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On the botanic model of plant growth with an intermediate vegetative-reproductive stage

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Abstract

The application of dynamic optimization to mathematical models of ontogenetic biological growth has been the subject of much research, see e g Cohen (1971). Kozłowski and Ziółko (1988), and Ziółko and Kozłowski (1995) presented a model with **gradual transition from vegetative to reproductive growth**. The central point of their model is a **mixed state control constraint on the rate of reproductive growth** which leads to a mixed **vegetative-reproductive growth period**. Their model is modified here in order to take into account the difference of photosynthesis use efficiency when energy is accumulated in the vegetative, and in the reproductive organs of the plant, respectively. The **correct mathematical solution of the optimal control problem** is presented, and the numerical example from Kozłowski and Ziółko (1988) is solved correctly. The influence of the length of the growing season, the relative photosynthesis use efficiency, and the potential sink demand of the reproductive organs on the location and duration of the mixedvegetative-reproductive period is investigated numerically.

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Why do plants behave as they do?

- Darwin (1859): **natural selection leads to an optimization process**, whereby organisms better fitted to their environment have a selective advantage.
- D. Cohen (1971) considered a **linear optimization model**, which **maximizes the amount of seeds** in a given growth period, whereby the optimal solution has two distinct intervals:
  - first, in the vegetative period, **all photosynthetic production is allocated to the vegetative organs** (leaves, stems, and roots).
  - then, in the reproductive period, **all material is allocated to the fruits/seeds**.
- However, multiple biological observations show that **the switch from the pure vegetative to the pure reproductive stage is** not abrupt, but smooth, or **gradual**.

Why do plants behave as they do?

- Kozłowski and Ziółko (1988), and Ziółko and Kozłowski (1995), considered a nonlinear model with a **constraint for the maximal value of reproductive accumulation to be the reason for such a gradual transition**.
- Kozłowski and Ziółko, however, solved their ensuing optimal control problem incorrectly.
- **Here, the correct mathematical solution of the KZ-problem is given**.
- Moreover, we introduce **different photosynthesis use efficiency** for vegetative and reproductive growth, see e.g. also Seginer and Ioslovich (1998).
- We investigate numerically the **influence of the climate** on the lengths of the vegetative, mixed, and reproductive periods.

The Kozłowski and Ziółko (KZ) model

$$\frac{dx}{dt} = \left(1 - u(t)\right) f\left(x(t)\right)$$

$$\frac{dy}{dt} = u(t) f\left(x(t)\right)$$

$$x(0) = x_0 \quad y(0) = 0$$

$$0 \leq u(t) \leq 1$$

$$u(t) f\left(x(t)\right) \leq g\left(y(t)\right)$$

$$y(T) \longrightarrow \max$$

$x(t)$ = energy of vegetative organs [cal/m^2],
$y(t)$ = energy of reproductive organs [cal/m^2],
$u(t)$ = partitioning factor control variable [-],

$f(x)$ = available power due to photosynthesis, a smooth and increasing fcn of x [cal/m^2/day],

$g(y)$ = constraint on the power for accumulation in the reproductive organs, or ”potential sink demand of the reproductive organs”, a smooth and increasing function of y [cal/m^2/day],

T = growing season [days].

The Modified Botanic Model (MBM)

$$\frac{dx}{dt} = k\left(1 - u(t)\right) f\left(x(t)\right)$$

$$\frac{dy}{dt} = u(t) f\left(x(t)\right)$$

$$x(0) = x_0 \quad y(0) = 0$$

$$0 \le u(t) \le 1$$

$$u(t) f\left(x(t)\right) \le g\left(y(t)\right)$$

$$y(T) \longrightarrow \max$$

$x(t)$ = energy of vegetative organs [kcal/m^2],
$y(t)$ = energy of reproductive organs [kcal/m^2],
$u(t)$ = partitioning factor control variable [-],

$f(x)$ = available power due to photosynthesis, a smooth and increasing fcn of x [kcal/m^2/day],

$g(y)$ = constraint on the power for accumulation in the reproductive organs, or ”potential sink demand of the reproductive organs”, a smooth and increasing function of y [kcal/m^2/day],

T = growing season [days].

- $k = k_v/k_r$ =relative photosynthesis use efficiency coefficient [-],
- climate dependence.

Climate dependence in MBM

Light and temperature

$f=m(t)F(x)$, where

$m(t)$= photosynthesis flux [kcal/m^2/day]

$F(x)$=light interception factor [-]

$g=s(\Theta(t))G(y)$ where

$s(\Theta(t))$ is an increasing function of **temperature** Θ**,** [kcal/m^2/day],

$G(y)$ [-].

