

Optimal allocation strategies of perennial plants

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Abstract—In this paper we propose a novel optimal allocation model for perennial plants. We consider not only favorable for photosynthesis periods, but analyze the whole life of a perennial plant. This provides more information about strategies of a plant during transitions between favorable and unfavorable seasons. One of predictions of our model is that a plant can begin re-establishment of vegetative tissues some time before the beginning of the favorable conditions, so as to come into the better environmental conditions with a certain amount of already developed vegetative tissues.

In the second part of the paper we extend the model by assuming that a plant controls not only a distribution of carbohydrates, but also a size of a seed. We provide sufficient conditions under which the optimal strategy for a plant is to produce as much seeds as possible. These results can be applied, in particular, for colonizing species and plants living in open environments.

Keywords: biological systems; optimal control; modeling; perennial plants

I. INTRODUCTION

The pioneering work [1] gave rise to a new class of mathematical models of plants, based on the methods of optimal control theory. In these models it is assumed that a plant can control itself in order to maximize its fitness to environment, often identified with the mass of seeds produced by a plant during its life.

The first models have been devoted to the development of annual plants. In them it is assumed that a plant consists of a number of compartments, at least of a vegetative compartment (leaves, roots, stems) and reproductive compartment (seeds and auxiliary tissues), but also can include storage and defensive tissues. The basic model of this type [2] results in a bang-bang transition from allocation to vegetative tissues to allocation into seeds.

This model of an annual plant has been extended in many directions. In particular, in [3] a model with multiple vegetative compartments has been analyzed, in works [4], [5] a model with additional physiological constraints has been considered that results in periods of mixed growth (where both vegetative and reproductive parts of a plant grow simultaneously). The optimal allocation strategies in stochastic environments have been investigated in particular in [6]. Allocation to defensive tissues was encountered, to cite a few, in [7], [8]. The overview of the early works in

this field is provided in a paper [9]. For general overview of the resource allocation in plants see [10] and [11].

In contrast to annual plants less attention has been devoted to the modeling of optimal phenology of perennials. Usually behavior of perennials is modeled in the following way [12], [13], [14]: the life-time of a perennial plant is divided into discrete seasons, which environmental conditions are favorable to the photosynthesis. The model of a plant in every season is continuous and is treated with the methods used in annual plant models. To model the behavior of a plant between seasons (when a weather is unfavorable) some simple transition rules are used that show which parts of compartments are saved during the season and which are not. The solution of such problems is divided into two parts: firstly the model on one season is solved using Pontryagin's Maximum Principle (see, e.g. [15]) and then one seeks a solution of the whole model using dynamic programming method.

Although these models provide interesting qualitative results of behavior of perennial plants, they have an important disadvantage: a subtle qualitative behavior of a plant within the season contrasts to the simple jump from the end of one season to the beginning of the next one.

In this paper we propose a continuous-time model of a perennial plant. This allows us to describe more precisely the dynamics of a plant during seasons with unfavorable for photosynthesis environmental conditions and to avoid the introduction of additional parameters for description of jumps between seasons. In particular one of predictions of the model is that the plant begins to generate the vegetative tissues not at the time when the environment conditions are favorable for photosynthesis, but some time before, so as to come into the suitable period with developed vegetative tissues.

In the second part of the paper we investigate a trade-off between size and number of seeds. A lot of attention is devoted to this topic in the scientific literature. The basic model has been proposed in a seminal work [16], where it was assumed that the fitness of the plant is equal to the sum of the fitnesses of the descendants. Since that this model has been generalized in many directions (for a survey see [17]). In this framework the optimal size is sought depending on the properties of the fitness function. This makes possible quite general treatment of size-number trade-offs, but the questions how to formalize the dependency of the fitness on size and number of seeds and how to find the properties of the function that characterizes this dependency, remain unsolved.

Our aim is to investigate the trade-offs between number

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and size of a seed in the context of the optimal allocation models. Within this framework the fitness is properly formalized, and we can investigate the optimal size of a seed depending on the properties of photosynthetic rate function, and other physiological parameters of a plant that are more distinct criteria than the abstract fitness. We provide the analysis for the model developed in Section II of this paper, but the results are valid also for a number of other optimal allocation models.

