Constrained growth flips the direction of optimal phenological responses among annual plants

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Summary

- Phenological changes among plants due to climate change are well documented, but often hard to interpret. In order to assess the adaptive value of observed changes, we study how annual plants with and without growth constraints should optimize their flowering time when productivity and season length changes. We consider growth constraints that depend on the plant's vegetative mass: self-shading, costs for nonphotosynthetic structural tissue and sibling competition.
- We derive the optimal flowering time from a dynamic energy allocation model using optimal control theory. We prove that an immediate switch (bang-bang control) from vegetative to reproductive growth is optimal with constrained growth and constant mortality.
- Increasing mean productivity, while keeping season length constant and growth unconstrained, delayed the optimal flowering time. When growth was constrained and productivity was relatively high, the optimal flowering time advanced instead. When the growth season was extended equally at both ends, the optimal flowering time was advanced under constrained growth and delayed under unconstrained growth.
- Our results suggests that growth constraints are key factors to consider when interpreting phenological flowering responses. It can help to explain phenological patterns along productivity gradients, and links empirical observations made on calendar scales with life-history theory.

Introduction

Changes in the phenology of plants are well-documented effects of increased temperatures (see Menzel *et al.*, 2006; Parmesan, 2007; Wolkovich *et al.*, 2012; for reviews and meta-analyses). Although there is a general pattern of advancing spring phenologies (Fitter & Fitter, 2002; Menzel *et al.*, 2006; Parmesan, 2007; Primack *et al.*, 2009), there is also great variation in rates of phenological changes, both among species and different phenological traits (CaraDonna *et al.*, 2014). It is often unclear how to interpret this variation. Is the long-term persistence of species that show little phenological change at risk (Willis *et al.*, 2008)? What constitutes a sufficient change to avoid negative fitness consequences (Munguía-Rosas *et al.*, 2011; Iler *et al.*, 2013; Santos-del-Blanco *et al.*, 2013)?

Some guidance for the aforementioned questions is provided by dynamic energy allocation models based on optimal control theory (reviewed by Iwasa, 2000). Here energy refers to the biomass production rate. These models enable analyses of how trade-offs between reproduction, growth and survival shape the evolution of life histories. For annual plants there is a tight link between phenology and life history, and some early models of optimal allocation considered the onset of reproduction in annual plants (Cohen, 1971, 1976). Recently, Johansson *et al.* (2013) applied a model of this kind to predict how the optimal flowering time should respond to changes in seasonal growth conditions. An interesting finding of that study is that the seasonal distribution of productivity (e.g. temperature and precipitation) can affect the size and even the direction of the optimal response of the flowering time to certain types of environmental change, such as increased productivity or increased season length. As with many other studies (King & Roughgarden, 1982; Shitaka & Hirose, 1993), Johansson *et al.* (2013) assumed that plant growth rate is proportional to the vegetative mass during the growth season. Although this may be reasonably representative for the growth rate of some annual plants, growth is often

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†Dedicated to the memory of Niclas Jonzén, May 1973 to May 2015.

constrained, leading to a saturating growth curve. Paine *et al.* (2012) suggest saturating nonlinear plant growth (i.e. constrained growth) as the general growth type for all plants, due to self-shading, increased costs of structural tissue and decreasing local nutrient levels. Biomass data from the annual forb *Cerastium diffusam* are provided as an example of constrained growth. Exceptions, where growth is not constrained, include algae growing in a chemostat where light and nutrients are abundant.

A small seedling with only a few leaves could place these leaves almost anywhere and still not be affected by self-shading limitations to growth. However, as it grows an increasing ratio of the total biomass needs to be allocated to nonphotosynthetic structural tissue in order to avoid self-shading, increase seed dispersal and to display flowers to pollinators (Fig. 1). The increasing demand of investment into structural, nonphotosynthetic tissue contributes to saturating growth patterns. Another reason for constrained growth is competition from other plants of the same species; that is, sibling competition (Yoda *et al.*, 1963; White & Harper, 1970). Growth is also closely related to metabolism, which in turn is often described by (nonlinear) power laws. West *et al.* (1999) argued that metabolic rate scales as a ¾ power of mass, but deviations from that empirically based rule can also be expected (see Brown *et al.*, 2004, and Price *et al.*, 2012, for reviews). A general ontogenetic growth model proposed by West *et al.* (2001) based on the ¾ metabolic scaling captures animals (Moses *et al.*, 2008), but has been criticized for not capturing crop growth (Shi *et al.*, 2013). As an example, the total leaf area, which roughly corresponds to leaf mass, for the annual prostrate desert plant *Chamaesyce setiloba* follows an estimated 0.9 power law (Koontz *et al.*, 2009). In other words the leaf mass is proportional to total aboveground biomass to the power of 0.9. This plant is nearly two-dimensional as it grows on the ground and does not need to allocate many resources into structural tissue to avoid self-shading, because competition for light is low.

