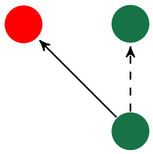
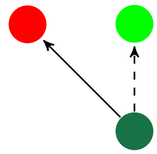
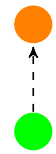
Unbranched, determinate case



(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 generating a floral meristem

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

The optimal control problem we are interested in is

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

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 5A) or an inflorescence and vegetative meristem (Figure 5B).
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.

The Hamiltonian is

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

The optimality conditions are

$$\frac{\partial H}{\partial p} = (PV)(\lambda_1 - \lambda_3)q = 0 \text{ at } p^* \tag{3}$$

$$\frac{\partial H}{\partial q} = (PV)(\lambda_1 - \lambda_3)p - IV\lambda_4 + PV\lambda_3 + PV\lambda_2 - PV\lambda_1 = 0 \text{ at } q^* \tag{4}$$

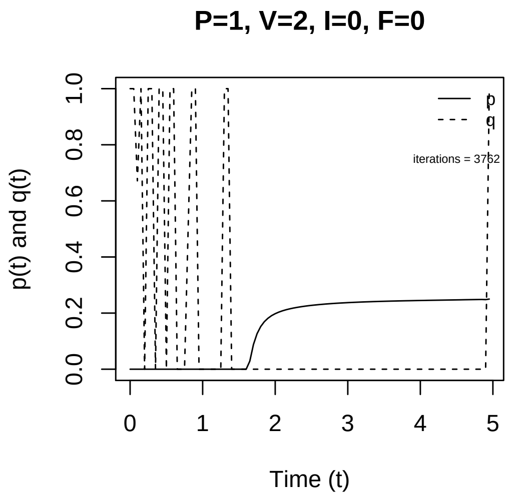
The transversality condition is

$$\lambda_1(T) = \lambda_2(T) = \lambda_3(T) = \lambda_4(T) = 0. \tag{5}$$

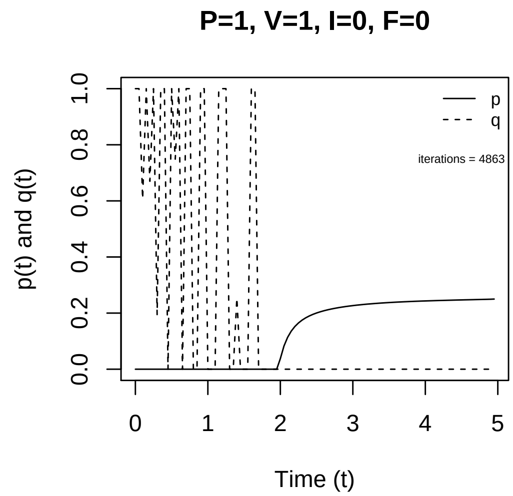
The adjoint equations are

$$\begin{aligned}
-\frac{\partial H}{\partial P} &= \dot{\lambda_1} = -((V\lambda_1 - V\lambda_3)p + V\lambda_3 + V\lambda_2 - V\lambda_1)q \\
-\frac{\partial H}{\partial V} &= \dot{\lambda_2} = -((P\lambda_1 - P\lambda_3)p - I\lambda_4 + P\lambda_3 + P\lambda_2 - P\lambda_1)q - I\lambda_4 \\
-\frac{\partial H}{\partial I} &= \dot{\lambda_3} = V\lambda_4 q - V\lambda_4 \\
-\frac{\partial H}{\partial L} &= \dot{\lambda_4} = -\frac{1}{F}
\end{aligned} \tag{6}$$

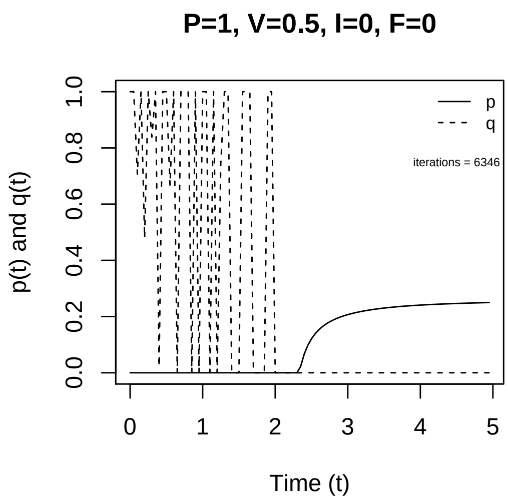
I used an adapted forward-backward sweep. The figures on the following pages summarize some solutions for different initial conditions and show the general trajectory of state variables and adjoint variables.



