

Optimal phenology of annual plants under grazing pressure

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Received 2 October 2006; received in revised form 10 January 2007; accepted 10 January 2007

Available online 20 January 2007

Abstract

Plants show phenological responses to herbivory. Some enclosure experiments have demonstrated that the onset of the peak flowering season is dependent on grazing pressure. We constructed a mathematical model using Pontryagin's maximum principle to investigate changes in flowering time by examining shifts in resource allocation from vegetative to reproductive plant components. We represented a primary production of a plant individual by two types of function of vegetative part size, a linear function and a convex non-linear function. The results of a linear production model indicate that optimal phenology follows a schedule that switches from the production of vegetative parts to that of reproductive parts at a given time ('bang–bang' control). However, in a non-linear model, a singular control, wherein the plant invests in both productive and reproductive parts, may be included between obligate production and reproduction periods. We assumed that the peak of the flowering season occurs immediately following the exclusive investment in reproduction. In a linear production model, differential herbivory rates on the vegetative and reproductive parts of a plant resulted in shifts in the peak flowering time. A higher herbivory rate on the vegetative components advanced the peak, whereas it was delayed when grazing pressure focused on reproductive components of the plant. In the non-linear production model, increased grazing pressure tended to postpone the flowering peak. These results corresponded well with results of enclosure experiments, thus suggesting adaptive control of flowering time in plants.

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Keywords: Dynamic optimization; Grazing; Mathematical model; Plant phenology; Singular solution

1. Introduction

A major developmental transition in flowering plants is the switch from vegetative to reproductive development. To maximize reproductive success, it is essential that the timing of this transition is correct. Many plants respond to environmental cues such as changes in day length and temperature, the molecular mechanisms of which have been well studied (Simpson and Dean, 2002). Moreover, plants respond phenologically to herbivory (Karban and Baldwin, 1997; Rose et al., 2005). For example, Young et al. (1994) and Ru and Fortune (1999) showed that increased grazing pressure delayed flowering time. Using enclosure experiments in Mongolian grasslands, Fujita et al. (2002) demonstrated that the peak

flowering season in edible plants was delayed as a result of herbivory.

Plants may respond to herbivory by prolonging periods of vegetative growth to compensate for biomass loss during predation. However, this is likely to depend on a variety of conditions. For example, if herbivores only consume the vegetative components of a plant and leave the reproductive organs intact, shortening vegetative growth may prevent biomass loss. Therefore, to understand plant responses to herbivory, it is necessary to understand the schedule of biomass allocation or phenology and its reproductive consequence. One way of doing this is to analyze the optimal growing schedule of plants using a mathematical approach.

The evolution of the schedule of plant biomass allocation was initially investigated theoretically by Cohen (1971, 1976), and has since been the topic of numerous reports (King and Roughgarden, 1982a, b, 1983; Schaffer, 1983;

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Iwasa and Roughgarden, 1984; Iwasa and Cohen, 1989; Iwasa, 1991, 2000; Yamamura and Tsuji, 1995; Iwasa et al., 1996; Iwasa and Kubo 1997; Day and Taylor, 2000; Yamauchi and Yamamura, 2004). These studies have used dynamic optimization models to explain patterns of resource allocation between tissues throughout the plant lifecycle. However, Yamamura and Tsuji (1995), Iwasa et al. (1996), and Yamauchi and Yamamura (2004) conducted the only studies that have considered the effects of continuous grazing on phenology. Yamamura and Tsuji (1995) investigated the strategy of resource allocation for vegetative and defensive plant parts while ignoring the reproductive parts. Similarly, Iwasa et al. (1996) analyzed the defense schedule of plants but failed to consider differences in productive and reproductive components. Yamauchi and Yamamura (2004) analyzed strategy of resource allocation between vegetative and reproductive parts during herbivory; however, they limited their focus to conditions of grazing optimization, considering nutrient dynamics in the soil. Therefore, no previous study has clarified the effects of herbivory on resource allocation dynamics between vegetative and reproductive parts.

Here we used the dynamic optimization method to construct a mathematical model that allowed us to investigate the relationship between grazing pressure and the timing of resource allocation switching between various plant tissues.

2. Methods

2.1. General mathematical equations

We consider an annual plant species that reproduces once at the end of the growing season. In this analysis, the biomass of an individual plant was divided into two parts: vegetative (V) and reproductive (R). At the start of the season $V = V_0$ (i.e., seed size) and $R = 0$.