We focus on the flowering time of annual plants and consider environmental change in the form of increased productivity, in turn representing the increased temperatures, increased CO$_2$ concentrations or longer growth seasons representative of climate change resulting from global warming (Menzel & Fabian, 1999; CaraDonna *et al.*, 2014; Reyes-Fox *et al.*, 2014). We extend previous theory (Johansson *et al.*, 2013) both by considering nonlinear growth functions and by considering changes in season length. Although motivated by understanding phenological responses to climate change, this study is relevant to any type of environmental change that influences productivity, for example fertilization or improved light conditions such as in tree fall gaps.

Description

Here we will investigate how growth constraints affect optimal flowering time responses to changed environmental conditions. The optimal flowering time is here conceived as a fitness-maximizing strategy and it can thus be expected to evolve under natural selection in a given environment (Pianka, 1976; Roff, 1992; Stearns, 1992). Evolution can be fast. For example, the flowering time for the annual plant *Brassica rapa* evolved within a few generations to escape drought stress (Franks *et al.*, 2007). Although there are many potential reasons, including genetic constraints, why organisms may not attain the optimal strategy by evolution, we consider the optimal strategy a useful reference point against which observed phenological responses can be compared and evaluated, regardless of whether these responses have a genetic,

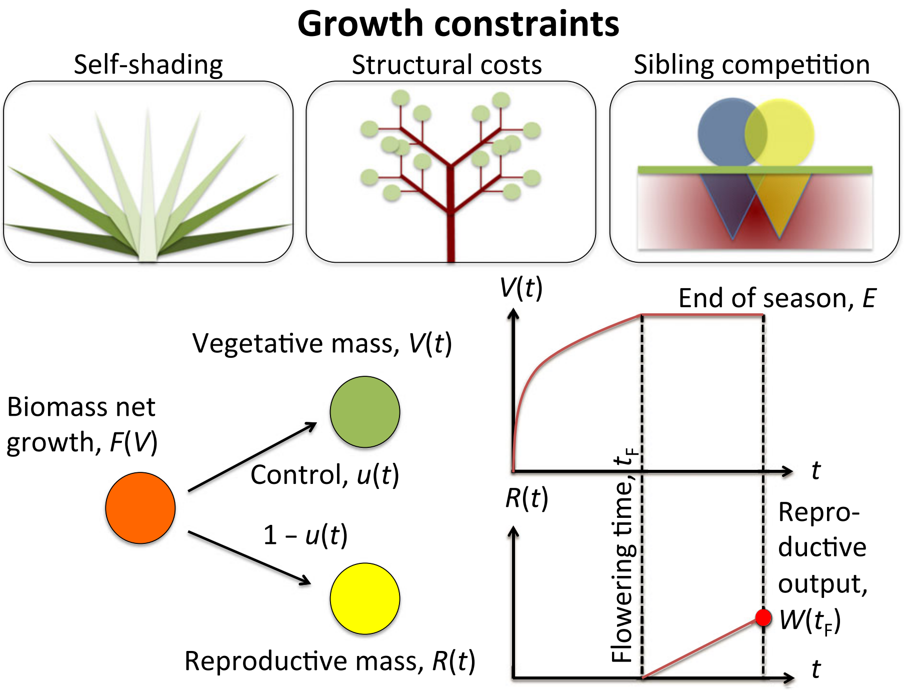

Fig. 1 Growth constraints increasing with size and mass can take many forms, for example: self-shading by leaves and branches, increasing costs for branches necessary for transportation and structural stability, and sibling competition for common resources. Growth of vegetative mass $V(t)$ and reproductive mass $R(t)$ is controlled by $u(t)$. The net biomass growth $F(V)$ depends only on the vegetative mass. With bang-bang reproduction, vegetative growth ceases at the flowering time t_F, and reproductive mass is starting to grow as $F(V(t_F))$, until the end of the season E. The reproductive output $W(t_F)$ is the reproductive mass at the end of the season E, and this is used as a measure of the plant fitness.

behavioural or other basis. In order to elucidate the effect of growth constraints on the optimal flowering time we compare three types of growth: (1) exponential, (2) logistic and (3) West–Brown–Enquist (WBE). The exponential (or linear) growth model describes growth without constraints and has previously been used in optimal control models (see, for example, King & Roughgarden, 1982). The logistic model is a standard model of constrained growth in mathematical biology, and has successfully been applied to crops (Shi *et al.*, 2013). The WBE model (2001) is a more recent constrained growth model that has been validated with data on various organisms. Examples of growth constraints are self-shading by leaves and branches, costs for branches and sibling competition (Fig. 1). These three models are described further later.