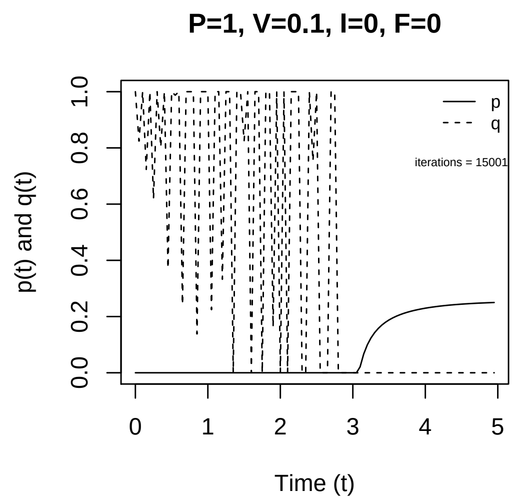
(a) ...



(b) ...



(c) ...



(d) ...

Figure 2: Trajectories of controls p (solid line) and q (dashed line) for a range of initial conditions. The optimal control suggests no division of primary meristems ($p(t) = 0$) initially with oscillating allocation of photosynthate to vegetative growth. I cut off the solutions at 15000 iterations, so the controls in Panel d have not converged. See next two pages for figures corresponding to state trajectories and adjoint variables for Panel d.