The assimilation rate of a plant can be considered to be dependent on individual photosynthetic ability, which should increase with the size of the vegetative component of the plant. However, photosynthetic ability may increase more slowly than the size of the vegetative component because a large vegetative part may be accompanied by increased maintenance costs or lower light intensity due to self-shading. Thus, the assimilation ability is assumed to be either a linear or convex function of the size of the vegetative part, $g(V)$. The assimilated products are allocated between the growth of vegetative and reproductive parts at a given time. The allocation schedule is optimized to maximize the final size of the reproductive component, $R(T)$, where T represents the end of the season. The resource allocation to the reproductive components at time t is denoted by $x(t)$, where $0 \leq x(t) \leq 1$. Given these assumptions, the dynamics of biomass allocation to vegetative and reproductive parts of a plant are described by the following equations:

$$\frac{dR}{dt} = x(t)g(V) - hR, \tag{1a}$$

$$\frac{dV}{dt} = (1 - x(t))g(V) - kV, \tag{1b}$$

where h and k represent the grazing rates on the reproductive and vegetative parts, respectively. The individual plant in question uses an $x(t)$ that maximizes the final size of the reproductive part, $R(T)$. This type of problem can be solved by Pontryagin's maximum principle (Pontryagin et al., 1962; see also the textbook by Kot, 2001). Based on the dynamics (1a), (1b), the Hamiltonian formulation is

$$\begin{aligned} H &= \frac{dR}{dt} + \lambda_R \frac{dR}{dt} + \lambda_V \frac{dV}{dt} \\ &= x(t)g(V)(1 + \lambda_R - \lambda_V) - (1 + \lambda_R)hR + \lambda_V(g(V) - kV), \end{aligned} \tag{2a}$$

where λ_R and λ_V represent costate variables accompanying reproductive and vegetative part sizes, respectively. In Eq. (2a), the first term represents a differentiation of objective function that should be maximized, while other terms are differentiations of state variables that are weighted by costate variable. It should be noted that when the objective function coincides with one of state variable, those are often unified into a single term (e.g. King and Roughgarden, 1982a; Iwasa and Roughgarden, 1984), accompanying a modification of terminal condition of the concerned costate variable (see below). In this system, canonical equations are as follows:

$$\frac{d\lambda_R}{dt} = -\frac{\partial H}{\partial R} = (1 + \lambda_R)h, \tag{2b}$$

$$\frac{d\lambda_V}{dt} = -\frac{\partial H}{\partial V} = -x(t)g'(V)(1 + \lambda_R - \lambda_V) - \lambda_V(g'(V) - k). \tag{2c}$$

According to the maximum principle, the dynamics of λ_R and λ_V are constrained by conditions such that both $\lambda_R(T)$ and $\lambda_V(T)$ equal zero at the end of season T because the state variables are not constrained at the terminal time. Given that $\lambda_R(T) = 0$, we can use Eq. (2b) to calculate that $\lambda_R = \text{Exp}[-h(T-t)] - 1$. By substituting this into Eqs. (2a)–(2c), we derive:

$$H = x(t)g(V)(e^{-h(T-t)} - \lambda_V) - e^{-h(T-t)}hR + \lambda_V(g(V) - kV). \tag{3a}$$

$$\lambda_R = e^{-h(T-t)} - 1, \tag{3b}$$

$$\frac{d\lambda_V}{dt} = x(t)g'(V)(\lambda_V - e^{-h(T-t)}) + \lambda_V(k - g'(V)). \tag{3c}$$

The maximum principle states that the optimal resource allocation schedule $x^*(t)$ can be derived by choosing $x(t)$ such that it maximizes the Hamiltonian (H) at a given time. According to Eq. (3a), we can obtain the optimal schedule

as follows:

$$x^*(t) = \begin{cases} 0 & \text{if } \lambda_V > e^{-h(T-t)}, \\ \text{between 0 and 1} & \text{if } \lambda_V = e^{-h(T-t)}, \\ 1 & \text{if } \lambda_V < e^{-h(T-t)}, \end{cases} \quad (4)$$

When $\lambda_V = \text{Exp}[-h(T-t)]$, the trajectory of optimal solution may be a singular control. By substituting this into Eq. (3c), the dynamics of λ_V under the singular control become

$$\frac{d\lambda_V}{dt} = e^{-h(T-t)}(k - g'(V)). \quad (5)$$

For tracing the singular trajectory, λ_V must simultaneously satisfy both $\lambda_V = \text{Exp}[-h(T-t)]$ and Eq. (5), giving $g'(V) = k - h$. This implies that the plant adopts a singular schedule when the vegetative part reaches a certain size, V^* , at which the increasing rate of assimilation ability against the vegetative part size [$g'(V^*)$] coincides with the difference in grazing rates between vegetative and reproductive parts ($k - h$). As such, the individual plant simultaneously allocates assimilated products to both vegetative and reproductive parts during a certain period, thereby maintaining the vegetative part size at V^* , which is a condition for the optimal control $x^*(t)$ on the singular trajectory.