We prove that, according to our model of a plant, if the photosynthetic rate function is concave (that is, if rate of photosynthesis per unit mass decays with increase of a size of a plant), then the seeds have to be as small as possible. This behavior is common in particular for the colonizing species (see Section III-B).

The outline of the article is as follows: in Section II-A we introduce the model of a perennial plant. In Section II-B we provide its analysis, using Pontryagin's Maximum Principle. Then, in Section II-C we summarize the results of the model, provide a general scheme of plant development and consider some special cases (annual and monocarpic plants).

In Section III we consider a trade-off between size and number of seeds. The results of the paper are discussed in the Section III-B.

II. OPTIMAL ALLOCATION MODEL

A. Model description

Usually it is assumed that all the allocated photosynthate is immediately used for construction of the tissues. In the models taking into account a presence of a storage compartment a plant can also allocate the resources from the storage with some maximal rate (depending on the mass of the storage).

Such a method ignores that a photosynthate is not immediately allocated to certain structures, but exists for some time in a free state. We are going to take this effect into account and assume that there exists an intermediate stage, when the carbohydrates have already been photosynthesized, but have not been permanently allocated to a given structure yet.

Let a plant consist of three parts: vegetative compartment, reproductive compartment and nonstructural carbohydrates (free glucose, starch etc.).

Let $x_1(t)$ be the mass of the vegetative compartment at time t , $x_2(t)$ be the mass of the reproductive compartment at time t , and $x_3(t)$ be the mass of nonstructural carbohydrates at time t .

We model dynamics of a plant by the following equations:

$$\begin{aligned} \dot{x}_1 &= v_1(t)g(x_3) - \mu(t)x_1, \\ \dot{x}_2 &= (v(t) - v_1(t))g(x_3), \\ \dot{x}_3 &= \zeta(t)f(x_1) - v(t)g(x_3) - \omega(t)x_3. \end{aligned} \quad (1)$$

Here $f(x_1)$ shows the rate of photosynthesis of the plant with the vegetative mass x_1 in the optimal environmental conditions, and $g(x_3)$ - the maximal rate of allocation of nonstructural carbohydrates, if their mass is x_3 . It is natural to assume that f and g are monotonically increasing and $f(0) = g(0) = 0$.

The influence of a climate is modeled by three functions: $\zeta : [0, T] \rightarrow [0, 1]$ and $\mu, \omega : [0, T] \rightarrow [0, \infty)$.

- $\zeta(t)$ shows the dependence of the rate of photosynthesis on the climate ($\zeta(t) = 0$ if at time t no photosynthesis is possible).
- $\mu(t)$ is the deconstruction rate of vegetative tissues per unit mass at time t .
- $\omega(t)$ is the deconstruction rate due to external factors (spoilage, grazing by animals etc.) of the storage parts per unit mass at time t .

Note that photosynthesized carbohydrates firstly enlarge the mass of nonstructural carbohydrates.

We assume that a plant can control the total allocation rate with the control $v(t) \in [0, 1]$, and allocation rate to the vegetative tissues $v_1(t) \in [0, v(t)]$, consequently the allocation rate to reproductive tissues at time t is $v_2(t) = v(t) - v_1(t)$.

At the moment $t = 0$ a mass of the seed and all its compartments is given a priori (the question of optimal mass of a seed will be considered in Section III):

$$x_i(0) = x_i^0, \quad i = 1, 2, 3. \quad (2)$$

The seed dormancy is modeled as an ability of a plant to choose the time of germination $t_0 \in [0, T]$. For simplicity we assume that a seed cannot spoil, and it does not use any resources for life-sustaining activities, thus:

$$x_i(t_0) = x_i(0) = x_i^0, \quad i = 1, 2, 3. \quad (3)$$

To model a mortality of a parental plant, we introduce the function $\tilde{L} : [0, T] \rightarrow [0, 1]$. $\tilde{L}(t)$ shows the probability of survival of a parental plant to the age of t .