We start from an ontogenetic growth function put forward by Moses *et al.* (2008)

$$F(V) = AV^a - BV^b \qquad \text{Eqn 1}$$

(V, dry mass of the vegetative part of the plant; $F(V)$, rate at which new biomass is produced; AV^a, first term corresponding to assimilation of metabolic energy; BV^b, second term corresponding to maintenance costs such as respiration). Here $F(V)/V$ corresponds to $\mathrm{d}V/\mathrm{d}t \times 1/V$; in other words the relative growth rate (RGR). Productivity, as defined later, is equivalent to RGR for exponential growth. Notation is according to Johansson *et al.* (2013) to facilitate comparisons. There is no general answer to how assimilation and respiration respond to increased productivity, which could be correlated to, for example, increased temperature and CO_2 levels. We assume that $A = P$, where P is the productivity of the environment where the plant is growing. This is a flexible formulation that can be used to represent the three different growth models described earlier: (1) by setting $a = 1$ and $B = 0$ we obtain an exponential growth model (Shitaka & Hirose, 1993); (2) a logistic growth model (Deng *et al.*, 2012) is obtained by setting $a = 1$, $B = P/V_{\max}$ and $b = 2$; and (3) the WBE growth model by West *et al.* (2001) is obtained by setting $a = 3/4$, $B = PV_{\max}^{-1/4}$ and $b = 1$.

Here $V_{\max}$ is the asymptotic, or maximal mass, which we assume not be influenced by the productivity parameter P. In the ontogenetic growth model by West *et al.* (2001) the parameter P is closely related to fundamental cellular properties, and according to Gillooly *et al.* (2002) $P(T_K) \propto \exp(-e/(kT_K))$ (e, average energy for cellular metabolism; k, Boltzmann's constant; T_K, absolute temperature in Kelvins). We assume that the productivity is constant during the growth season, but discuss how variable productivity can be handled in an alternative model formulation based on physiological time described later. The season starts at $t = S$ and ends at $t = E$, which means that the season length is $T = E - S$.

We embed the growth function into a dynamic energy allocation model (reviewed by Iwasa, 2000). Produced biomass is partitioned between the dry mass of the vegetative part of the plant (V) and the dry mass of the reproductive part (R) according to a time-dependent control function $u(t)$. We assume that the vegetative part grows according to:

$$\frac{\mathrm{d}V}{\mathrm{d}t} = u(t)F(V) \text{ with } V(t_0) = V_0 \qquad \text{Eqn 2}$$

and the reproductive part grows according to:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = (1 - u(t))F(V) \qquad \text{Eqn 3}$$

We prove using optimal control theory that the functional form which maximizes reproductive output for both constrained and unconstrained growth will be of bang-bang type; that is, a sudden switch from none to maximal reproductive investment (Supporting Information Methods S1, Theorem 1; Cohen, 1971, 1976). The time point for the switch from vegetative growth to reproduction is denoted flowering time, t_F (cf Johansson *et al.*, 2013). We thus think of flowering as the initial stage of the reproductive phase and that other important and energy-demanding stages such as production and growth of seeds occur later. In principle the model is silent on the exact timing and nature of specific reproductive stages. Schaffer (1977) refers to the switch as date of first flowering, also reflecting that flowering is an early stage but leaving open how extended it is, and more generally t_F may be thought of as timing of maturation. The timing of first flowering might be a poor predictor of the timing of peak flowering, but peak flowering is more challenging to measure in the field (CaraDonna *et al.*, 2014). Mathematically, this means that $u(t) = 1$ for $t < t_F$ and $u(t) = 0$ for $t > t_F$. Because we have this single switch it is easy to find analytic expressions for the vegetative growth in all three growth models (Eqns S2a.1, S2b.1, S2c.1 in Methods S2).

We equate the fitness of a strategy with its average lifetime reproductive output (Metz *et al.*, 1992). The optimal flowering time t_F^* maximizes the reproductive output W, which has the form:

$$W(t_F) = \int_{t_F}^{E} F(V)\mathrm{d}t = F(V(t_F))(E - t_F) \qquad \text{Eqn 4}$$

because $F(V(t))$ is assumed to be constant after the flowering time (Fig. 1), implying $F(V(t)) = F(V(t_F))$ for all $t \geq t_F$. This equation reflects the fact that all biomass growth after the onset of flowering is allocated to reproductive structures. There is a life-history trade-off between growth and reproduction. If reproduction (i.e. flowering) starts too early then the plant will not have gained enough mass (or energy), but if reproduction is delayed too long then the remaining season will be too short (Kozłowski, 1992). In the Supporting Information we describe how the optimal flowering time is determined by differentiating the reproductive output (Eqns S2a.2, S2b.2, S2c.2 in Methods S2).