Using these equations and assuming that the assimilation ability is a convex increasing function [$g'(V) > 0$, $g''(V) < 0$], we can divide the growing season into three periods. In the first period, vegetative part size V is sufficiently small, thereby allowing $g'(V)$ to be large, such that $g'(V) > k$. Additionally, if λ_V is large enough to allow $\lambda_V > \text{Exp}[-h(T-t)]$, the plant invests all assimilation products into vegetative parts [$x^*(t) = 0$], resulting in a growth increment of V [i.e., decrement of $g'(V)$]. When $g'(V) = k - h$, $\lambda_V = \text{Exp}[-h(T-t)]$ occurs simultaneously, thus forcing the optimal control to enter into a singular trajectory. During singular control, the plant keeps vegetative part size at V^* , meaning that assimilation products are invested in both reproductive and vegetative parts, thus compensating for loss of biomass due to grazing. During this period, λ_V follows $\lambda_V = \text{Exp}[-h(T-t)]$, although λ_V must eventually reach zero at the end of the season [$\lambda_V(T) = 0$]. This means that λ_V must leave the singular trajectory at a given time, thereby becoming $\lambda_V < \text{Exp}[-h(T-t)]$. Thereafter, the plant invests all assimilation products into reproductive parts [$x^*(t) = 1$]. During this period, the vegetative component of the plant gradually decreases as a result of grazing pressure ($V < V^*$), and the dynamics of λ_V follow $d\lambda_V/dt = -g'(V)\text{Exp}[-h(T-t)] + \lambda_V k$ from Eq. (3c).

In summary, the plant generally invests exclusively in the vegetative component early in the season, whereas it contributes to both vegetative and reproductive parts in the middle of the season and only to the reproductive part toward the end of the season. In some situations, however, this general pattern cannot hold. For example,

when the growing season is short, or when the assimilation ability of plant is relatively low, it may not be able to reach V^* , by which an intermediate period with singular control does not take place. In such situations, the plant allocates all of its resources to vegetative growth early in the season and reproductive growth later in the season. Therefore, the resource allocation pattern of an individual suddenly changes at a given time. In dynamic optimization this is often referred to as ‘bang–bang’ control. If grazing pressure is absent, this type of schedule is the only option (Cohen, 1971, 1976). This is the case in our model, because the condition for the singular control, $g'(V) = k - h$ does not hold when $k = h = 0$.

We have derived a general pattern of the optimal phenology of plant resource allocation under grazing pressure. However, this can only be calculated for an explicit functional form of assimilation ability $g(V)$. We assume that $g(V)$ equals αV^β ($0 \leq \beta \leq 1$), where $g'(V) > 0$ and $g''(V) \leq 0$. In this case, when the plant allocates all assimilation products to vegetative part in the absence of herbivory, its growth coincides with von Bertalanffy growth curve (or Richards curve with a slope of the allometric line being smaller than 1) with which maintenance costs are absent or the maximum size is sufficiently large (von Bertalanffy, 1957; Richards, 1959; Hunt, 1982). To ensure that the vegetative growth (1b) is initially positive we must have $\alpha > kV_0^{1-\beta}$, where V_0 is the initial size of the vegetative part.

2.2. Non-linear $g(V)$, $0 \leq \beta < 1$

First, we consider a case, where the assimilation ability $g(V)$ is a non-linear function of vegetative part size ($\beta < 1$). If the optimal phenology involves singular control (see Appendix A), we can denote the times for changing resource allocation patterns as

$$\tau_1 = \frac{1}{k(1-\beta)} \ln \left[\frac{(k-h)(\alpha - kV_0^{1-\beta})}{\alpha\{k(1-\beta) - h\}} \right] \quad (6a)$$

and

$$\tau_2 = T - \frac{1}{k\beta - h} \ln \left[\frac{k-h}{k(1-\beta)} \right]. \quad (6b)$$

The plant invests assimilation products exclusively in vegetative parts when $0 < t < \tau_1$, whereas it invests in both vegetative and reproductive parts when $\tau_1 < t < \tau_2$, and solely in reproductive parts when $\tau_2 < t < T$. Conversely, when τ_1 and τ_2 are such that $\tau_1 > \tau_2$, there is no possibility of singular control. In such cases, the optimal phenology is bang–bang control, in which the plant invests in vegetative components in the earlier season and then switches to reproductive components toward the end of the season. That is, the plant never invests simultaneously in both vegetative and reproductive parts. As described in the Appendix A, the optimal switching time

τ_b is a solution of

$$\left(\frac{\alpha}{\alpha - kV_0^{1-\beta}} e^{k(1-\beta)\tau_b} - 1 \right) \frac{h}{k\beta} - \frac{\alpha}{\alpha - kV_0^{1-\beta}} e^{(k-h)\tau_b - (k\beta-h)T} + 1 = 0. \tag{7a}$$