Remark 1: We assume in this paper that mortality is only age-dependent, and does not depend on the time and size of a plant.

Since the time of germination may vary, it makes sense to introduce the function L_{t_0} , defined by the relation $L_{t_0}(t) = \tilde{L}(t_0 - t)$. In what follows we write for short $L = L_{t_0}$.

It is natural to assume that L is a non-increasing function and that $L(t) > 0$ for all $t \in [0, T)$. Really, if $L(t) \equiv 0$ on $[T - \varepsilon, T]$ for some $\varepsilon > 0$, then this means, that already at the moment $T - \varepsilon$ a plant will be dead, and we can consider the optimal control problem on the time-period $[0, T - \varepsilon]$.

We assume that a plant maximizes the expectation of a total yield of seeds over the period:

$$\int_{t_0}^T L(s)\dot{x}_2(s)ds = \int_{t_0}^T L(s)(v(s) - v_1(s))g(x_3(s))ds \rightarrow \max. \quad (4)$$

To achieve this aim, a plant may choose an appropriate germination time t_0 and controls v and v_1 defined on $[t_0, T]$.

We assume that the functions in the right hand side of equations (1) are smooth enough to guarantee existence and uniqueness of solutions of (1). Also we assume that the system (1) is forward complete, that is, for all initial conditions and all admissible controls the solution of (1) exists for all time. From the biological viewpoint it means that it is impossible to achieve endless yield in finite time.

Also we assume, that a solution of the optimal control problem exists (1), (2), (4) in the class of piecewise-continuous controls. In particular this excludes the Fuller's phenomenon (bang-bang controls with infinite number of switches on the finite interval) [23]. For applications of our model these assumptions are not restrictive.

B. Model analysis

For analysis of (1) we exploit Pontryagin's Maximum Principle (see, e.g. [15]). Note that we can drop the equation for x_2 , since the other equations of (1) as well as the cost functional (4) after substitution of \dot{x}_2 do not depend on x_2 .

The Hamiltonian of (1), (4) is defined by:

$$H = p_1(t)(v_1(t)g(x_3(t)) - \mu(t)x_1(t)) + \lambda_0 L(t)(v(t) - v_1(t))g(x_3(t)) + p_3(t)(\zeta(t)f(x_1(t)) - v(t)g(x_3(t)) - \omega(t)x_3(t)). \quad (5)$$

Here p_1, p_3 are so-called adjoint functions and $\lambda_0 \geq 0$. The equations determining their dynamics will be given later.

To simplify the notation, we will frequently write in equations simply p_1, x_2 , etc. instead of $p_1(t), x_2(t)$, if there arises no ambiguity.

We rewrite expression (5) in a more suitable form

$$H = p_3 \zeta(t) f(x_1) - p_1 \mu(t) x_1 + g(x_3)(v_1(t)(p_1 - \lambda_0 L(t)) + v(t)(\lambda_0 L(t) - p_3)) - p_3 \omega(t) x_3. \quad (6)$$

Equations for the adjoint function p are as follows

$$\begin{aligned} \dot{p}_1 &= p_1 \mu(t) - p_3 \zeta(t) \frac{\partial f}{\partial x_1}(x_1), \\ \dot{p}_3 &= -\frac{\partial g}{\partial x_3}(x_3)(v_1(p_1 - \lambda_0 L(t)) + v(\lambda_0 L(t) - p_3)) + p_3 \omega(t). \end{aligned} \quad (7)$$

The corresponding boundary conditions are

$$p_1(T) = p_3(T) = 0. \quad (8)$$

If $\lambda_0 = 0$, then from (8) and (7) we obtain that $p_i \equiv 0$ on $[t_0, T]$, from which it follows that all the controls are possible. Let $\lambda_0 > 0$. We can take in this case $\lambda_0 = 1$.