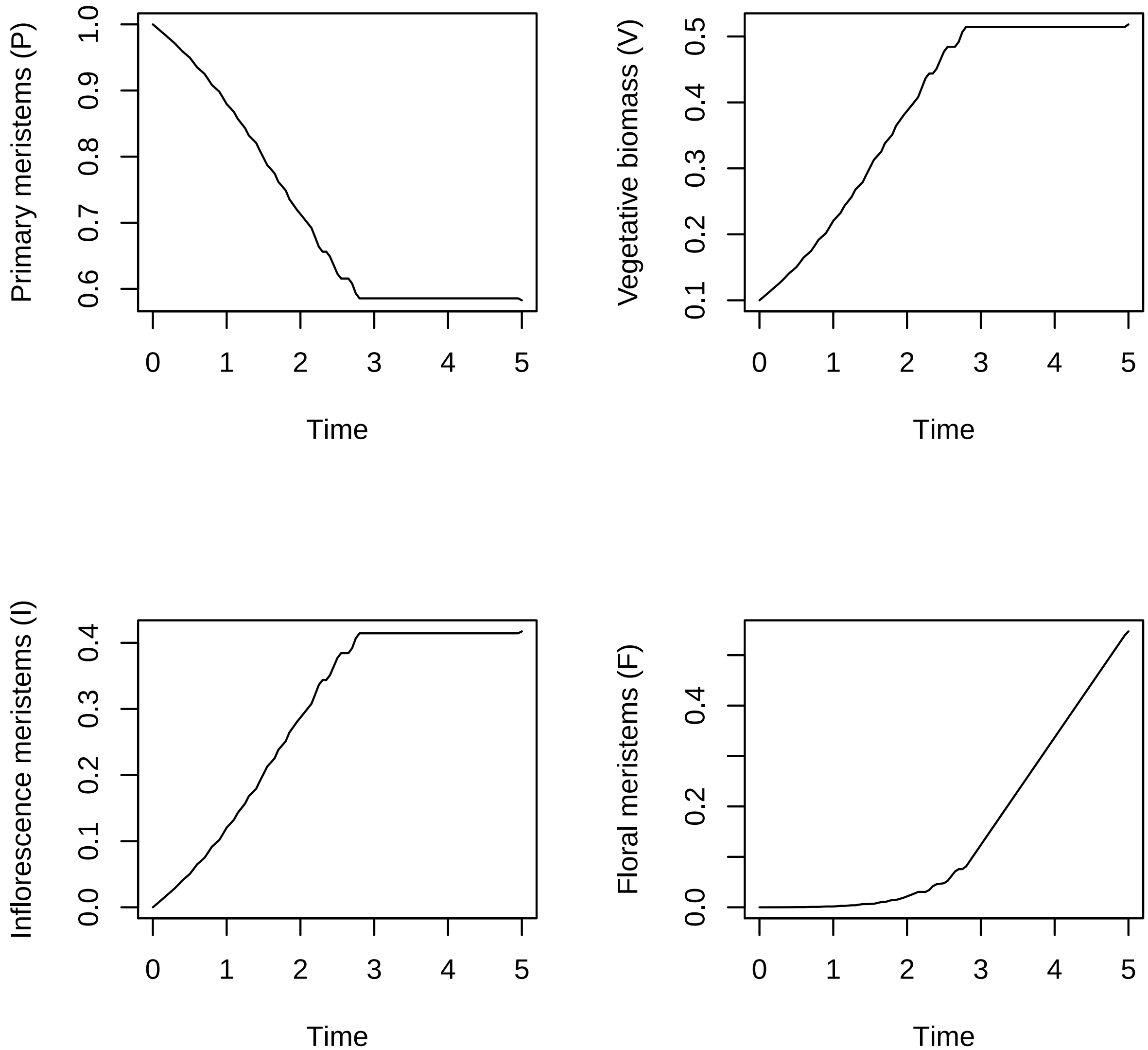


Figure 3: Trajectories of state variables for the case where the initial conditions are $P(0) = 1,\ V(0) = 0.1,\ I(0) = 0,\ F(0) = 0$.

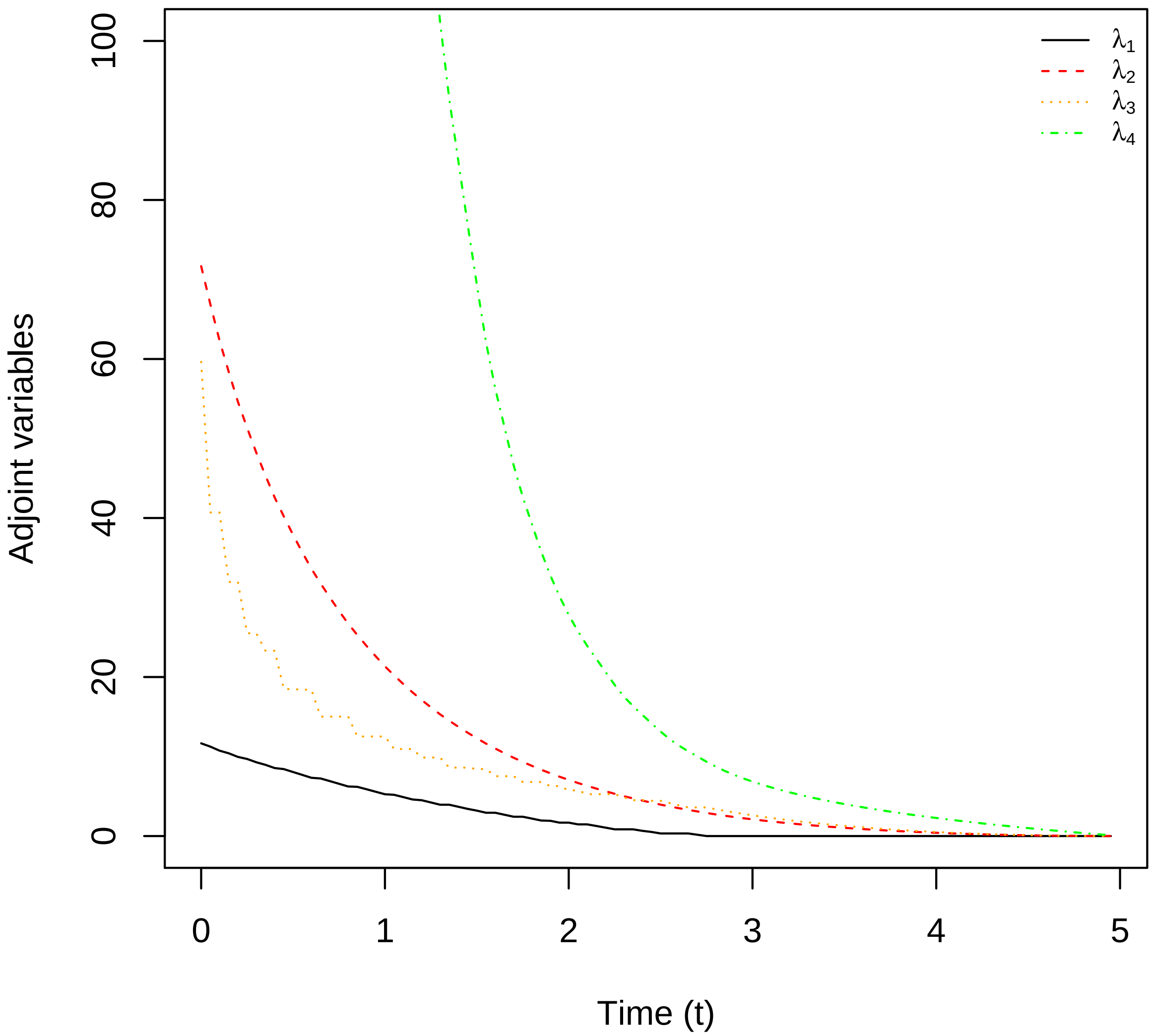
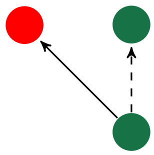
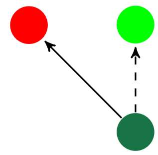