This equation can be explicitly solved for two special cases. First, if the reproductive part of the plant is not grazed (i.e., $h = 0$), the optimal switching time of resource allocation is

$$\tau_b = \beta T - \frac{1}{k} \ln \left[\frac{\alpha}{\alpha - kV_0^{1-\beta}} \right]. \tag{7b}$$

This is a decreasing function of k because $\alpha > kV_0^{1-\beta}$. On the other hand, when grazing pressure is identical between reproductive and vegetative parts ($h = k$), the optimal switching time can be calculated as

$$\tau_b = \frac{1}{k(1-\beta)} \times \ln \left[\frac{\alpha - kV_0^{1-\beta}}{\alpha} \left\{ \beta \left(\frac{\alpha}{\alpha - kV_0^{1-\beta}} e^{k(1-\beta)T} - 1 \right) + 1 \right\} \right]. \tag{7c}$$

2.3. Linear $g(V)$, $\beta = 1$

When $g(V)$ is a linear function of vegetative part size and $\beta = 1$, the singular solution cannot occur because Eq. (6a) diverges. Thus, the optimal phenology always follows the bang–bang control. By substituting $\beta = 1$ into Eq. (7a), the optimal time for switching resource allocation is calculated as follows:

$$\tau_b = T - \frac{1}{k-h} \ln \left[\frac{\alpha}{\alpha - (k-h)} \right]. \tag{8}$$

In the limit of $k = h$, τ_b is defined as $T - 1/\alpha$. This is a well-known formula for calculating the time of resource allocation switching in the case of a linear growth function (Cohen, 1976).

3. Results

Using the above equations, we can examine the parameter dependence of optimal phenology. Fig. 1 illustrates the dependence on seasonal length (T) as well as on the coefficient of vegetative part size in the assimilation function (α), and on the order of vegetative part size in the assimilation function (β). Fig. 1a shows that as the length of the growing season increases, the optimal schedule is more likely to involve singular control. Fig. 1b shows that for any α value, the phenology always includes singular control, although this is dependent on other parameter values. The supplemental calculations illustrate that additional parameter sets may result in the disappearance of singular control at a high α . Accordingly,