To obtain the values of v, v_1 , we solve the problem

$$H \rightarrow \max, \quad 0 \leq v \leq 1, \quad 0 \leq v_1 \leq v.$$

It is not hard to check that its solution is given by

1) If $L(t) - p_3(t) > 0$, then $v(t) = 1$, and

$$v_1(t) = \begin{cases} v(t) & \text{if } p_1(t) - L(t) > 0, \\ 0 & \text{if } p_1(t) - L(t) < 0, \\ \in [0, v] & \text{if } p_1(t) - L(t) = 0. \end{cases} \quad (9)$$

2) If $L(t) - p_3(t) = 0$, then

$$\begin{aligned} p_1(t) - L(t) > 0 &\Rightarrow v(t) = 1, v_1(t) = v(t) \\ p_1(t) - L(t) = 0 &\Rightarrow v(t), v_1(t) - \text{EAC} \\ p_1(t) - L(t) < 0 &\Rightarrow v(t) - \text{EAC}, v_1(t) = 0 \end{aligned} \quad (10)$$

3) If $L(t) - p_3(t) < 0$, then

- if $p_1(t) - L(t) \leq 0$ then $v(t) = v_1(t) = 0$.
- if $p_1(t) - L(t) > 0$ then

$$\begin{aligned} p_1(t) - p_3(t) < 0 &\Rightarrow v(t) = v_1(t) = 0 \\ p_1(t) - p_3(t) = 0 &\Rightarrow v(t) - \text{EAC}, v_1(t) = v(t) \\ p_1(t) - p_3(t) > 0 &\Rightarrow v(t) = v_1(t) = 1 \end{aligned} \quad (11)$$

Here the abbreviation EAC stands for "every admissible control".

We introduce three main periods characterized by different values of controls:

(V) Vegetative period: $p_1(t) > \max\{L(t), p_3(t)\}$. In this case $v(t) = v_1(t) = 1$, that is the vegetative parts are being constructed with the maximal rate.

Equations (7) in the vegetative period take form

$$\begin{aligned} \dot{p}_1 &= p_1(t)\mu(t) - p_3(t)\zeta(t)\frac{\partial f}{\partial x_1}(x_1(t)), \\ \dot{p}_3 &= -\frac{\partial g}{\partial x_3}(x_3(t))(p_1(t) - p_3(t)) + \omega(t)p_3. \end{aligned} \quad (12)$$

(R) Reproductive period: $L(t) > \max\{p_1(t), p_3(t)\}$. In this case $v(t) = 1, v_1(t) = 0$ and reproductive tissues are being constructed with the maximal rate.

Equations (7) within this period take the form

$$\begin{aligned} \dot{p}_1 &= p_1(t)\mu(t) - p_3(t)\zeta(t)\frac{\partial f}{\partial x_1}(x_1(t)), \\ \dot{p}_3 &= -\frac{\partial g}{\partial x_3}(x_3(t))(L(t) - p_3(t)) + \omega(t)p_3(t). \end{aligned} \quad (13)$$

(S) Storage period: $p_3(t) > \max\{p_1(t), L(t)\}$. In this case $v(t) = v_1(t) = 0$ and all allocated energy goes to storage.

The corresponding equations (7) take the form

$$\begin{aligned} \dot{p}_1 &= p_1(t)\mu(t) - p_3(t)\zeta(t)\frac{\partial f}{\partial x_1}(x_1(t)), \\ \dot{p}_3 &= \omega(t)p_3. \end{aligned} \quad (14)$$

We are going to analyze these periods more deeply and find out in what order these periods can arise in a life of a plant. To this end we investigate equations (7) from the end of the life of a plant.

Controls v and v_1 maximize the value of $(v_1(p_1 - L(t)) + v(L(t) - p_3))$, therefore for optimal v, v_1 it holds that

$$(v_1(p_1 - L(t)) + v(L(t) - p_3)) \geq 0. \quad (15)$$

Note that in case, when $\omega(t) \equiv 0$ (that is, if storage parts cannot be destructed due to external factors) this inequality and monotonicity of g imply that p_3 is a non-increasing function on $[t_0, T]$.

Let us analyze the behavior of Lagrange multipliers p_i and values of controls at the neighborhood of the time T .

