New Phytologist Supporting Information:
Constrained growth flips the direction of optimal phenological responses among annual plants

Magnus Lindh, Jacob Johansson, Kjell Bolmgren,
Niklas L.P. Lundström, Åke Brännström, Niclas Jonzén

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Methods S1: Mortality and bang-bang theorem

We first show the influence of mortality on our model predictions as a robustness check, and second we show that the optimal control is of bang-bang type, with one unique switch, for annuals with constrained growth, fixed season length, and constant mortality.

How mortality affects our results

As a robustness check we extend the model with constant background mortality rate m. We assume that the vegetative part grows according to

$$\frac{dV}{dt} = u(t)F(V) \text{ with } V(0) = V_0, \tag{S1.1}$$

and that the reproductive part grows according to

$$\frac{dR}{dt} = (1 - u(t)F(V))s(t), \tag{S1.2}$$

where

$$s(t) = e^{-mt} \tag{S1.3}$$

is the survival function and m is the mortality rate. The reproductive mass depends on the survival, but the vegetative mass does not since we would otherwise account for the survival twice. According to Cohen (1976) the optimal control is a bang-bang control of reproduction. Below we provide an alternative proof of this fact, based on optimal control theory, showing also that there

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will be one unique switch called the optimal flowering time t_F^* (Theorem 1). Therefore, the reproductive output is

$$W(t_F^*) = \int_{t_F^*}^{T} F(V)s(t)dt = \frac{F(V(t_F^*))}{m}\left(e^{-mt_F^*} - e^{-mT}\right),$$

where T the end of the season.

In Fig. S1 we show the optimal flowering time as a function of productivity for a few different mortality rates. We find in Fig. S1a that there is no internal maximum for the optimal flowering time, and in Fig. S1b,c that there is always an internal maximum for intermediate productivity, regardless of the mortality. This indicates that (low) mortality rates does not qualitatively change our results. Moreover, increasing the mortality always advances the optimal flowering time (higher mortality implies that it is better to reproduce earlier since then the risk of dying before reproduction decreases) and the effect of mortality decreases as productivity increases.
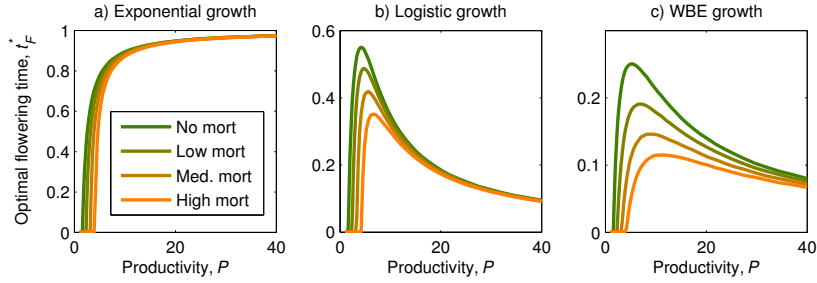

Figure S 1: Mortality decreases the survival, and affects the optimal flowering times as a function of productivity. Mortality is $m = 0, 1, 2, 3$, corresponding to no, low, intermediate and high mortality rate. The season length is $E = 1$ and the default mass values are $V_{max} = 1$ and $V_0 = 0.02$.

In the case of exponential growth, when mortality is included in the form of a survival function (Figure S1.a), we show how to find the optimal flowering time t_F^* analytically. In particular, in this case $F(V) = PV$ and hence, using the bang-bang control in Theorem 1, the solution of (S1.1) becomes

$$V(t) = V_0 e^{Pt}$$

for $0 \le t \le t_F$, where t_F is the flowering time. To find t_F^* we maximize the reproductive output

$$W(t_F) = \frac{PV_0}{m}e^{Pt_F}\left(e^{-mt_F} - e^{-mT}\right)$$

with respect to t_F. Differentiating w.r.t. t_F and setting the derivative to zero yield

$$\frac{dW(t_F)}{dt_F} = \frac{PV_0}{m}e^{Pt_F}\left((P-m)e^{-mt_F} - Pe^{-mT}\right) = 0.$$

This implies that the optimal flowering time for exponential growth with mortality m is

$$t_F^* = T - \frac{1}{m}\log\left(\frac{P}{P-m}\right).$$

This is a maximum when the second derivative w.r.t. t_F of the reproductive output is negative, that is

$$\frac{d^2W(t_F)}{dt_F^2} = \frac{PV_0}{m}\left(e^{-mt_F}(P-m)^2 - P^2e^{-mT}\right)e^{-Pt_F} < 0,$$

which holds true for $t_F = t_F^*$.