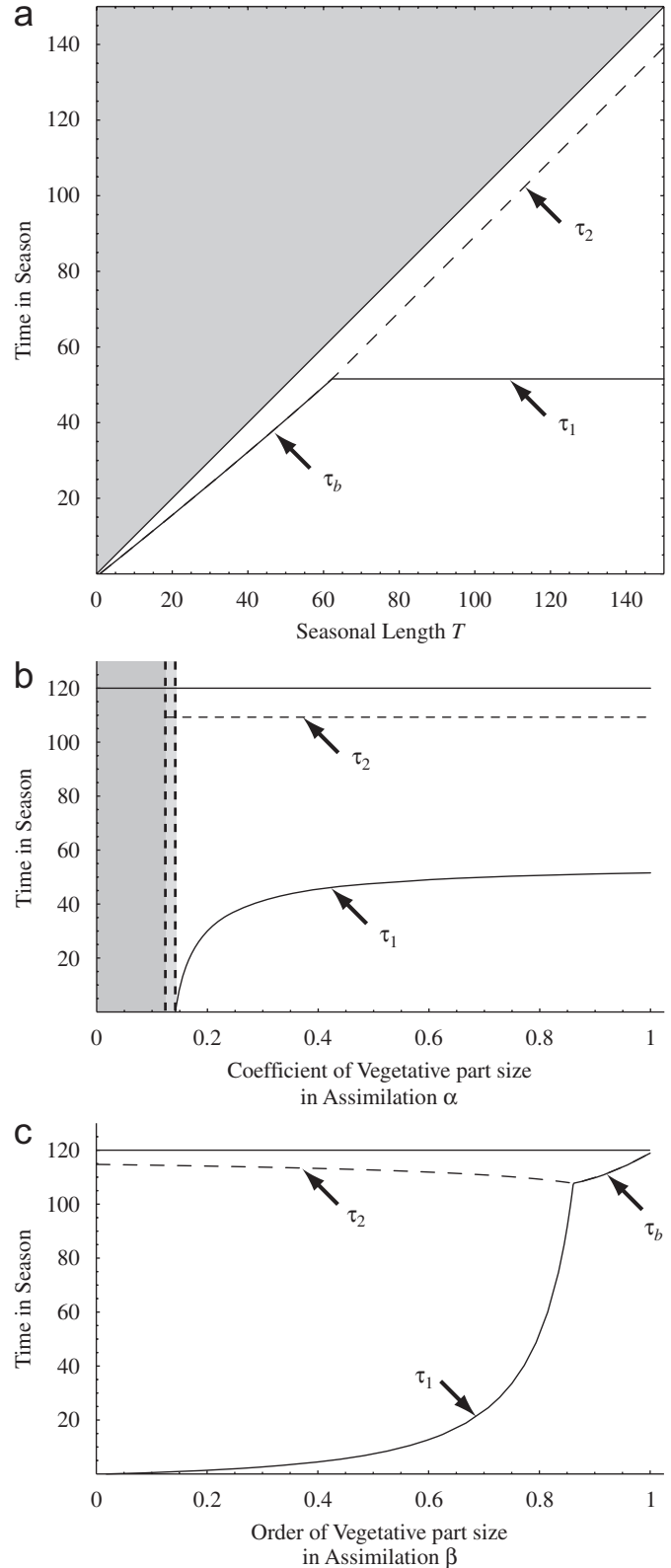


Fig. 1. Optimal phenologies with respect to (a) seasonal length, T , (b) coefficient of vegetative part size in the assimilation function, α , and (c) the order of vegetative part size in the assimilation function, β . Basic parameters are $h = 0.02$, $k = 0.2$, $\alpha = 1$, $\beta = 0.8$, $T = 120$, and $V_0 = 0.1$.

depending on conditions, the optimal schedule of resource allocation tends to include singular control with a lower coefficient of vegetative part size α . Fig. 1c indicates that the optimal schedule tends to involve singular control with the decreasing order of vegetative part size β .

In Fig. 1b, the gray areas indicate impracticable parameters. Two such cases are possible. The first is represented by the dark gray region (smaller α), which corresponds to situations where the plant cannot grow at all. The second, indicated by the light gray region (larger α), represents situations where the initial size of the vegetative part (i.e., V_0 immediately after germination) is larger than that for singular control V^* . In such cases, the plant initially invests all of its resources toward the growth of the reproductive parts, thus resulting in the reduction of the vegetative parts via herbivory. When the size of vegetative part reaches V^* , the plant begins to follow a singular trajectory with simultaneous investment in both vegetative and reproductive parts. At the end of the season, the plant again invests all resources in reproductive growth. This means that the plant has two peaks of reproductive activity during a single season, once immediately after germination and again at the end of season. Given that this is highly unrealistic, we conclude that this schedule is

unfeasible and have therefore excluded it from the optimal schedule illustrated in Fig. 1b.

Fig. 2 shows that the optimal phenology is dependent on the grazing pressures on (a) reproductive parts and (b) vegetative parts for a non-linear model ($\beta < 1$). A singular solution period tends to occur when the herbivory of vegetative parts is relatively high compared to that of reproductive parts. Fig. 3 illustrates the dependency of the schedule of resource allocation on grazing pressure in a linear model ($\beta = 1$), in which case the optimal phenology always follows bang–bang control without a singular solution period. The switching time τ_b is an increasing function of h and a decreasing function of k .

4. Discussion

It is well documented that plant species demonstrate altered growing schedules in response to herbivory. For example, Young et al. (1994) and Ru and Fortune (1999) reported that some plant species delayed flowering as herbivory increased. Fujita et al. (2002) showed that increased grazing pressure delayed the peak flowering season of edible plant species in Mongolian grasslands. These studies were conducted by artificially controlling