If the last period would be vegetative, then the equations, governing the dynamics of p_1, p_3 would be (12). Due to well-posedness of (12), and since the conditions (8) hold, we obtain, that $p_1(t) \equiv 0$ and $p_3(t) \equiv 0$ in the neighborhood of time T . Since $L(t) > 0$ for all $t < T$, we come to a contradiction with an assumption that the last period is vegetative. Analogously one can show that also the storage period cannot be the last period of a plant's life. This proves, that *the last period of a plant development is a reproductive period*.

From equations (15) and (7) using monotonicity of g and inequality $\omega \geq 0$ we have that if for some $\tau \in [t_0, T]$ $p_3(\tau) < 0$, then $p_3(t) < 0$ for all $t \in [\tau, T]$, which contradicts to (8). Thus, $p_3 \geq 0$ on $[t_0, T]$. Analogously one can prove that $p_1 \geq 0$ on $[t_0, T]$.

Now let us find out, what period can precede to the reproductive period. According to equations (14) and due to $\omega \geq 0$

we see, that p_3 cannot decrease during the reproductive period. Since L is a nonincreasing function, we see, that starting in a reproductive period ($p_3 > L$) we cannot obtain $p_3 < L$ at the end of this period. This tells us that *before reproduction period the storage period is impossible*.

If the climate conditions (functions μ and ζ) are such that $p_1(t) = L(t)$ for all $t \in [t_s, t_1]$ for some $t_s < t_1$, then according to (9) a plant can have the period with mixed control $v_1 \in [0, v]$ for $t \in [t_s, t_1]$. Although this possibility cannot be excluded in general, but such mixed controls can arise only due to very specific climate conditions and we do not separate it as a special period of plant life.

If $p_1(t) - L(t)$ is increasing from the left at $t = t_1$, then one can distinguish one more reproductive period $[t_1 - s, t_1]$ for some $s > 0$. Throughout this paper we follow the agreement to combine all such periods together with stages with mixed controls between these periods into one reproductive period.

Let $p_1(t) - L(t)$ be decreasing. Then for some time interval preceding to the reproductive period we have $p_1(t) > L(t) > p_3(t)$ and therefore on this time interval a plant has a vegetative period. We call it period V.1, in contrast to period V.2 characterized by relation $p_1(t) > p_3(t) > L(t)$ (this distinction will be useful for monocarpic plants).

There are 2 possibilities for the plant behavior before period V.1: either it will have one more R-period (if p_1 decreases lower than $L(t)$ while it remains true that $p_3 < L(t)$), or it will exist $t_2 < t_1$: $p_3(t_2) = L(t_2)$. As mentioned before, we neglect the possibility of mixed controls and consider the case $\dot{p}_3(t_2) < 0$.

In this case period V.2 characterized by $p_1(t) > p_3(t) > L(t)$ precedes the period V.1. Although the allocation pattern is the same in both periods V.1 and V.2, the distinction between these periods is useful for the study of phenology of monocarpic plants. To understand this difference let us consider the case, when the nonstructural carbohydrates cannot be deconstructed due to external factors (i.e. $\omega \equiv 0$, which implies, as was mentioned earlier, that p_3 is non-increasing) and the probability of survival remains constant throughout the whole period ($L \equiv const$). This implies that before period V.2 the reproduction periods are not possible ($p_3 > L$) and consequently *the plant exploits monocarpic strategy*.

In the general case, when $\omega \neq 0$ both periods R and S can precede the V-period, or all the previous life of a plant can consist of one vegetative period. In the first case a plant possesses one more reproduction period, which has been already analyzed. If before vegetative period there is no other period, then the *plant is annual*.

Let now the S-period precedes to the V-period. Then there exist t_4, t_3 : $t_4 < t_3 < t_2$, such that p_1 increases on $[t_4, t_3]$ (due to the unfavorable climate conditions) and $p_1(t_4) = p_3(t_4)$. We separate period between t_4 and t_3 in the season V.2.1 ($p_1 > p_3 > L(t)$, but p_1 increasing), which distinctive feature is that *although the climate conditions are not comfortable for photosynthesis a plant anyway allocates some part of stored resources to the construction of the vegetative tissues, so as to come into the better conditions with a certain amount*

of already developed vegetative mass.

