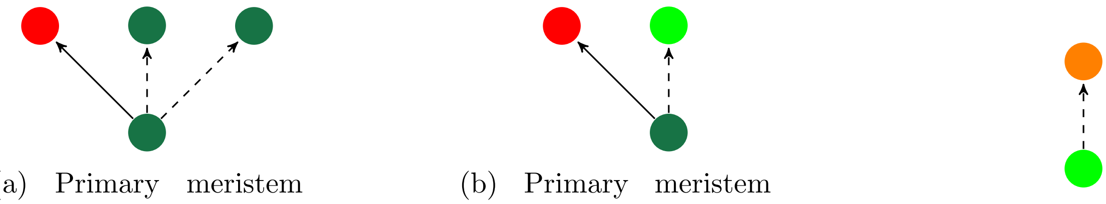
From the above equation, $\eta = 0$ when $V - (\beta_1 P + \beta_2 I) > 0$ (off the constraint). On the other hand, $\eta > 0$ when $V - (\beta_1 P + \beta_2 I) \leq 0$ (on the constraint).

When we are not on the boundary, $(V - (\beta_1 P + \beta_2 I) > 0)$.

We do the following on the boundary

$$\phi = \frac{(P(\lambda_3 - \lambda_1)(1-u) + \lambda_2) - (I(\lambda_4 - \lambda_3)}{P - I} \tag{17}$$

Branched, determinate case



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

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

(c) Inflorescence meristem generating a floral meristem

Figure 2: Meristem transitions in an unbranched plant with a determinate inflorescence.

The optimal control problem we are interested in is

$$\begin{aligned} &\max_u \int_0^T \log(F(t))dt \\ \text{subject to } &\dot{P} = [q(t)V][p(t)P] - [q(t)V][(1-p(t))P], \\ &\dot{V} = [q(t)V][p(t)P] + [q(t)V][(1-p(t))P], \\ &\dot{I} = [q(t)V][(1-p(t))P], \\ &\dot{F} = [(1-q(t))V]I, \\ &P(0) > 0;\ V(0),\ I(0),\ F(0) \geq 0, \\ &0 \leq p(t), q(t) \leq 1. \end{aligned} \tag{18}$$

The Hamiltonian is

Term	**Description**
P	Primary meristems
V	Vegetative biomass
I	Inflorescence meristems
F	Floral meristems
p	The probability that a primary meristem division produces a primary and vegetative meristem. A primary meristem division either produces a primary and vegetative meristem (Figure **??**A) or an inflorescence and vegetative meristem (Figure **??**B).
q	The fraction of photosynthate that is allocated to vegetative growth. Here, vegetative growth consists of primary meristem divisions. Any photosynthate not allocated to primary meristem divisions is allocated to inflorescence meristem divisions.

$$H = \log F + ((2PV\lambda_1 - PV\lambda_3)p - IV\lambda_4 + PV\lambda_3 + PV\lambda_2 - PV\lambda_1)q + IV\lambda_4 \tag{19}$$

The optimality conditions are

$$\frac{\partial H}{\partial p} = (PV)(2\lambda_1 - \lambda_3)q = 0 \text{ at } p^* \tag{20}$$
$$\frac{\partial H}{\partial q} = (PV)(2\lambda_1 - \lambda_3)p - IV\lambda_4 + PV\lambda_3 + PV\lambda_2 - PV\lambda_1 = 0 \text{ at } q^* \tag{21}$$

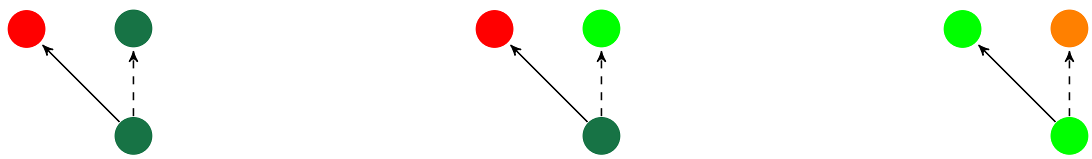
The transversality condition is

$$\lambda_1(T) = \lambda_2(T) = \lambda_3(T) = \lambda_4(T) = 0. \tag{22}$$

The adjoint equations are

$$\begin{aligned}
-\frac{\partial H}{\partial P} &= \dot{\lambda_1} = -((2V\lambda_1 - V\lambda_3)p + V\lambda_3 + V\lambda_2 - V\lambda_1)q \\
-\frac{\partial H}{\partial V} &= \dot{\lambda_2} = -((2P\lambda_1 - P\lambda_3)p - I\lambda_4 + P\lambda_3 + P\lambda_2 - P\lambda_1)q - I\lambda_4 \\
-\frac{\partial H}{\partial I} &= \dot{\lambda_3} = V\lambda_4 q - V\lambda_4 \\
-\frac{\partial H}{\partial L} &= \dot{\lambda_4} = -\frac{1}{F}
\end{aligned} \tag{23}$$

Unbranched, indeterminate case



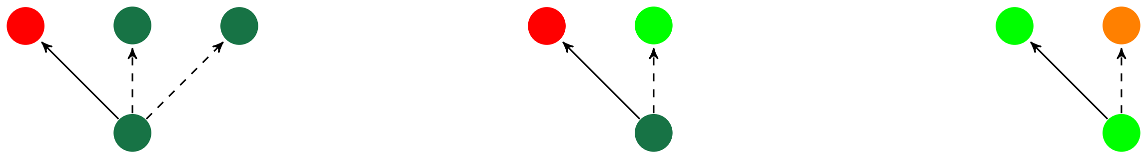
(a) Primary meristem transitioning to one vegetative meristem and generating one primary meristem.

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

(c) Inflorescence meristem transitioning to one inflorescence meristem, and generating a floral meristem

Figure 3: Meristem transitions in an unbranched plant with an indeterminate inflorescence.

Branched, indeterminate case



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

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

(c) Inflorescence meristem transitioning to one inflorescence meristem, and generating a floral meristem

Figure 4: Meristem transitions in an unbranched plant with an indeterminate inflorescence.