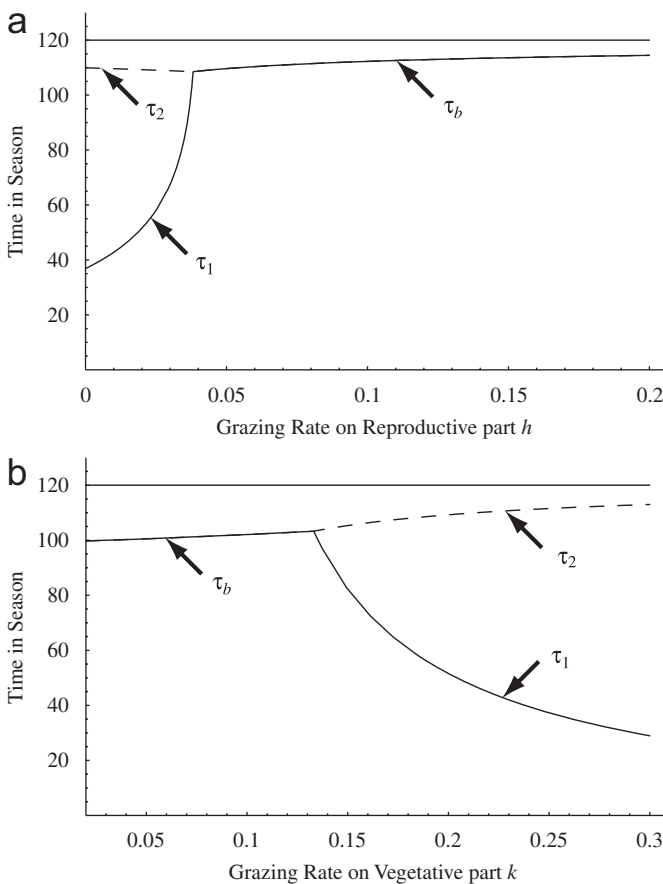


Fig. 2. Dependence of the optimal phenology in the non-linear model on grazing rates on (a) reproductive parts, and (b) vegetative parts. Basic parameters are $h = 0.02$, $k = 0.2$, $\alpha = 1$, $\beta = 0.8$, $T = 120$, and $V_0 = 0.1$.

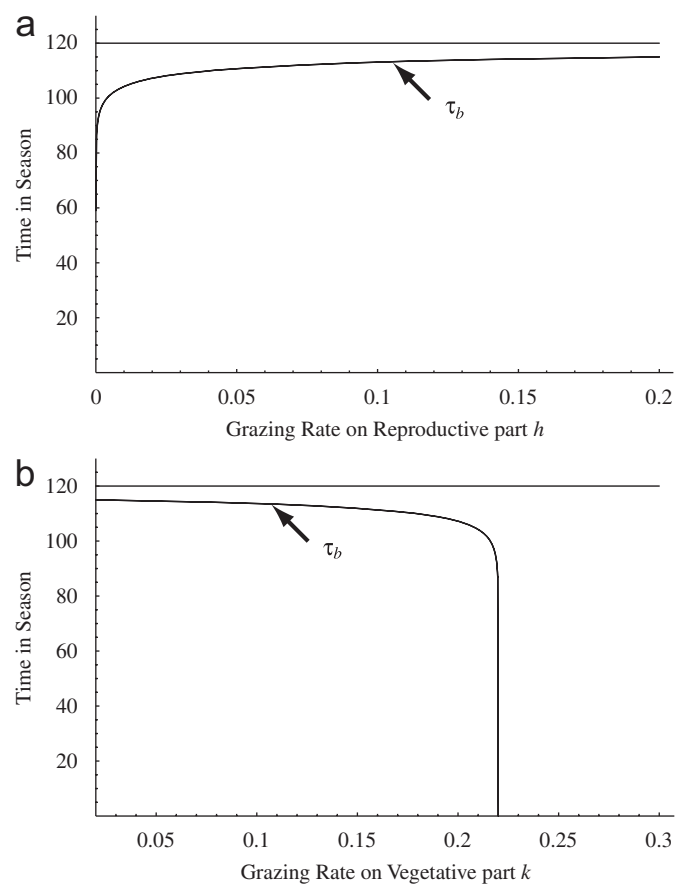


Fig. 3. Dependence of the optimal phenology in the linear model on grazing rate on (a) reproductive parts and (b) vegetative parts. Basic parameters are $h = 0.02$, $k = 0.2$, $\alpha = 0.2$, $\beta = 1$, $T = 120$ and $V_0 = 0.1$.

herbivory conditions using techniques such as enclosure experiments. However, the responses of plants to novel conditions were measured over experimental periods that were far too short to observe evolutionary responses. Therefore, the observed changes in flowering season could be a result of phenotypic plasticity, which may have been selected for depending on the cost of the plasticity and reliability of the environmental cues (Scheiner, 1993; Moran, 1992; DeWitt et al., 1998; Tufto, 2000). Here we have focused on the evolution of phenology under selection pressure resulting from herbivory. However, our model can also be applied toward adaptive phenotypic plasticity. Grazing pressure at the earlier season can be a reliable cue for plants so as to plastically alter its phenology for the following season. Thus, it is possible that the changes in flowering time observed in previous experiments can be explained by our model system.

Our model initially focuses on a linear situation, where the assimilation ability is a linear function of vegetative part size (i.e., $\beta = 1$). In this case, the optimal phenology is always a bang–bang schedule, whereby resource allocation completely switches from an investment solely in vegetative growth to that of reproductive growth at time τ_b . The analysis shows that the flowering time (τ_b) increases with increasing grazing intensity on the reproductive parts (h), but decreases with the herbivory of vegetative parts (k) (Fig. 3).