Now let there exist some r : $p_1(t) < p_3(t)$ for all $t \in [r, t_4)$. Then a plant enters a storage period.

If the climate conditions are unfavorable for all $t < t_4$, that is, $p_1(t) < p_3(t)$ for all $t \in [0, t_4)$, then the first period of time is only the storage of allocated photosynthate (this is hardly possible because a seed has a possibility to stay this period in dormancy). If it is not the case, then there exist some moments $t_6, t_5, t_6 < t_5 < t_4$, such that p_1 is decreasing on $[t_6, t_5]$ and $p_1(t_6) = p_3(t_6)$.

We separate the period (t_5, t_4) , which we call period S.1 (when the climate conditions are disadvantageous and all the allocated material is stored), and time-span (t_6, t_5) called period S.2 (when the climate conditions are kindly, but all the allocated material is anyway stored for a preparation to the unfavorable climate conditions).

Both reproductive and vegetative periods can precede to the storage period. It depends on the climate conditions and values of x^0 .

We consider in the next subsection the case, when the first period after germination is a vegetative.

C. Predictions of the model

In this section we conclude our investigations. The development of the plant according to the model (1) consists of 3 main periods that can be further subdivided into subperiods and that can follow each other as depicted in the Figure 1.

These periods are:

- D - Dormancy.
 - V - Vegetative period.
 - S.2 - Preparing for the unfavorable climate conditions.
 - S.1 - Life in unfavorable climate conditions.
 - V.2 - Vegetative period, which starts after storage period.
- In the beginning of this period, a plant starts the allocation to vegetative tissues as a preparation for the climate conditions favorable for the photosynthesis.
- V.1 Allocation to vegetative tissues before reproduction.
 - R - Reproduction.

Important special cases of this scheme are:

- 1) Annual plant with multiple reproduction periods: see Figure 2 (period V we identify with V.1 for simplicity). Multiple reproduction periods appear because of losses of vegetative mass due to external factors that are modeled by the function μ . This particular case has been analyzed in the early work [18]. If $\mu \equiv 0$, then the multiple reproductive periods for annual plants are not possible.
- 2) Monocarpic plants. Sufficient (but not necessary) condition for a plant to be monocarpic (in case where there is no mortality) is negligibility of ω (in particular, if $\omega \equiv 0$), in other words, the mass of storage cannot decrease due to the external factors. In this case transitions $R \rightarrow S.2$ and $V.1 \rightarrow V.2$ are not possible, see Figure 3.

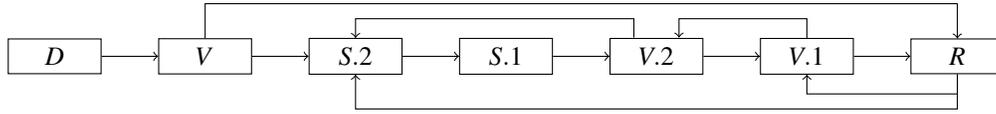


Fig. 1. Stages of perennial plant development

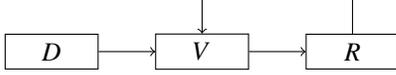


Fig. 2. Life-stages of annual plants

III. OPTIMIZATION OF THE SEED MASS

In the previous sections we have defined fitness of a plant as an expectation of the mass of reproductive tissues produced by the plant during its life. To maximize the fitness, a plant controls the allocation of photosynthate.

However, it is well-known, that the fitness depends (for plants that propagate exclusively through seeds) crucially on the quantity (and size) of seeds, that a plant produces. Current models of optimal allocation do not provide this information, and a mass of a seed is treated as an external parameter. But essentially a choice of a mass of the seed is an additional control, which a plant can use in order to allocate the photosynthate efficiently. Therefore in the next section we extend the model from the previous section, giving to a plant an additional control over the mass of a seed.