Alternative model formulation based on physiological time

Our model is originally formulated in calendar time, but here we formulate it in physiological time. Many empirical models set out to predict the seasonal timing of biological events based on temperature sums or other measures of physiological time

(Bonhomme, 2000; Wilczek *et al.*, 2009). All three types of growth presented earlier can be written in the form:

$$F(V) = \frac{dV}{dt} = P(T_K)U(V) \qquad \text{Eqn 5}$$

where $P(T_K)$ is a productivity function depending on temperature in Kelvin, and $U(V)$ is unitless. For exponential growth $U(V) = V$, for logistic growth $U(V) = V(1 - V/V_{max})$ and for WBE growth $U(V) = V^{3/4}(1-(V/V_{max})^{1/4})$. The rate at which physiological time passes relative to calendar time is defined as:

$$\frac{d\tau}{dt} = c^{-1}P(T_K) \qquad \text{Eqn 6}$$

where c is a process-dependent proportionality constant (van Straalen, 1983). Alternatively, the aforementioned equation can be written in the form:

$$\tau(t) = c^{-1}\int_S^t P(T_K(t'))dt' \qquad \text{Eqn 7}$$

which shows that physiological time (τ-time) depends on the productivity, that is, τ-time is proportional to the cumulative productivity. Here, S is the start of the growth season in calendar time, that is, the first time of the year when $P(T_K(t)) > 0$, which, in turn, defines the point at which the physiological time equals zero. If P is a linearly increasing function of temperature (above a certain baseline), where P is essentially zero at temperature zero, then $\tau(t)$ is well-approximated by the number of degree-days or the temperature sum at day t (van Straalen, 1983). The season length in physiological time is $\tau(E)$, corresponding to the total productivity integral over the season. Applying the chain rule, the growth rate in physiological τ-time becomes:

$$F_\tau(V) = \frac{dV}{d\tau} = \frac{dV}{dt}\bigg/\frac{d\tau}{dt} = \frac{P(T_K)U(V)}{c^{-1}P(T_K)} = cU(V) \qquad \text{Eqn 8}$$

The derivation given earlier is valid independent of the relationship assumed between temperature and productivity, and independent of how temperature varies during the growth season. The dependencies will, however, affect the season length in physiological time, $\tau(E)$, and consequently also the optimal flowering strategy. The potential benefits of using physiological time will be considered in the Discussion section.

Results

We first study the effect of growth constraints and productivity on the optimal flowering time (Fig. 2) and second we study the effect of changing season length jointly with the growth constraints and productivity (Fig. 3).

Scenario 1: optimal flowering time and productivity

Here we assume a fixed season length T starting at time $S = 0$, and ending at time $E = T$. In order to understand how growth constraints influence optimal flowering times we first compare the three different growth models and their influence on relative growth rates (Fig. 2a–c), and vegetative mass trajectories (Fig. 2d–f). Exponential growth corresponds to constant RGR (Fig. 2a,d). Under logistic growth RGR decrease linearly with mass (Fig. 2b) and under WBE growth RGR is a decreasing nonlinear function of mass with its sharpest decrease at low masses (Fig. 2c). In the latter two cases, the vegetative mass trajectory is saturating (Fig. 2e,f).

Optimal flowering time is an increasing function of productivity under exponential growth (Fig. 2g), but has an intermediate maximum under logistic or WBE growth (Fig. 2h,i), and can thus either increase or decrease when productivity increases (Eqns S2a.3, S2b.3, S2c.3 in Methods S2). We show that there is an unique intermediate maximum by investigating the sign of the derivative of dt_F/dP (Eqns S2a.4, S2b.4, S2c.4 in Methods S2). Optimal flowering time is delayed in plants with exponential growth when productivity increases because, by postponing reproduction, they can grow large towards the end of the season (circles in Fig. 2d) and are thereby able to produce more resources for reproduction. Plants with constrained growth, by contrast, cannot gain much in final size by postponing reproduction in productive environments. By flowering earlier (circles in Fig. 2e,f), they can use the increased productivity to invest in reproduction under a longer period of time. Advanced reproduction at increasing productivity is thus found both for WBE and for logistic growth (Fig. 2h,i).

The differences in relative growth rate when productivity is varied for logistic and WBE growth (Fig. 2b,c) also suggest an explanation for why the corresponding optimal flowering time curves have a maximum (Fig. 2h,i). At low productivity the relative growth rate has only a weak negative slope (brown curves in Fig. 2b,c), and the plants can thus be expected to postpone flowering when productivity increases in a similar fashion to plants with exponential growth and a constant relative growth rate. At higher productivity the relative growth rates have steeper, negative slopes (green curves in Fig. 2b,c) and therefore it instead pays off to reproduce early and utilize a longer period with reproductive investment.