Ref: Seginer and Ioslovich (1998)

Biological time

Assume a strong correlation between mean daily temperature and photosynthesis, namely

$$m(t) / s(\Theta(t)) = k_c$$

Then biological time τ can be introduced via

$$\mathrm{d}\tau/\mathrm{d}t = m(t)$$

...

Climate dependent MBM

$$\frac{dx}{d\tau} = k\left(1 - u(\tau)\right)F(x) \qquad 0 \le u(\tau) \le 1$$

$$\frac{dy}{d\tau} = u(\tau)F(x) \qquad u(\tau)F(x) \le G(y)/k_c$$

$$x(0) = x_0 \quad y(0) = 0 \qquad y(\Psi) \longrightarrow \max$$

Intuitive solutions

$$\frac{dx}{dt} = k\left(1-u(t)\right) f\left(x(t)\right)$$

$$\frac{dy}{dt} = u(t) f\left(x(t)\right)$$

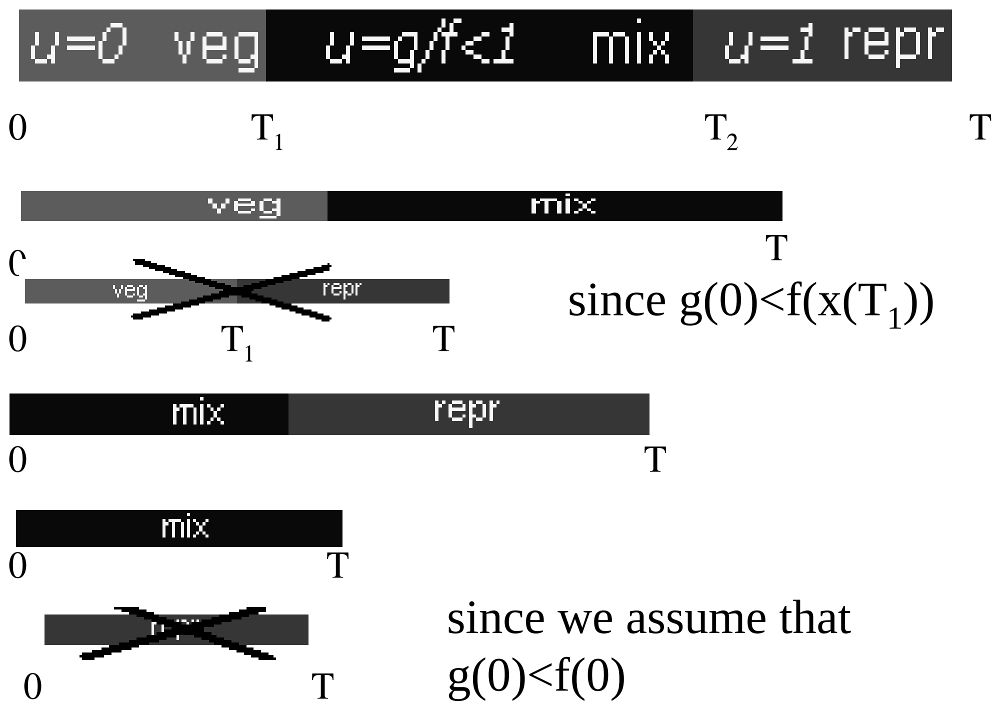
$$x(0) = x_0 \quad y(0) = 0$$

$$0 \le u(t) \le 1$$

$$u(t) f\left(x(t)\right) \le g\left(y(t)\right)$$

$$y(T) \longrightarrow \max$$

Depending on T, f, g, one can envisage:



In any case, there is no ”going back” to a previous stage

Pontryagin's Maximum Principle

$$\frac{dx}{dt} = k\left(1 - u(t)\right) f\left(x(t)\right)$$

$$\frac{dy}{dt} = u(t) f\left(x(t)\right)$$

$$x(0) = x_0 \quad y(0) = 0$$

$$0 \le u(t) \le 1$$

$$u(t) f\left(x(t)\right) \le g\left(y(t)\right)$$

$$y(T) \longrightarrow \max$$

- The **costate variables** represent the sensitivities of the criterion function to the state variables:

$$p_x(t) = \frac{\partial y(T)}{\partial x(t)} \qquad p_y(t) = \frac{\partial y(T)}{\partial y(t)}$$