A. Modeling and Analysis

Let $y_0 = (y_1^0, y_2^0, y_3^0)$ be the total mass of the seeds (the vector consisting of the masses of three components of a plant within seeds) that has to be divided between a seeds, $a \in [1, \infty)$ and a can be either natural or real number.

We assume that the mass of each seed is $s = \frac{y_0}{a}$.

We model the dynamics of a plant as follows

$$\begin{aligned} \dot{x}_1 &= v_1(t)g(x_3) - \mu(t)x_1, \\ \dot{x}_2 &= (v(t) - v_1(t))g(x_3), \\ \dot{x}_3 &= \zeta(t)f(x_1) - v(t)g(x_3) - \omega(t)x_3, \\ x(0) &= \frac{1}{a}y_0. \end{aligned} \quad (16)$$

Here $x(0) = (x_1(0), x_2(0), x_3(0))$.

The aim of a plant we define as maximization of the total mass of reproductive tissues produced by all direct descendants:

$$\max_{0 \leq v(t) \leq 1, 0 \leq v_1(t) \leq v(t), a \in [1, \infty)} Q_a = a\xi \int_{t_0}^T L(s)\dot{x}_2(s)ds, \quad (17)$$

where a constant ξ shows the percentage of the seeds, which germinate to the total quantity of produced seeds. We assume, that ξ doesn't depend on the size of a seed.

Important special case is when f and g are concave functions, i.e., the rate of photosynthesis and maximal speed of chemical reactions in a plant are saturated with the growth

of the mass of a plant (due to self-shading of leaves, nutrient depletion in the soil etc.). We have the following result:

Proposition 1: Consider an optimal control problem (16), (17). Let $f, g : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ be concave, $f(0) = g(0) = 0$, $a \in [1, \infty)$. Then Q_a increases, when a increases.

Proof: The problem (16), (17) can be written in equivalent form, using new variables $y_i(t) := ax_i(t)$, $i = 1, 2, 3$. Then we have:

$$\begin{aligned} \dot{y}_1 &= v_1(t)ag\left(\frac{y_3}{a}\right) - \mu(t)y_1, \\ \dot{y}_2 &= (v(t) - v_1(t))ag\left(\frac{y_3}{a}\right), \\ \dot{y}_3 &= \zeta(t)af\left(\frac{y_1}{a}\right) - v(t)ag\left(\frac{y_3}{a}\right) - \omega(t)y_3, \\ y(0) &= y_0. \end{aligned} \quad (18)$$

The corresponding maximum problem is:

$$\max_{0 \leq v(t) \leq 1, 0 \leq v_1(t) \leq v(t), a \in [1, \infty)} Q_a = \xi \int_{t_0}^T L(s)\dot{y}_2(s)ds. \quad (19)$$

Now the problem is similar to (1), (4), but with $af(\frac{y_1}{a})$ and $ag(\frac{y_3}{a})$ instead of $f(x_1)$ and $g(x_3)$.

Using concavity we have: $f(\frac{y_1}{a}) = f(\frac{1}{a}y_1 + \frac{a-1}{a} \cdot 0) \geq \frac{1}{a}f(y_1) + \frac{a-1}{a}f(0) = \frac{1}{a}f(y_1)$.

Thus, for every $y_1(t) \geq 0$, $a \geq 1$ it holds $af(\frac{y_1(t)}{a}) \geq f(y_1(t))$ and therefore $af(\frac{y_1(t)}{a})$ and $ag(\frac{y_3(t)}{a})$ are nondecreasing in a and $\sup_{a \in [1, \infty)} af(\frac{y_1(t)}{a})$ and $\sup_{a \in [1, \infty)} ag(\frac{y_3(t)}{a})$ yields, when $a \rightarrow \infty$.