Figure 4: Trajectories of adjoint variables for the case where the initial conditions are $P(0) = 1,\ V(0) = 0.1,\ I(0) = 0,\ F(0) = 0$.

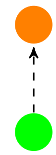
Unbranched, determinate case (budget constraint)



(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 5: Meristem transitions in an unbranched plant with a determinate inflorescence.

Term	**Description**
P	Primary meristems
V	Vegetative biomass
I	Inflorescence meristems
F	Floral meristems
$\beta_1(t)$	The per-capita rate of division by primary meristems.
$\beta_2(t)$	The per-capita rate of division by inflorescence 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).

The optimal control problem we are interested in is

$$\max_u \int_0^T \log(F(t))dt$$

subject to $\dot{P} = -[\beta_1(t)][(1-u(t))P]$,

$$\dot{V} = [\beta_1(t)][u(t)P] + [\beta_1(t)][(1-u(t))P] = \beta_1[P],$$

$$\dot{I} = [\beta_1(t)][(1-u(t))P] - [\beta_2(t)]I,$$

$$\dot{F} = [\beta_2(t)]I,$$

$$P(0) > 0;\ V(0),\ I(0),\ F(0) \geq 0,$$

$$0 \leq \beta_1(t), \beta_2(t) \leq M \qquad \text{Meristem constraint}$$

$$0 \leq \beta_1(t)P + \beta_2(t)I \leq V \qquad \text{Resource constraint}$$

$$0 \leq u(t) \leq 1. \tag{7}$$

The Hamiltonian is

$$H = \log F + \lambda_1[-\beta_1(1-u)P] + \lambda_2[\beta_1 P] + \lambda_3[\beta_1(1-u)P - \beta_2 I] + \lambda_4[\beta_2 I] \tag{8}$$