Scenario 2: optimal flowering time and season length

Changes in the length of the growth season may be due to variation in its start (S) or its end (E). We will first (case (1)) study how season length influences optimal flowering in relation to the *start* of the growth season, that is, on a relative time scale. We will then assume $S = 0$ and $E = T$. We will then study the effects on optimal flowering time given a scenario (case (2)) in which the season is *extended equally* at both ends. Specifically, we then assume that midseason is always at time $t = 0$, the beginning of the season occurs at time $S = -T/2$ and the end of the season occurs at time $E = T/2$, where T is the season length. For example, if season length increases by 2 d, the start of the season is advanced by 1 d and the end of the season is delayed by 1 d. Fig. 3 shows how variation in productivity and season length affects optimal flowering time for our three growth functions in

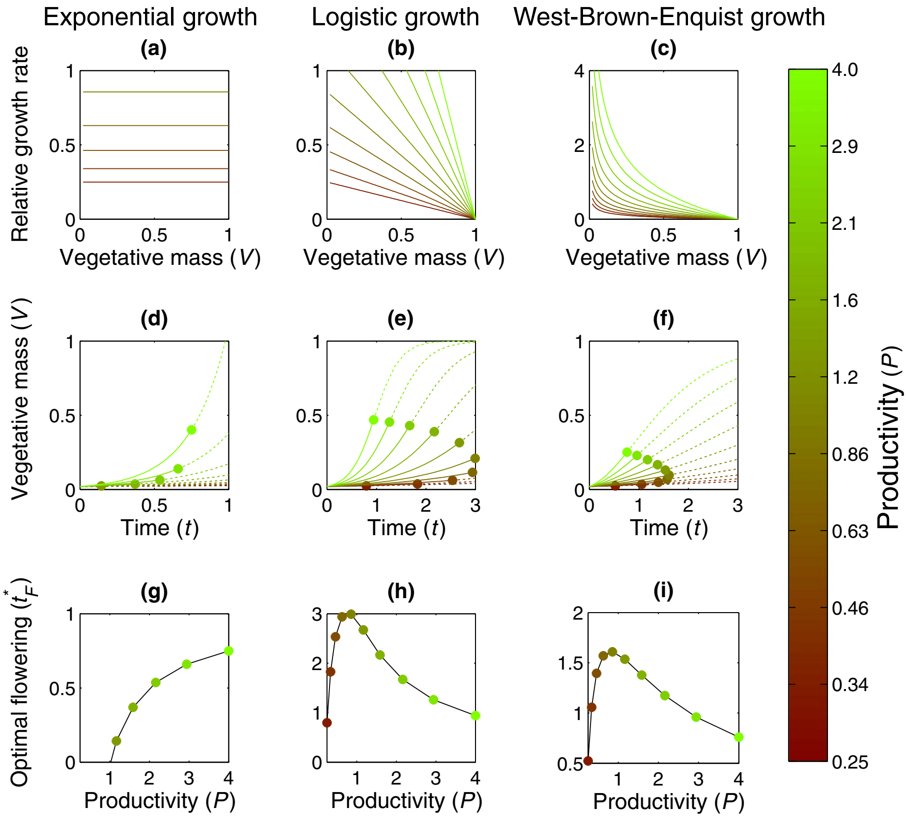

Fig. 2 The relative growth rate is constant for (a) exponential growth, but decreasing for (b) logistic growth and (c) West–Brown–Enquist (WBE) growth. The vegetative mass at optimal flowering time t^*_F (coloured circles) always increases with productivity (d–f). Increasing productivity *P* always delays optimal flowering time t_F for exponential growth (d, g), but this is not true for logistic (e, h), and WBE growth (f, i). Closed circles represent the optimal flowering times and each circle in (d, e) corresponds to a circle in (g–i) for comparison. The colours of lines and circles represent different levels of productivity (green for high levels). The dotted lines (d–f) indicate vegetative mass, had flowering not occurred. The default mass values are $V_{max} = 1$ and $V_0 = 0.02$.

