Optimal allocation patterns and optimal seed mass of a perennial plant

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Outline

Basic ideas

- A plant is an autonomously controlled dynamical system.
- A plant consists of n compartments:
  1. vegetative compartment (roots, shoots etc.)
  2. reproductive compartment
  3. storage compartment
  4. ...
- A fitness is formalized in a certain way
- A plant aims to maximize fitness by using admissible controls.

A basic OAM of an annual plant

State variables of a system

- x_1 is a mass of a vegetative compartment
- x_2 is a mass of a reproductive compartment

A simple annual plant model

$$\begin{cases} \dot{x}_1(t) = (1 - u(t))f(x_1(t)), \\ \dot{x}_2(t) = u(t)f(x_1(t)), \\ x_1(0) = x_0, \\ x_2(0) = 0, \end{cases}$$

$$\max_{0 \le u(t) \le 1} Q = x_2(T).$$

Tool for analysis of a problem

Pontryagin's maximum principle

OAM of perennial plants

Common approach

- The whole life is divided into discrete periods with favorable conditions
- Within the period the OA problem is solved via PMP
- Then OA problem is solved for all life via dynamic programming

- W. M. Schaffer. The application of optimal control theory to the general life history problem. The American Naturalist 121 (3) (1983) 418–431.
- Y. Iwasa, D. Cohen. Optimal growth schedule of a perennial plant, The American Naturalist 133 (4) (1989) 480–505.
- A. Pugliese, J. Kozłowski. Optimal patterns of growth and reproduction for perennial plants with persisting or not persisting vegetative parts, Evolutionary Ecology 4 (1990) 75–89.

Motivation

In the above models annuality and perenniality are assumptions:

1. The annual plants do not have storage
2. Perennial plants "jump" from the end of the season n to the beginning of the season $n + 1$.

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We want to obtain more precise description of life-strategies during unfavourable periods

Continuous-time model of a perennial plant

Compartments of a plant

- $x_1(t)$ is a mass of vegetative compartment at time t,
- $x_2(t)$ is a mass of reproductive compartment at time t,
- $x_3(t)$ is a mass of nonstructural carbohydrates at time t.

Available controls

- $v(t) \in [0, 1]$ - total allocation rate
- $v_1(t) \in [0, v(t)]$ - allocation rate to vegetative tissues

Equations, describing a development of a plant

$$\begin{cases} \dot{x}_1 = v_1(t)g(x_3) - \mu(t)x_1, \\ \dot{x}_2 = (v(t) - v_1(t))g(x_3), \\ \dot{x}_3 = \nu(t)f(x_1) - v(t)g(x_3) - \omega(t)x_3. \end{cases}$$

Goal: Maximization of a fitness

$$\max_{0 \le v(t) \le 1,\ 0 \le v_1(t) \le v(t)} = x_2(T).$$

Stages of perennial plant development

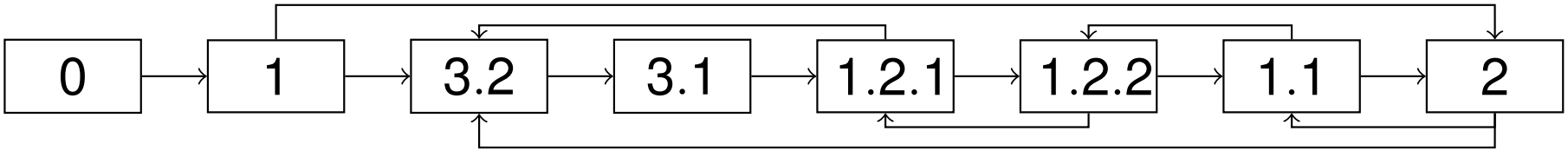

Figure : Stages of perennial plant development

- 0 - Dormancy.
- 1 - Vegetative period.
- 3.2 - Preparing for the unfavorable climate conditions.
- 3.1 - Life in unfavorable climate conditions.
- 1.2.1 - Allocation to vegetative tissues as a preparation for the climate conditions favorable for the photosynthesis.
- 1.2.2 - A vegetative period that is important for the characterization of monocarpic plants (see below).
- 1.1 Allocation to vegetative tissues before reproduction.
- 2 - Reproduction.