- Clearly, the **transversality conditions** at $t=T$ are:

$$p_x(T) = 0 \qquad p_y(T) = 1$$

The Hamiltonian

$$\frac{dx}{dt} = k\left(1-u(t)\right) f\left(x(t)\right)$$

$$\frac{dy}{dt} = u(t) f\left(x(t)\right)$$

$$x(0) = x_0 \quad y(0) = 0$$

$$0 \le u(t) \le 1$$

$$u(t) f\left(x(t)\right) \le g\left(y(t)\right)$$

$$y(T) \longrightarrow \max$$

- The Hamiltonian, H, has to be maximized

  w.r.t. u, given the constraints,

  $$H = p_x(1-u)kf(x) + p_y uf(x) = (uS + kp_x) f(x)$$

  where the **switching function** is

  $$S = p_y - kp_x$$

- $S<0 \Rightarrow u=0$ (lower bound, v)
- $S>0 \Rightarrow u=\min(g/f, 1)$ (upper bound, m/r)

The optimal solution in the v-m-r case

$$\frac{dx}{dt} = k\left(1-u(t)\right)f\left(x(t)\right)$$
$$\frac{dy}{dt} = u(t)f\left(x(t)\right)$$
$$x(0) = x_0 \quad y(0) = 0$$
$$0 \le u(t) \le 1$$
$$u(t)f\left(x(t)\right) \le g\left(y(t)\right)$$
$$y(T) \longrightarrow \max$$

$$H = \left(uS + kp_x\right)f(x)$$
$$S = p_y - kp_x$$
$$S<0 \Rightarrow u=0$$
$$S>0 \Rightarrow u=\min(g/f,\, 1)$$
$$p_x(T)=0 \quad p_y(T)=1$$

- It is natural to assume that

$$p_x(0) = \frac{\partial y(T)}{\partial x(0)} > 0 \qquad p_y(0) = \frac{\partial y(T)}{\partial y(0)} > 0$$

such that $S(0)<0 \Rightarrow$ ***u*(0)=0**, i.e. the growth starts with a **vegetative period** until $t=T_1$ when $S(T_1)=0$.

- **Costate equations during the veg. period**:

$$\frac{dp_x}{dt} = -\frac{\partial H}{\partial x} - \left(uS + kp_x\right)\frac{\partial f}{\partial x} = -kp_x\frac{\partial f}{\partial x} < 0 \Rightarrow p_x \xrightarrow{\neq} 0$$

$$\frac{dp_y}{dt} = -\frac{\partial H}{\partial y} = 0 \Rightarrow p_y = p_y(0) > 0 \quad \text{(constant)}$$

- Hence, S(t) increases, with $S(T_1)=0$

The mixed period

$$\frac{dx}{dt} = k\left(1 - u(t)\right) f\left(x(t)\right)$$
$$\frac{dy}{dt} = u(t) f\left(x(t)\right)$$
$$x(0) = x_0 \quad y(0) = 0$$
$$0 \le u(t) \le 1$$
$$u(t) f\left(x(t)\right) \le g\left(y(t)\right)$$
$$y(T) \longrightarrow \max$$

$$S = p_y - kp_x$$

$S>0$ and $u=\min(g/f, 1)=g/f$

$$p_x(T) = 0 \qquad p_y(T) = 1$$

- Mixed state-control constraint active

$$H = \left(uS + kp_x\right) f(x) - \lambda\left(uf(x) - g(y)\right), \quad \lambda \ge 0$$

$$\frac{\partial H}{\partial u} = 0 \Rightarrow \lambda = S \qquad \frac{\partial H}{\partial \lambda} = 0 \Rightarrow u = \frac{g(y)}{f(x)}$$

$$\frac{dp_x}{dt} = -\frac{\partial H}{\partial x} = -kp_x \frac{\partial f}{\partial x} < 0 \Rightarrow p_x \xrightarrow{\neq} 0 \quad \text{as above}$$

$$\frac{dp_y}{dt} = -\frac{\partial H}{\partial y} = -\lambda \frac{\partial g}{\partial y} = -S \frac{\partial g}{\partial y} < 0$$

$$\frac{dS}{dt} = -S \frac{\partial g}{\partial y} + k^2 p_x \frac{\partial f}{\partial x} > 0 \quad \text{when } S \text{ near } 0, \Rightarrow S>0$$

- At $t=T_2$, $f(x(T_2))=g((y(T_2))$, switch to reproductive period

The reproductive period

$$\frac{dx}{dt} = k\left(1 - u(t)\right) f\left(x(t)\right)$$
$$\frac{dy}{dt} = u(t) f\left(x(t)\right)$$
$$x(0) = x_0 \quad y(0) = 0$$
$$0 \le u(t) \le 1$$
$$u(t) f\left(x(t)\right) \le g\left(y(t)\right)$$
$$y(T) \longrightarrow \max$$

$$S = p_y - kp_x$$

***S*>0** and ***u*=min(*g*/*f*, 1)=1**

$$p_x(T) = 0 \qquad p_y(T) = 1$$

- The mixed state-control constraint is **inactive**

$$H = \left(uS + kp_x\right) f(x)$$

$$\max_u H \Rightarrow u = 1 \ \text{ since } S > 0, \ \text{ and } \ H = p_y f(x)$$