This proves that, in the case of exponential growth, increasing the mortality always advances the optimal flowering time t_F^*, and the effect of mortality decreases as productivity increases.

Proof of optimal flowering bang-bang control with constrained growth and constant mortality

The dynamic model for vegetative mass $V = V(t)$ is given by

$$\frac{dV}{dt}(t) = u(t)F(V(t)), \quad 0 < t < T, \quad V(0) = V_0 > 0 \qquad \text{(S1.4)}$$

where T is the end of the season, $F(V)$ is the growth function and $u(t) \in A$ is the control, in which

$$A = \{u(t) : [0,T] \to [0,1] \text{ and } u(t) \text{ is measurable}\}$$

denotes the set of admissible controls. We will prove results on properties on controls $u(t)$ maximizing the reproductive output

$$W = \int_0^T (1-u(t))s(t)F(V(t))dt. \qquad \text{(S1.5)}$$

In particular, we prove the following theorem.

Theorem 1. *Suppose that the growth function $F(V)$ is positive, that $\frac{dF}{dV}(V)$ is a non-increasing function of V, and that the survival function is given by $s(t) = e^{-mt}$, where $m \geq 0$ is a constant mortality. Let $f(m,T) = \frac{m}{1-e^{-mT}}$ with $f(0,T) = \frac{1}{T}$. Assume that $u^*(t)$ is an optimal control maximizing the reproductive output in (S1.5). If $\frac{dF}{dV}(V_0) > f(m,T)$, then there exists an optimal flowering time $t_F^* \in (0,T)$ and $u^*(t)$ is given by the bang-bang control*

$$u^*(t) = \begin{cases} 1 & if \quad 0 \leq t \leq t_F^* \\ 0 & if \quad t_F^* < t \leq T. \end{cases}$$

If $\frac{dF}{dV}(V_0) \leq f(m,T)$, then the optimal control is $u^*(t) = 0$ for all $t \in [0,T]$, that is, the optimal strategy is to flower immediately.

Proof. We intend to apply the Pontryagin maximum principle. Since the survival function $s(t)$ depends on time we first extend the dynamic model for vegetative mass (S1.4) by regarding time t as an additional variable $\hat{t}(t) = t$ satisfying the differential equation $\frac{d\hat{t}}{dt}(t) = 1$ for $0 \leq t \leq T$. Next, we define, for any $x_1, x_2, p_1, p_2 \in \mathbb{R}, a \in [0,1]$, the Hamiltonian

$$H(x_1, x_2, p_1, p_2, a) = \begin{pmatrix} aF(x_1) \\ 1 \end{pmatrix} \cdot \begin{pmatrix} p_1 \\ p_2 \end{pmatrix} + (1-a)s(x_2)F(x_1)$$
$$= F(x_1)s(x_2) + p_2 + aF(x_1)(p_1 - s(x_2)).$$

Assume that $u^*(t)$ is the optimal control for (S1.4), (S1.5) and let $V^*(t)$ be the corresponding trajectory for vegetative mass. Then the Pontryagin maximum principle, see e.g. Theorem 4.3 in Evans (1983), implies the existence of costates $p_1^*(t), p_2^*(t) : [0,T] \to \mathbb{R}$, satisfying the adjoint equations with $x_1 = V$ and $x_2 = t$

$$\frac{dp_1^*}{dt}(t) = -\frac{dH}{dV} = -\frac{dF}{dV}(V^*(t))s(t) - u^*(t)\frac{dF}{dV}(V^*(t))(p_1^*(t) - s(t)), \quad \text{(S1.6)}$$
$$\frac{dp_2^*}{dt}(t) = -\frac{dH}{dt} = m(1 - u^*(t))s(t)F(V^*(t))$$

with terminal conditions

$$p_1^*(T) = 0, \quad p_2^*(T) = 0.$$

The second adjoint equation, related to $\frac{d\hat{t}}{dt}(t) = 1$, will not be used below. Using the maximum principle we get

$$H(V^*(t), t, p_1^*(t), p_2^*(t), u^*(t))$$
$$= \max_{a \in [0,1]} \left\{ F(V^*(t))s(t) + p_2^*(t) + aF(V^*(t))(p_1^*(t) - s(t)) \right\}.$$