The optimality conditions are

$$\frac{\partial H}{\partial u} = (\lambda_1 - \lambda_3)\beta_1 P = 0 \text{ at } \beta_1^*, \beta_2^* \tag{9}$$

$$\frac{\partial H}{\partial \beta_1} = (\lambda_3(1-u) - \lambda_1(1-u) + \lambda_2)P = 0 \text{ at } u^*, \beta_2^* \tag{10}$$

$$\frac{\partial H}{\partial \beta_2} = (\lambda_4 - \lambda_3)I = 0 \text{ at } u^*, \beta_1^* \tag{11}$$

The transversality condition is

$$\lambda_1(T) = \lambda_2(T) = \lambda_3(T) = \lambda_4(T) = 0. \tag{12}$$

The adjoint equations are

$$\begin{aligned}
-\frac{\partial H}{\partial P} &= \dot{\lambda_1} = \beta_1(\lambda_1(1-u) - \lambda_2 - \lambda_3(1-u)) \\
-\frac{\partial H}{\partial V} &= \dot{\lambda_2} = 0 \\
-\frac{\partial H}{\partial I} &= \dot{\lambda_3} = \beta_2(\lambda_3 - \lambda_4) \\
-\frac{\partial H}{\partial L} &= \dot{\lambda_4} = -\frac{1}{F}
\end{aligned} \tag{13}$$

Unbranched, determinate case without resource constraint

To start, if we ignore the resource constraint the problem becomes one of solving

$$\max_u \int_0^T \log(F(t))dt$$

subject to $\dot{P} = -[\beta_1(t)][(1-u(t))P]$,

$$\dot{V} = [\beta_1(t)][u(t)P] + [\beta_1(t)][(1-u(t))P] = \beta_1[P],$$

$$\dot{I} = [\beta_1(t)][(1-u(t))P] - [\beta_2(t)]I,$$

$$\dot{F} = [\beta_2(t)]I,$$

$$P(0) > 0;\ V(0),\ I(0),\ F(0) \geq 0, \qquad \text{System of ODEs, initial conditions}$$

$$0 \leq \beta_1(t), \beta_2(t) \leq M \qquad \text{Meristem constraint}$$

$$0 \leq u(t) \leq 1 \qquad \text{Control constraint.}$$

We can write the Hamiltonian as

$$H = \log F + \lambda_1[-\beta_1(1-u)P] + \lambda_2[\beta_1 P] + \lambda_3[\beta_1(1-u)P - \beta_2 I] + \lambda_4[\beta_2 I] \tag{14}$$

The derivative of the Hamiltonian with respect to the control gives us our switching functions

$$\frac{\partial H}{\partial u} = (\lambda_1 - \lambda_3)\beta_1 P = \Phi_1(t) \text{ at } \beta_1^*, \beta_2^* \tag{15}$$

$$\frac{\partial H}{\partial \beta_1} = (\lambda_3(1-u) - \lambda_1(1-u) + \lambda_2)P = \Phi_2(t) \text{ at } u^*, \beta_2^* \tag{16}$$

$$\frac{\partial H}{\partial \beta_2} = (\lambda_4 - \lambda_3)I = \Phi_3(t) \text{ at } u^*, \beta_1^* \tag{17}$$

The adjoint equations are

$$\begin{aligned}
-\frac{\partial H}{\partial P} &= \dot{\lambda_1} = \beta_1(\lambda_1(1-u) - \lambda_2 - \lambda_3(1-u)) \\
-\frac{\partial H}{\partial V} &= \dot{\lambda_2} = 0 \\
-\frac{\partial H}{\partial I} &= \dot{\lambda_3} = \beta_2(\lambda_3 - \lambda_4) \\
-\frac{\partial H}{\partial F} &= \dot{\lambda_4} = -\frac{1}{F}
\end{aligned} \tag{18}$$

The transversality condition is

$$\lambda_1(T) = \lambda_2(T) = \lambda_3(T) = \lambda_4(T) = 0. \tag{19}$$

Without a resource constraint, 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. 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.