Annual plant with multiple reproduction periods

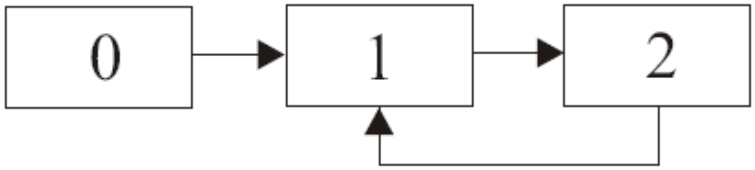

Figure : Life-stages of annual plants

Causes of occurring of multiple reproduction periods

Multiple reproduction periods appear due to losses of vegetative mass, which are caused by external factors (modeled by $\mu(\cdot)$).
This particular case has been analyzed in

- D. King, J. Roughgarden, Multiple switches between vegetative and reproductive growth in annual plants, Theoretical Population Biology 21 (2) (1982) 194 – 204.

If $\mu \equiv 0$, then the multiple reproductive periods for annual plants are not possible.

Monocarpic plants

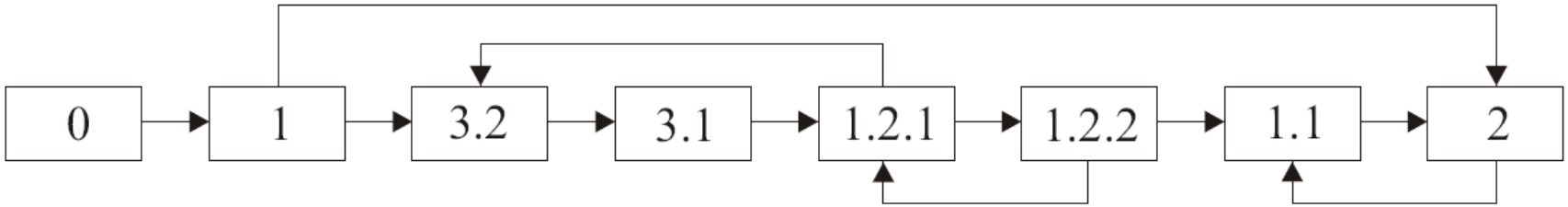

Figure : Life-stages of monocaprics

Transition 1.1 $\rightarrow$ 1.2 (= 1.2.1 + 1.2.2) is not possible.

Sufficient condition ensuring monocarpicity

Sufficient (but not necessary) condition for a plant to be monocarpic is negligibility of ω, in other words, the mass of storage cannot decrease due to the external factors.

Model of size/number trade-offs

Main assumptions

- There is a number of resources, which a parent should divide between its descendants.
- The fitness of a parent depends on the fitness of the number and quality of the offspring.
- The more resources are invested into an offspring, the greater is its fitness.

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Goals

- How many descendants should be produced?
- How much resources should be invested into the single offspring?

- C. C. Smith, S. D. Fretwell, The Optimal Balance between Size and Number of Offspring, The American Naturalist 108 (962) (1974) 499–506.

Optimization of a mass of a seed

Main assumptions

- Fitness of the parent is equal to the sum of fitnesses of all its descendants
- The probability of germination k does not depend on the size of the seed.

Equations, governing the dynamics of a plant

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

Maximization of a fitness

$$\max_{0 \le v(t) \le 1,\ 0 \le v_1(t) \le v(t),\ a \in [1,\infty)} Q_a = kax_2(T).$$

Concavity of photosynthetic rate

Theorem

Let f, g be concave functions, $f(0) = g(0) = 0$. Then a plant should produce as much seeds as possible.

The sense of concavity

Efficiency of photosynthesis declines with the growth of a plant

- Self-shading
- boundedness of resources
- etc.

Some consequences

- colonizing species
- plants, living in open environments

should have small seeds

Convexity of photosynthetic rate

Theorem

Let f, g be convex functions, $f(0) = g(0) = 0$. Then the size of the seeds should be as large seeds as possible.

Above theorem implies:

- In the closed and shady environments
- under mineral shortage
- if there is a strong competition with the established vegetation

The size of seeds cannot be too small

If f and g are linear functions then all partition strategies are equivalent!

Applications to life strategies of the animals

For animals the fitness of the parent may not be equal to the sum of the fitnesses of the descendants

- G. P. Brown, R. Shine, Beyond size-number trade-offs: clutch size as a maternal effect., Philosophical transactions of the Royal Society of London. Series B, Biological sciences 364 (1520) (2009) 1097–1106.

Conclusion

- A continuous-time OAM of a perennial plant has been developed
- We have studied the special cases of
  1. Monocarpic plants
  2. Annual plant with multiple reproduction periods
- Within OAM framework size-number (of seeds) trade-offs have been analyzed

Where the length of the life comes from?

Why a plant doesn't grow to infinity?