Since $p_1^*(T) = 0$ and $s(T) > 0$ we deduce, using continuity of solutions of (S1.6), that $p_1^*(t) < s(t)$ for $t \leq T$ close enough to T. Define t_0 as the smallest number in $[0,T]$ such that $p_1^*(t) < s(t)$ holds for all $t_0 < t \leq T$. Using $F(V) > 0$ and

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that $u^*(t)$ maximizes H we see that as long as $t_0 < t \leq T$ we have $u^*(t) = 0$. Therefore, the costate equation (S1.6) simplifies to

$$\frac{dp_1^*}{dt}(t) = -\frac{dF}{dV}(V^*(t))s(t), \quad \text{for} \quad t_0 < t \leq T. \tag{S1.7}$$

We assume in the rest of the proof that $m > 0$, however, the case $m = 0$ follows by similar calculations. Integrating (S1.7) from t_0 to T yields

$$p_1^*(t_0) = \int_{t_0}^T \frac{dF}{dV}(V^*(t))s(t)dt = \frac{dF}{dV}(V^*(t_0)) \int_{t_0}^T e^{-mt}dt \tag{S1.8}$$
$$= \frac{1}{m}\frac{dF}{dV}(V^*(t_0)) \left[e^{-mt_0} - e^{-mT}\right].$$

If $t_0 = 0$, then we must have $p_1^*(0) \leq s(0) = 1$ and so, by (S1.8),

$$\frac{dF}{dV}(V_0) \leq \frac{m}{1 - e^{-mT}}. \tag{S1.9}$$

If $t_0 > 0$, then $p_1^*(t_0) = s(t_0) = e^{-mt_0}$ and (S1.8) implies

$$\frac{dF}{dV}(V^*(t_0)) = \frac{m}{1 - e^{m(t_0 - T)}}. \tag{S1.10}$$

By assumption $\frac{dF}{dV}$ is a non-increasing function of V and $F(V)$ is positive. Therefore, from (S1.4) it follows that $V_0 \leq V^*(t_0)$ and thus $\frac{dF}{dV}(V_0) \geq \frac{dF}{dV}(V^*(t_0))$. Moreover, since $t_0 > 0$ we have $\frac{m}{1 - e^{m(t_0 - T)}} > \frac{m}{1 - e^{-mT}}$ and hence

$$\frac{dF}{dV}(V_0) > \frac{m}{1 - e^{-mT}}. \tag{S1.11}$$

We can conclude that (S1.9) holds if and only if $t_0 = 0$, and (S1.11) holds if and only if $t_0 > 0$. Setting $t_F^* = t_0$, this proves the result on when it is optimal to flower immediately.

It remains to show that the optimal control is of bang-bang type and that there exists only one switch. In particular, we will show that the optimal control is given by

$$u^*(t) = \begin{cases} 1 & \text{if} \quad 0 \leq t \leq t_0 \\ 0 & \text{if} \quad t_0 < t \leq T. \end{cases} \tag{S1.12}$$

To do so we first observe that if $t_0 = 0$ then $u^*(t) = 0$ for all $t \in (0, T]$ and, therefore, we are done.

Assume that $t_0 > 0$. If we can show that $p_1^*(t) > s(t)$ for all $t \in [0, t_0)$, then $u^*(t) = 1$ for all $t \in [0, t_0)$ and, therefore, we are done. From (S1.10) and since $0 < e^{m(t_0 - T)} < 1$, we find the inequality

$$\frac{dF}{dV}(V^*(t_0)) > m. \tag{S1.13}$$

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We also know that $\frac{dF}{dV}$ is a non-increasing function of V, and since $F(V)$ is positive it follows from (S1.4) that V is a non-decreasing function of t. Therefore, (S1.13) yields

$$\frac{dF}{dV}(V^*(t)) > m \qquad\qquad (S1.14)$$

for all $t \in [0, t_0)$. Since $u^*(t) = 0$ if $p_1^*(t) < s(t) = e^{-mt}$, and $u^*(t) = 1$ if $p_1^*(t) > s(t) = e^{-mt}$, we see that $u^*(t)(p_1^*(t)e^{mt} - 1) \geq 0$ for all $t \in [0, T]$. Hence, (S1.14) yields

$$\frac{dF}{dV}(V^*(t))\left[1 + u^*(t)(p_1^*(t)e^{mt} - 1)\right] > m$$

for all $t \in [0, t_0)$. We obtain, according to (S1.6)

$$-\frac{dp_1^*}{dt}(t) = \frac{dF}{dV}(V^*(t))\left[e^{-mt} + u^*(t)(p_1^*(t) - e^{-mt})\right] > me^{-mt} = -\frac{ds}{dt}(t)$$

which is equivalent to

$$\frac{dp_1^*}{dt}(t) < \frac{ds}{dt}(t)$$

for all $t \in [0, t_0)$. Recalling that $p_1^*(t_0) = s(t_0)$, the above inequality shows that (S1.12) is true. This proves the theorem for $t_F^* = t_0$. $\qquad\square$