In the non-linear model, the assimilation ability is a convex function of vegetative part size (i.e., $\beta < 1$). In this case, both bang–bang and singular controls are possible. When the optimal phenology follows a bang–bang schedule, τ_b increases as both grazing on reproductive parts (h) and on vegetative parts (k) increases (right and left halves of Fig. 2a and b, respectively). Conversely, when the optimal phenology involves singular control, the timing of the switch (τ_1) from the exclusive investment in vegetative growth to simultaneous investment in both vegetative and reproductive growth is prolonged with increasing h and decreasing k (left and right halves of Fig. 2a and b, respectively). Additionally, τ_2 , or the timing of the switch from simultaneous investment to exclusive investment in reproductive growth, increases with decreasing h and increasing k (left and right halves of Fig. 2a and b, respectively). If we focus on a timing of initiation of exclusive investment toward reproduction (i.e., τ_b or τ_2), this timing is delayed with the increment of grazing on vegetative parts (k) in both the bang–bang and singular control cases.

In the linear model, the flowering time (τ_b) was moved forward when grazing focused on vegetative components of the plant. However, the peak was delayed under identical conditions in the non-linear model, if we define the peak of the flowering season as notable blooming resulting from the exclusive investment in the reproductive components of the plant (i.e., τ_b or τ_2). Therefore, the peak of the flowering season changed in response to grazing intensity, depending on the functional form of assimilation ability to vegetative part size. Accordingly, our results suggest that the

assimilation rate $g(V)$ is a non-linear function of vegetative part size V in plants that were observed the delay of flowering when herbivory increased. However, if plants have experienced only a small variation of grazing pressure during evolutionary period, they could not evolve ability for adaptive response to significant change of grazing pressure. Accordingly, the adaptive phenotypic plasticity should be considered, taking account of a range of variation of grazing pressure during evolutionary time scale.

We considered an annual plant species, where a criterion of plant performance is a size of reproductive part at the end of season. If reproductive part is not grazed ($h = 0$), all investments for reproductive part at each moment are accumulated without loss until the terminal time. The same concept may be applicable on perennial plants, in which investment for reproductive part at each moment (year) is immediately exchanged to reproductive output, by evaluating plant performance as the summation of those reproductions. Tree species are typical perennial plants, where their growths often become very slow or almost stop when they reach the mature size. Such a growth pattern could be considered from two viewpoints; (1) a game for light in the presence of cost for height (Iwasa et al., 1985), and (2) the optimal phenology under herbivory (the presented model). Basically, both are based on balancing between cost and benefit accompanied by plant height. The former considers interactions among individuals, resulting in taller height so as to dominate in competition for light. On the other hand, the latter includes effect of the terminal time, predicting more significant reproduction at older stage near the terminal time. In real nature, both factors may be important determinants of tree life-histories.

Yamauchi and Yamamura (2004) analyzed conditions for grazing optimization using the dynamic optimization method. They considered the dynamics of vegetative and reproductive part sizes of individual plants as well as nutrient concentrations in the soil, thereby revealing the conditions under which grazing pressure promotes plant performance as a result of herbivore-driven nutrient cycle mediation. They concluded that the optimal plant phenology will always follow a bang–bang control, even in the presence of grazing pressure. Our model, however, predicts otherwise. Optimal plant phenology possibly follows singular control, depending on the given conditions. Fortunately, in their numerical analysis, the singular control never appears under the chosen parameters, implying that their results were correct at least under the given settings. Future studies should therefore expand on their model by addressing the possibility of singular schedules of resource allocation, clarifying general conditions for grazing optimization driven by nutrient cycling.

Acknowledgments

We thank the members of the Center for Ecological Research at Kyoto University for their comments

and encouragement. We also appreciate two anonymous reviewers for their helpful comments. This research was partially supported by the Ministry of Education, Culture, Sports, Science, and Technology (MEXT), and the Grant-in-Aid for Scientific Research for N.Y. (No. 14405037), N.F. (No. 14405037) and A.Y. (No. 13640629). This work was also supported by the MEXT Grant for Biodiversity Research of the 21st Century COE (A14).

Appendix A. Optimal phenology with $g(V) = \alpha V^\beta$

A.1. Case 1: The solution including singular control

Assuming that $g(V) = \alpha V^\beta$, we can calculate that $V^* = \{\alpha\beta/(k-h)\}^{1/(1-\beta)}$ from $g'(V^*) = k-h$, which is the size of the vegetative part under singular control.