1. Due to mortality?
2. Due to physiological restrictions?
3. Or due to other factors?

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Possibilities to resolve this problem

1. Choose another definition of a fitness
2. To pass into populational optimal allocation models.

Introduction of plants into new habitat

Equations in the native environment

$$\begin{cases} \dot{x}_1 = v_1(t)g(x_3) - \mu(t)x_1, \\ \dot{x}_2 = (v(t) - v_1(t))g(x_3), \\ \dot{x}_3 = \nu(t)f(x_1) - v(t)g(x_3) - \omega(t)x_3. \end{cases}$$

Central assumption of OAM

A plant "knows" its dynamical equations as well as all parameters of environment during its whole life

Goal: Maximization of a fitness

$$\max_{0 \le v(t) \le 1,\ 0 \le v_1(t) \le v(t)} = x_2(T). \tag{1}$$

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Equations in the new environment

$$\begin{cases} \dot{x}_1 = v_1(t)g(x_3) - \tilde{\mu}(t)x_1, \\ \dot{x}_2 = (v(t) - v_1(t))g(x_3), \\ \dot{x}_3 = \tilde{\nu}(t)f(x_1) - v(t)g(x_3) - \tilde{\omega}(t)x_3. \end{cases}$$

What is an information, available to the plant?

- According to what dynamical equations will optimize a plant its behavior?
- What information about the new environment ($\tilde{\mu}(t)$, $\tilde{\nu}(t)$, $\tilde{\omega}(t)$) can obtain a plant?

Model predictive control (MPC)

MPC is a paradigm for optimal control with moving horizon.

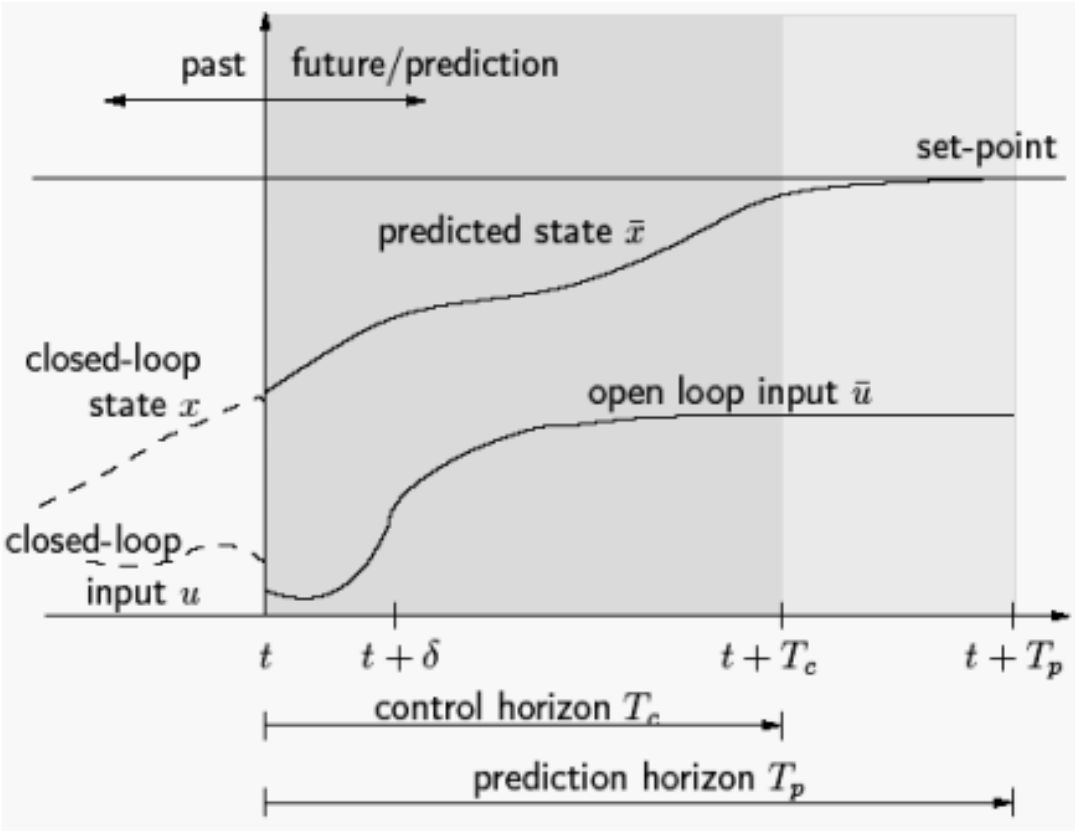

Fig. 1. Principle of model predictive control.

Populational optimal allocation models

Populational models would allow

1. To include interactions between the plants
2. To take into account spatial distribution of the species
3. To treat more precisely the models of single perennials
4. To treat the population as a unit of evolution

General way for modeling

Partial differential equations