Methods S2: Analysing the optimal flowering time

Here we go through the details in finding the optimal flowering time t_F^* that maximizes reproductive output W, as well as a few criteria that needs to be fulfilled. There are three steps in the derivations:

1. Find a solution $V(t)$ for the growth of the vegetative mass from the dynamics $dV/dt = u(t)F(V)$ with $V(0) = V_0$. The solution is easily found for our growth types $F(V)$.

2. Find the reproductive output. Using Theorem 1 we have the bang-bang reproduction

$$u(t) = \begin{cases} 1 & \text{if } 0 \leq t \leq t_F \\ 0 & \text{if } t_F < t \leq T. \end{cases}$$

   This means that the vegetative mass does not grow after the flowering time t_F, and the reproductive mass does not grow before time t_F. The reproductive output in this case is: $W(t_F) = F(V(t_F))\int_{t_F}^{T} dt = F(V(t_F))(T - t_F)$, where T is the end of season.

3. Finally, in order to find the optimal flowering time t_F^* we solve $dW/dt_F = 0$. We also need to ascertain that $d^2W/dt_F^{*2} < 0$ so that the optimal flowering time is a maximum, exclude the possibility of more than one local maximum, and the possibility of a maximum on the boundary.

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We are interested in three types of growth:

(a) Exponential growth: $F(V) = PV$,

(b) Logistic growth: $F(V) = PV(1 - V/V_{max})$, and

(c) West-Brown-Enquist growth: $F(V) = PV^{3/4}(1 - (V/V_{max})^{1/4})$.

(a) Exponential growth

The plant grows according to

$$\frac{dV}{dt} = u(t)F(V) = u(t)PV,$$

where the allocation to vegetative growth is $u(t)$. Assuming the bang-bang control the differential equation has the solution

$$V(t) = V_0 e^{Pt}, \tag{S2a.1}$$

for $0 \le t \le t_F$ where V_0 is the initial mass at time $t = 0$. The reproductive output, with the bang-bang control having flowering time t_F, is easy to find since $F(V(t_F))$ is constant after flowering,

$$W(t_F) = F(V(t_F)) \int_{t_F}^{T} dt = PV_0 e^{Pt_F}(T - t_F). \tag{S2a.2}$$

To find the optimal flowering time we differentiate this w.r.t. t_F and set the derivative to zero,

$$\frac{dW}{dt_F} = -PV_0 e^{Pt_F}(P(t_F - T) + 1) = 0.$$

The solution is the optimal flowering time

$$t_F^* = T - \frac{1}{P}.$$

This is a maximum when the second derivative w.r.t. t_F of the reproductive output,

$$\frac{d^2 W}{dt_F^2} = -V_0 P^2 e^{Pt_F}(P(t_F - T) + 2), \tag{S2a.3}$$

is negative, which is the case when $t_F = t_F^* = T - \frac{1}{P}$. There is no productivity that maximizes t_F since the derivative of t_F^* w.r.t P is always positive, meaning that the optimal flowering time always increases with increasing productivity,

$$\frac{dt_F^*}{dP} = \frac{d}{dP}\left(T - \frac{1}{P}\right) = \frac{1}{P^2} > 0. \tag{S2a.4}$$

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(b) Logistic growth

The plant grows according to

$$\frac{dV}{dt} = u(t)PV\left(1 - \frac{V}{V_{max}}\right).$$

Assuming the bang-bang control the differential equation has the solution

$$V(t) = \frac{V_{max}V_0 e^{Pt}}{V_{max} + V_0(e^{Pt} - 1)}, \tag{S2b.1}$$

for $0 \leq t \leq t_F$, where V_{max} is the maximum vegetative mass. The reproductive output at the flowering time t_F is

$$W(t_F) = F(V(t_F)) \int_{t_F}^{T} dt = PV(t_F)\left(1 - \frac{V(t_F)}{V_{max}}\right)(T - t_F), \tag{S2b.2}$$

and we find the optimal flowering time t_F^* when $dW/dt_F = 0$. The derivative has the same sign as