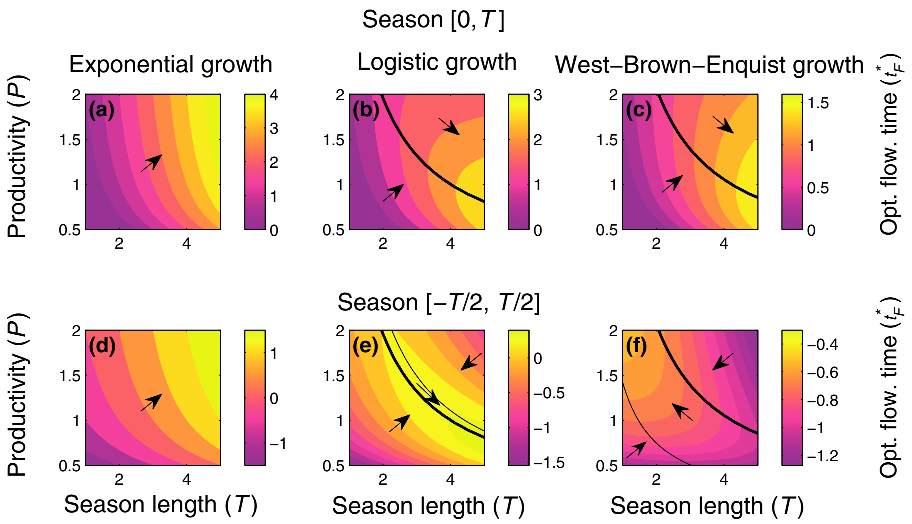

Fig. 3 Optimal flowering time (t^*_F) is advanced or delayed at increasing productivity (*P*), depending on the type of growth, the season length and the productivity. We investigate two types of seasons: (0, *T*) the season always start at time zero, and a longer season delays the end of the season (a–c), and (−*T*/2, *T*/2) a longer season equally advances the beginning of the season and delays the end of the season (d–f). Optimal flowering time is defined in relation to season start and is shown with colours (purple, early; yellow, late), with three types of growth: exponential growth, logistic growth and West–Brown–Enquist growth. The arrows show the direction in which optimal flowering time is getting later, that is, they indicate the gradient of the optimal flowering time. For exponential growth, when the season is defined without an offset, then the optimal flowering time is always delayed as productivity or season length increases (a), and this is also true when the season has an offset (d). The t^*_F advances with increased *P* above the thick black line in (b, c, e, f), elsewhere t^*_F is delayed with increased *P*. The t^*_F advances with increased season length (*T*) to the right of the thin line in (e, f), elsewhere t^*_F is delayed with increased *T*. The default mass values are $V_{max} = 1$ and $V_0 = 0.02$.

these two cases. In case (1), the optimal flowering time is always delayed (Fig. 3a–c) when the season length is increased. In other words, increased season length always causes the optimal flowering time to occur later in relation to the start of the season. When the season length is increased in case (2), and productivity is held constant, the optimal flowering time is still delayed for exponential growth (Fig. 3d), but advanced for logistic and WBE growth, to the right of the thin black line where productivity is high and season length is long (Fig. 3e,f). Increasing the season length can delay the optimal flowering time, to the left of the thin black line at low productivity and short seasons (Fig. 3e,f). If instead season length is held constant and the productivity is increased, the optimal flowering time is delayed under exponential growth (Fig 3a) but may be either advanced (above the black line in Fig. 3b,c,e,f) or delayed (below the black line in Fig. 3b,c, e,f) under constrained growth. This occurs because optimal flowering time is a hump-shaped function of productivity as shown above (the black line in Fig. 3b,c corresponds to the maximum in Fig. 2h,i). Note that the productivity level that maximizes optimal flowering time decreases with increasing season length (the black line has a negative slope in Fig. 3b,c). In sum, the optimal phenological response to increased season length depends on whether growth is constrained or not. When growth is constrained, season length can influence the direction of the phenological response to increased productivity, and productivity can influence the direction of the phenological response to a longer season.

Discussion

Our results suggest that life-history strategies may explain variation in phenological responses to a changing climate. In essence we suggest that when optimizing reproductive output, plants with less constrained vegetative growth will respond to increasing productivity (e.g. increasing temperature, rainfall, nitrogen or CO_2) by delaying their flowering time whereas plants with more constrained vegetative growth may respond to increased productivity either by delaying or advancing their flowering time, depending on the productivity and season length. Similarly, when season length is extended equally at the start and the end of the growing season, optimal flowering time is either delayed, for unconstrained growth, or advanced, for constrained growth. Growth is constrained in the logistic or WBE growth models when productivity is high and/or season length is long, giving a large vegetative mass.

Because growth rate depends on plant architecture, self-shading and metabolic costs, this work establishes new links between phenological adaptation and fundamental plant traits. As an example, species of annual forbs advanced their flowering times whereas grass species delayed their flowering times in relation to the start of the growth season when subjected to increased CO_2 (Cleland *et al.*, 2006). These opposing shifts may reflect different physiological responses to environmental cues which are optimal according to our model if increased CO_2 increases productivity and if the optimal flowering time in grasses is in the less constrained part of the growth curve whereas that of forbs is in the more constrained part of the growth curve (Fig. 2). It has previously been shown that increased CO_2 extends season length (Reyes-Fox *et al.*, 2014), possibly because increased CO_2 level means less water is lost through transpiration, which could promote senescence. In the experiments by Cleland *et al.* the start of the season was equal for all plants, because it was controlled by the first fall rains, and thus corresponds to our case (1) in Fig. 3. According to our model, the optimal response to a longer season is to flower later in relation to the start of the season, regardless of whether growth is constrained or not (Fig. 3a–c). This would then indicate that the grasses but not the forbs are responding in the optimal direction in Cleland's experiment. In this context it should be noted that increasing temperatures and increasing CO_2 might increase the season length, but other factors also associated with global warming will likely shorten the growth season, such as more frequent drought, which can increase mortality, and cause increased variance in expected life span.