16 Unbranched, determinate case with resource constraint

Including a resource constraint makes this a problem of the kind discussed by Kamien and Schwartz in the Chapter on ‘State Variable Inequality Constraints’ (p 231). They solve these problems with the following approach.

$$\max \int_{t_0}^{t_1} f(t,x,u)dt + \phi(x(t_1))$$

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

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

To solve the problem, associate a multiplier λ with the system of ODEs and a multiplier η with the state variable constraint. The Hamiltonian is then

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

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

$$\begin{aligned}
&\frac{\partial H}{\partial u} = \frac{\partial f}{\partial u} + \lambda \frac{\partial g}{\partial u} = 0 && \text{Optimality conditions}\\
&\frac{\partial H}{\partial x} = -\dot{\lambda} = \frac{\partial f}{\partial x} + \lambda \frac{\partial g}{\partial x} + \eta \frac{\partial k}{\partial x} && \text{Adjoint equations}\\
&\lambda(t_1) = \frac{\partial \phi}{\partial x}(x(t_1)) && \text{Transversality condition/payoff}\\
&\eta \geq 0, \eta k(t,x) = 0 && \text{complementary slackness conditions}
\end{aligned} \tag{20}$$

We now rewrite our maximization problem, this time including a resource constraint

$$\max_u \int_0^T \log(F(t))dt$$

subject to $\dot{P} = -[\beta_1(t)][(1-u(t))P]$,

$$\dot{V} = [\beta_1(t)][u(t)P] + [\beta_1(t)][(1-u(t))P] = \beta_1[P],$$

$$\dot{I} = [\beta_1(t)][(1-u(t))P] - [\beta_2(t)]I,$$

$$\dot{F} = [\beta_2(t)]I,$$

$$P(0) > 0;\ V(0),\ I(0),\ F(0) \geq 0, \qquad \text{System of ODEs, initial conditions}$$

$$0 \leq \beta_1(t), \beta_2(t) \leq M \qquad \text{Meristem constraint}$$

$$0 \leq \beta_1(t)P + \beta_2(t)I \leq V \qquad \text{Resource constraint}$$

$$0 \leq u(t) \leq 1 \qquad \text{Control constraint.}$$

The Hamiltonian is then

$$H = \log F + \lambda_1[-\beta_1(1-u)P] + \lambda_2[\beta_1 P] + \lambda_3[\beta_1(1-u)P - \beta_2 I] + \lambda_4[\beta_2 I] + \eta[V - (\beta_1 P + \beta_2 I)] \tag{21}$$

The optimality conditions are

$$\frac{\partial H}{\partial u} = (\lambda_1 - \lambda_3)\beta_1 P = 0 \text{ at } \beta_1^*, \beta_2^* \tag{22}$$

$$\frac{\partial H}{\partial \beta_1} = (\lambda_3(1-u) - \lambda_1(1-u) + \lambda_2 - \eta)P = 0 \text{ at } u^*, \beta_2^* \tag{23}$$

$$\frac{\partial H}{\partial \beta_2} = (\lambda_4 - \lambda_3 - \eta)I = 0 \text{ at } u^*, \beta_1^* \tag{24}$$

The transversality condition is

$$\lambda_1(T) = \lambda_2(T) = \lambda_3(T) = \lambda_4(T) = 0. \tag{25}$$

The adjoint equations are

$$
\begin{aligned}
-\frac{\partial H}{\partial P} &= \dot{\lambda_1} = \beta_1(\lambda_1(1-u) - \lambda_2 - \lambda_3(1-u) + \eta\beta_1) \\
-\frac{\partial H}{\partial V} &= \dot{\lambda_2} = -\eta \\
-\frac{\partial H}{\partial I} &= \dot{\lambda_3} = \beta_2(\eta + \lambda_3 - \lambda_4) \\
-\frac{\partial H}{\partial F} &= \dot{\lambda_4} = -\frac{1}{F}
\end{aligned} \tag{26}
$$

And

$$
\eta \geq 0,\ \ \eta[V - (\beta_1 P + \beta_2 I)] = 0 \tag{27}
$$

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

$$
\phi = \frac{(P(\lambda_3 - \lambda_1)(1-u) + \lambda_2) - (I(\lambda_4 - \lambda_3)}{P - I} \tag{28}
$$