$$f(t_F) = V_{max} - V_0 - V_{max}PT + PTV_0 + P(V_{max} - V_0)t_F + V_0(1 + PT)e^{Pt_F}$$
$$- PV_0 t_F e^{Pt_F} = 0,$$

assuming that $V_{max} > V_0$. This equation has a unique solution for t_F, which we will only find numerically. The solution is unique because

$$\frac{df(t_F)}{dt_F} = P(V_{max} - V_0) + (T - t_F)P^2 V_0 e^{Pt_F} > 0, \tag{S2b.3}$$

since $V_{max} > V_0$ and $T > t_F$. Therefore $f(t_F)$ is a monotonically increasing function and there can be only one or zero solutions to $f(t_F) = 0$. Assuming that V_0 is small, there exists a unique solution, which is the optimal flowering time t_F^*, since $W(t_F)$ grows initially at $t_F = 0$, and decreases at $t_F = T$.

Now we show that increasing the productivity can either delay or advance the optimal flowering time. By implicit derivation of $f(t_F)$ we find that the sign of dt_F^*/dP is the same as the sign of

$$S = (T - t_F)(V_{max} - V_0) - (T + Pt_F(T - t_F))V_0 e^{Pt_F}. \tag{S2b.4}$$

The first term is positive since $T > t_F$ and $V_{max} > V_0$. For low values of P we get $dt_F^*/dP > 0$ (delayed optimal flowering) since the second negative term is small, but for large values of P we get $dt_F/dP < 0$ (advanced optimal flowering) since the second negative term is dominating.

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(c) West-Brown-Enquist growth

The plant grows according to (West et al., 2001)

$$\frac{dV}{dt} = u(t)PV^{3/4}\left(1 - (V/V_{max})^{1/4}\right).$$

Assuming the bang-bang control the differential equation has the solution

$$V(t) = V_{max}\left(1 - \left[1 - \left(\frac{V_0}{V_{max}}\right)^{1/4}\right]\exp\left(\frac{-Pt}{4V_{max}^{1/4}}\right)\right)^4,$$

for $0 \le t \le t_F$. The reproductive output is

$$W(t_F) = PV(t_F)^{3/4}\left(1 - \left(\frac{V(t_F)}{V_{max}}\right)^{1/4}\right)(T - t_F), \qquad \text{(S2c.2)}$$

and we find the optimal flowering time when $dW/dt_F = 0$. The derivative has the same sign as

$$f(t_F) = a + 4ab(T - t_F) - (1 + bT)e^{bt_F} + bt_F e^{bt_F} = 0,$$

where

$$a = \left[1 - \left(\frac{V_0}{V_{max}}\right)^{1/4}\right] \quad \text{and} \quad b = \frac{P}{4V_{max}^{1/4}}.$$

This equation has a unique solution for the optimal flowering time t_F^*, which we will only find numerically. The solution is unique because

$$\frac{df(t_F)}{dt_F} = -4ab - (T - t_F)b^2 e^{bt_F} < 0, \qquad \text{(S2c.3)}$$

since $V_{max} > V_0$ and $T > t_F$. Therefore $f(t_F)$ is a monotonically decreasing function and there can be only one or zero solutions to $f(t_F) = 0$. Assuming that V_0 is small, there exists a unique solution, which is the optimal flowering time t_F^*, since $W(t_F)$ grows initially at $t_F = 0$, and decreases at $t_F = T$.

Now we show that increasing the productivity can either delay or advance the optimal flowering time. By implicit derivation of $f(t_F)$ we find that the sign of dt_F^*/dP is the same as the sign of

$$S = 4a\frac{db}{dP}(T - t_F) - (T + bt_F(T - t_F))\frac{db}{dP}e^{bt_F}.$$

The first term is positive since $T > t_F$, $db/dP > 0$ and $a > 0$. For low values of b we get $dt_F/dP > 0$ (delayed optimal flowering) since the second negative term is small, but for large values of b we get $dt_F/dP < 0$ (advanced optimal flowering) since the second negative term is dominating.

References

[1] Cohen D. 1976. The optimal timing of reproduction. American Naturalist 110: 801-807.

[2] Evans LC. 1983. An introduction to mathematical optimal control theory version 0.2. Lecture notes available at `https://math.berkeley.edu/~evans/control.course.pdf`. [accessed 12 November 2014]

[3] West GB, Brown JH, Enquist BJ. 2001. A general model for ontogenetic growth. Nature 413: 628631.