Our study focuses on changes in flowering times among annual plants. The model, and the conclusions from our study, may also be representative for timing of reproduction in other annual organisms, including many insect species in temperate and other areas characterized by seasonality. To what extent our result also carries over to species with a perennial lifestyle is more of an open question. For instance, the perennial plant *Veratrum tenuipetalum* can reproduce clonally or sexually depending on summer temperatures (Iler & Inouye, 2013), which makes it challenging to compare it with a framework such as ours that only considers flowering phenology. In general, although reproductive timing often is tightly connected to energy allocation patterns in annual organisms, it may be more or less decoupled from growth phenology in perennial plants because of the use of stored resources to produce flowers (Johnson, 1993; Debussche *et al.*, 2004). Dynamic energy models of perennial plants with vegetative, reproductive and storage compartments (Iwasa & Cohen, 1989; Mironchenko & Kozłowski, 2014) might be a good starting point for further investigations. Under certain circumstances the optimal switch from vegetative growth to reproduction in the model considered here, would correspond to the optimal switch from vegetative growth to storage in dynamic energy models (Johansson *et al.*, 2013). It should also be noted that the only constraints on reproduction that we have considered here are season length and productivity. There are many other possible obstacles to reproduction, for example, temporal mismatch for pollination, seed dispersal and/or germination (Rafferty & Ives, 2011; Bolmgren & Eriksson, 2015; Ehrlén *et al.*, 2015). Considering poor synchronization with pollinators owing to climate change, constrained reproduction would be an interesting extension to this study.

We base all our calculations on a bang-bang control, where first all biomass production is put into vegetative growth, and from the flowering time (i.e. maturation time) until the end of the season, all biomass production is put into reproductive growth. Our use of a bang-bang control is supported by Cohen (1976) who showed that with constrained growth, the optimal allocation is to first put all resources to vegetative growth, and at some time switch to put all resources into reproduction until the end of the season. When survival was described instead by a decreasing function, Cohen (1976) also found a bang-bang control; we give an alternative proof of bang-bang control with exponentially decreasing survival corresponding to constant mortality in Methods S1. Notwithstanding this, we regard bang-bang control as an approximation: although shifts from vegetative to reproductive growth have been shown to occur relatively fast in some annual plants, for example *Lupinus nanus* (Pitelka, 1977), gradual transitions to reproductive growth appear more common (Rathcke & Lacey, 1985; and reference therein). A complex genetic network governs the crucial step from vegetative to reproductive growth (Huijser & Schmid, 2011), and this complexity makes a sudden switch unlikely. In one empirical test the timing of the sudden switch predicted by a model similar to ours coincided closely with the gradual transition to reproductive growth (King & Roughgarden, 1983). In our setting, we have proved that the fitness-maximizing strategy is a bang-bang control. This is not necessarily the case for other model variants. We show that adding constant mortality – that is, exponentially decreasing survival – does not change our qualitative results (Fig. S1).

In order to compare the predictions of this model with empirical data it is important to distinguish between changes of the flowering time on a calendar scale and changes in relation to the start of the growth season. In our investigation of effects of changed productivity (Fig. 2) the optimal flowering time is measured in relation to the start of the growth season ($S = 0$ and $E = T$), such that time refers to the age of the plant. On a calendar time scale, changes of this relative flowering time may be offset by a change in the start of the growth season. For example, if the growth season advances, a delayed flowering time on the relative time scale may be manifested as a nonchanging flowering time on the calendar time scale. In scenarios with strongly advanced start of the season, we thus predict that growth constraints may not necessarily flip the direction of the optimal phenological response on a calendar scale but rather influence whether the optimal response is to advance more or less.

Interannual variation and climate change may affect productivity, as well as the start and the end of the season, and the latter are often hard to define (Steltzer & Post, 2009). In our investigation of changed season length (Fig. 3), we considered two cases where: (1) only the end the season is changed ($S = 0$ and $E = T$), and (2) a constant midseason (and $S = -T/2$ and $E = T/2$). In case (1) we found that a longer season always delays the optimal flowering time for all types of growth, which is expected. In case (2), where an increased season length is caused by an equally large change in both ends of the season, we find an internal maximum of the optimal flowering time under constrained growth. Thus constrained growth can flip the direction of optimal phenological response for both increasing productivity and season length. Anyhow, in a scenario with unequal rates of change of the start and end of season, we would again need to translate the model predictions to the calendar scale.

When interpreting our results, it is also important to note that we only consider the optimal timing of reproduction, but not the exact mechanisms that control this timing and that our focus is on the ultimate explanations, not the proximate ones. Environmental cues such as ambient temperature, winter chilling and day length can, however, have a large impact on species phenologies. For example, Wilczek *et al.* (2009) found that environmental variation can produce different life histories in *Arabidopsis thaliana* such as germinating in early winter and flowering in early spring in the Mediterranean, germinating in late autumn and flowering in late spring in northern Scandinavia, and rapid-cycling ecotypes germinating in autumn, spring and summer without vernalization in England. No significant differences were found between the genotypes. When Wilczek *et al.* were looking closer at the different life histories they found that *A. thaliana* was always flowering after accumulating the same amount of photothermal units; in other words, they behave in the same way in physiological time. Thus, the observed differences in germination and flowering time for this species across environments are likely to be caused by the mechanisms that control the species' life history rather than local adaptation.