Define the optimal trajectories of the problem (16), (17) for a fixed a as $y(\cdot)$. Now take arbitrary $n > a$ and consider a system

$$\begin{aligned} \dot{y}_1 &= v_1(t)ag\left(\frac{y_3}{a}\right) - \mu(t)y_1, \\ \dot{y}_2 &= (v(t) - v_1(t))ag\left(\frac{y_3}{a}\right), \\ \dot{y}_3 &= \zeta(t)nf\left(\frac{y_1}{n}\right) - v(t)ag\left(\frac{y_3}{a}\right) - \omega(t)y_3, \\ y(0) &= y_0. \end{aligned} \quad (20)$$

The solution of this system at time t subject to optimality condition (18) we denote $\hat{y}(t)$. If $\zeta(0) > 0$, then from $nf(\frac{y_1(t)}{n}) > af(\frac{y_1(t)}{a})$ we have that $\hat{y}_3(0) > y_3(0, a)$ and therefore there exists $t^* > 0$: $\hat{y}_3(t) > y_3(t, a) \forall t \in [0, t^*)$. Hence $\hat{y}_3(t) > y_3(t, a)$ and $ag(\frac{\hat{y}_3(t)}{a}) > ag(\frac{y_3(t, a)}{a})$ for $t \in (0, t^*)$.

Let v and v_1 be the optimal controls for the system (18). There exist controls $0 \leq \hat{v} \leq v$, $0 \leq \hat{v}_1 \leq v_1$ for the system (20), such that $\hat{v}(t)ag(\frac{\hat{y}_3(t)}{a}) = v(t)ag(\frac{y_3(t, a)}{a})$ and $\hat{v}_1(t)ag(\frac{\hat{y}_3(t)}{a}) = v_1(t)ag(\frac{y_3(t, a)}{a})$.

Consequently, $\hat{y}_i(t) = y_i(t, a)$, $t \in [0, t^*)$, $i = 1, 2$. Constructing \hat{v} , \hat{v}_1 for all $t \in [0, T]$, we obtain that $\hat{y}_2(T) = y_2(T, a)$ and thus for a given a and $n > a$ the optimal trajectory of a system (20) produces no less output than the best trajectory of (18).

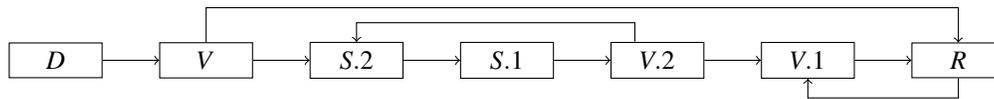


Fig. 3. Life-stages of monocarpics

Analogously, the output of the following system is not less than that of the system (20):

$$\begin{aligned} \dot{y}_1 &= v_1(t)ng\left(\frac{y_3}{n}\right) - \mu(t)y_1, \\ \dot{y}_2 &= (v(t) - v_1(t))ng\left(\frac{y_3}{n}\right), \\ \dot{y}_3 &= \zeta(t)nf\left(\frac{y_1}{n}\right) - v(t)ng\left(\frac{y_3}{n}\right) - \omega(t)y_3, \\ y(0) &= y_0. \end{aligned} \quad (21)$$

Hence Q_a is nondecreasing in a . ■

It follows from the previous proposition that in the case, when f and g are concave the best strategy for a plant is to produce as much seeds as possible.

Remark 2: Similar argument shows that for convex functions f , g the optimal mass of the seed has to be as large as possible (without additional restrictions on quantity of seeds $a = 1$).

Remark 3: Note that if both f and g are linear, then from (18) it follows that the yield of a plant does not depend on the mass of the seeds.

B. Discussion of results

We see that the optimal size of a seed depends crucially on the form of the functions f and g . For concave functions that are often used to take into account self-shading, boundedness of resources etc. (see e.g. [13]) we have proved that according to our model seeds have to be as small as possible.

For plants living in open environments and for species occupying early phases in succession (colonizing species) the assumption of concavity is not an oversimplification. The behavior that our model predicts, namely that the optimal strategy is to produce a vast amount of small seeds is common for these species [19].

However, in closed and shady environments, under mineral shortage, or if there is a strong competition with the established vegetation, the rate of photosynthesis per unit mass can increase with increasing of a mass of a plant, that is, the function f is convex on some $[0, p]$, $p > 0$ and the seeds cannot be too small. These predictions are, in general, in accordance with field data [20], [21], but see [22].

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