First, we determine τ_1 , the starting time of the second period, after which both vegetative and reproductive parts grow. In the first period, the plant grows vegetative parts only between V_0 to V^* [$x^*(t) = 0$], following

$$\frac{dV}{dt} = g(V) - kV = \alpha V^\beta - kV \tag{A.1}$$

from Eq. (1b). Eq. (A.1) can be solved as

$$V^{1-\beta} = \frac{1}{k} \{ \alpha - (\alpha - kV_0^{1-\beta}) e^{-k(1-\beta)t} \}, \tag{A.2a}$$

therefore,

$$t = \frac{1}{k(1-\beta)} \ln \left[\frac{\alpha - kV_0^{1-\beta}}{\alpha - kV^{1-\beta}} \right], \tag{A.2b}$$

representing a period for growth from V_0 to V . By substituting $V = V^* = \{\alpha\beta/(k-h)\}^{1/(1-\beta)}$ into Eq. (A.2b), we can obtain the starting time of the second period, within which both vegetative and reproductive parts grow, as follows:

$$\tau_1 = \frac{1}{k(1-\beta)} \ln \left[\frac{\alpha - kV_0^{1-\beta}}{\alpha \{1 - \beta k / (k-h)\}} \right]. \tag{A.3}$$

Next, we determine the starting time of the third period, τ_2 , after which only reproductive part grows. In this period, $x(t) = 1$ and vegetative part size reduces by grazing as follows:

$$\frac{dV}{dt} = -kV, \tag{A.4}$$

from $V^* = \{\alpha\beta/(k-h)\}^{1/(1-\beta)}$. Eq. (A.4) shows that $V = \{\alpha\beta/(k-h)\}^{1/(1-\beta)} \text{Exp}[-k(t-\tau_2)]$ within the third period. Conversely, in this period λ_V must eventually reach zero, following the dynamics

$$\begin{aligned} \frac{d\lambda_V}{dt} &= -g'(V)e^{-h(T-t)} + \lambda_V k = -\alpha\beta V^{\beta-1} e^{-h(T-t)} + \lambda_V k \\ &= -(k-h)e^{(k(1-\beta)+h)t-k(1-\beta)\tau_2-hT} + k\lambda_V. \end{aligned} \tag{A.5}$$

Since $\lambda_V = \text{Exp}[-h(T-t)]$ in the singular solution, $\lambda_V = \text{Exp}[-h(T-\tau_2)]$ at $t = \tau_2$. Accordingly, Eq. (A.5) can

be solved as

$$\lambda_V = \left\{ 1 - \frac{k-h}{\beta k-h} (1 - e^{-(k\beta-h)(t-\tau_2)}) \right\} e^{-h(T-\tau_2)+k(t-\tau_2)}. \tag{A.6}$$

Since λ_V must equal zero at $t = T$, Eq. (A.6) can be rewritten as

$$\tau_2 = T - \frac{1}{k\beta-h} \ln \left[\frac{k-h}{k(1-\beta)} \right]. \tag{A.7}$$

A.2. Case 2: The solution being ‘bang–bang’ control

If the optimal phenology is a bang–bang control, the resource allocation pattern completely switches from vegetative growth to reproductive growth at a given time, τ_b . When $0 < t < \tau_b$, all assimilation products are invested in vegetative parts, and growth dynamics are as follows:

$$\frac{dV}{dt} = g(V) - kV = \alpha V^\beta - kV. \tag{A.8}$$

Accordingly, vegetative part size at $t = \tau_b$ is

$$V_{\tau_b} = \left\{ \frac{\alpha}{k} - \left(\frac{\alpha}{k} - V_0^{1-\beta} \right) e^{-k(1-\beta)\tau_b} \right\}^{1/1-\beta}. \tag{A.9}$$

Conversely, when $\tau_b < t < T$, all assimilation products are invested in reproductive parts, during which time growth dynamics are such that

$$\frac{dR}{dt} = g(V) - hR = \alpha V^\beta - hR, \tag{A.10a}$$

$$\frac{dV}{dt} = -kV. \tag{A.10b}$$

From Eq. (A.10b), we can calculate vegetative part size after τ_b as $V = V_{\tau_b} \text{Exp}[-k(t-\tau_b)]$. Thus, based on Eq. (A.10a), reproductive part size at the end of the season is

$$\begin{aligned} R(T) &= \frac{\alpha}{k\beta-h} \left\{ \frac{\alpha}{k} - \left(\frac{\alpha}{k} - V_0^{1-\beta} \right) e^{-k(1-\beta)\tau_b} \right\}^{\beta/1-\beta} \\ &\quad \times (e^{-h(T-\tau_b)} - e^{-k\beta(T-\tau_b)}). \end{aligned} \tag{A.11}$$

The optimal switching time maximizes Eq. (A.11). Solving $\partial R(T)/\partial \tau_b = 0$, the optimal τ_b must satisfy

$$\begin{aligned} &\left(\frac{\alpha}{\alpha - kV_0^{1-\beta}} e^{k(1-\beta)\tau_b} - 1 \right) \frac{h}{k\beta} \\ &\quad - \frac{\alpha}{\alpha - kV_0^{1-\beta}} e^{(k-h)\tau_b - (k\beta-h)T} + 1 = 0. \end{aligned} \tag{A.12}$$

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