In order to avoid getting bogged down by details in seasonal productivity variation, transforming from calendar to physiological time can be useful for explaining how cues for germination and flowering work (Wilczek *et al.*, 2009), and why certain cues are used and certain life histories are selected for in a given environment. Our model is expressed in calendar time but could also be expressed in physiological time (Eqns 5–8). As shown here, the consequences of changed temperature or productivity for optimal flowering times may be hard to predict when considered in calendar time. This is not the case when viewed in physiological time. The optimal physiological time for flowering depends only on the cumulative productivity during the growth season, where the cumulative productivity is similar to a temperature sum if productivity is proportional to temperature above a certain baseline. If the cumulative productivity is increasing, flowering is delayed as measured in physiological time. *Otherwise*, flowering is advanced. This effect can be seen both in Fig. 2(d–f), where the optimal flowering time always occurs at a larger vegetative mass (i.e. higher cumulative productivity) when productivity increases, and in Fig. 3(a–c), where a longer season (i.e. increasing cumulative productivity) always gives a later flowering time. Thus we do not expect growth constraints to flip the optimal direction of change for the physiological time for flowering. To transform insights from physiological time to calendar time, it is necessary to consider how productivity changes during the season and how this affects the beginning and the end of the growing season. Both perspectives are useful, and whether one should work with calendar time or physiological time is ultimately determined by the research question.

Most field studies on long-term phenological change among annual plants show advancing first-flowering dates, usually explained by an advancing spring (Fitter & Fitter, 2002; Menzel *et al.*, 2006; Parmesan, 2007; Primack *et al.*, 2009). Our results suggest that under constrained growth advanced flowering may be an adaptive response to increased productivity, even if the start of the season would remain unchanged. Global warming can additionally increase the season length and we find when season length is extended equally at the start and the end of the growing season, optimal flowering is either delayed, for unconstrained growth, or advanced, for constrained growth. These two findings suggest that factors constraining growth, such as self-shading and sibling competition, are worth considering in phenological studies.

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Author contributions

M.L., J.J., K.B. and N.J. conceived the study. M.L. analysed the model and wrote the manuscript. M.L., N.L. and Å.B. proved Theorem 1 (Supporting Information Methods S1). All authors discussed the results and implications and revised the manuscript.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Influence of mortality on our model predictions.

Methods S1 Theorem 1 with proof showing that bang-bang control is optimal for constrained growth with constant mortality.

Methods S2 Derivations of analytic expressions for the optimal flowering time, and analysis of how variations in productivity affect our results.

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

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Niklas L.P. Lundström, Åke Brännström, Niclas Jonzén

8 September, 2015

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 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.

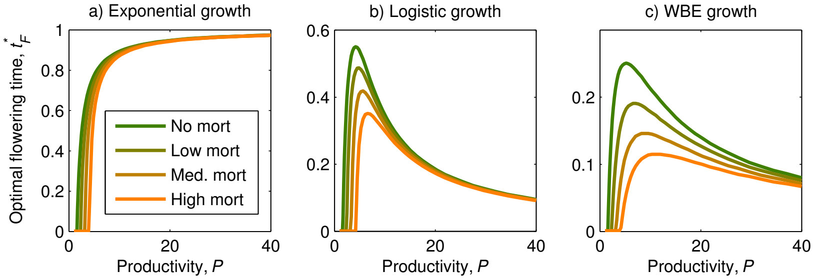

Figure S 1: Mortality decreases the survival, and affects the optimal flowering times as a function of productivity. Mortality is $m = 0, 1, 2, 3$, corresponding to no, low, intermediate and high mortality rate. The season length is $E = 1$ and the default mass values are $V_{max} = 1$ and $V_0 = 0.02$.

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

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

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

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

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

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

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*

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

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

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

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 $x_2 = t$

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

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

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

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 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

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

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

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

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

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

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 $t_F^* = t_0$. □

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

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

   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 $d^2W/d{t_F^*}^2 < 0$ 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.

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 $0 \leq t \leq t_F$ 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,

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

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,

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

(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

$$V(t) = \frac{V_{max}V_0e^{Pt}}{V_{max} + V_0(e^{Pt} - 1)}, \tag{S2b.1}$$

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

$$\begin{aligned} f(t_F) = {} & V_{max} - V_0 - V_{max}PT + PTV_0 + P(V_{max} - V_0)t_F + V_0(1 + PT)e^{Pt_F} \\ & - PV_0t_Fe^{Pt_F} = 0, \end{aligned}$$

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

$$\frac{df(t_F)}{dt_F} = P(V_{max} - V_0) + (T - t_F)P^2V_0e^{Pt_F} > 0, \tag{S2b.3}$$

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

$$S = (T - t_F)(V_{max} - V_0) - (T + Pt_F(T - t_F))V_0e^{Pt_F}. \tag{S2b.4}$$

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.

(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

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

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

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

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

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

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

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

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.

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