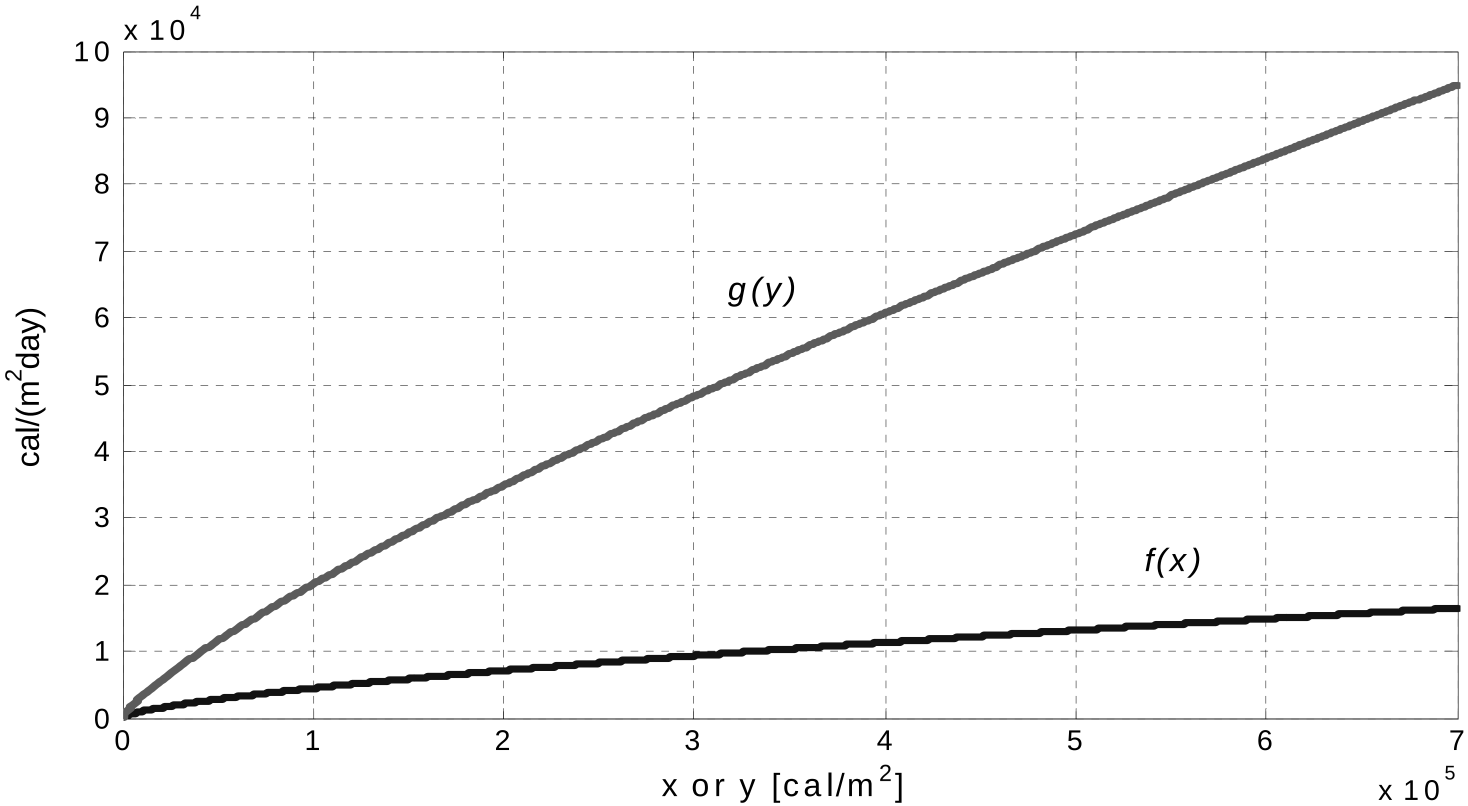
$$\frac{dp_y}{dt} = -\frac{\partial H}{\partial y} = 0, \ \text{ hence } \ p_y(t) = 1 \ \text{ for } \ t \in \left[T_2, T\right]$$

$$\frac{dp_x}{dt} = -\frac{\partial H}{\partial x} = -p_y \frac{\partial f}{\partial x} < 0 \ \text{ and } \ p_x(T) = 0$$

- $S(t)$ remains >0 for $t \in [\,T_2,\, T]$

The KZ88 example

- k=1, $x(0)$=100000 cal/m^2, $y(0)$=1 cal/m^2, T=100 days
- $f(x)=2x^{0.67}$ cal/(m^{2}day), $g(y)=2x^{0.80}$ cal/(m^{2}day),



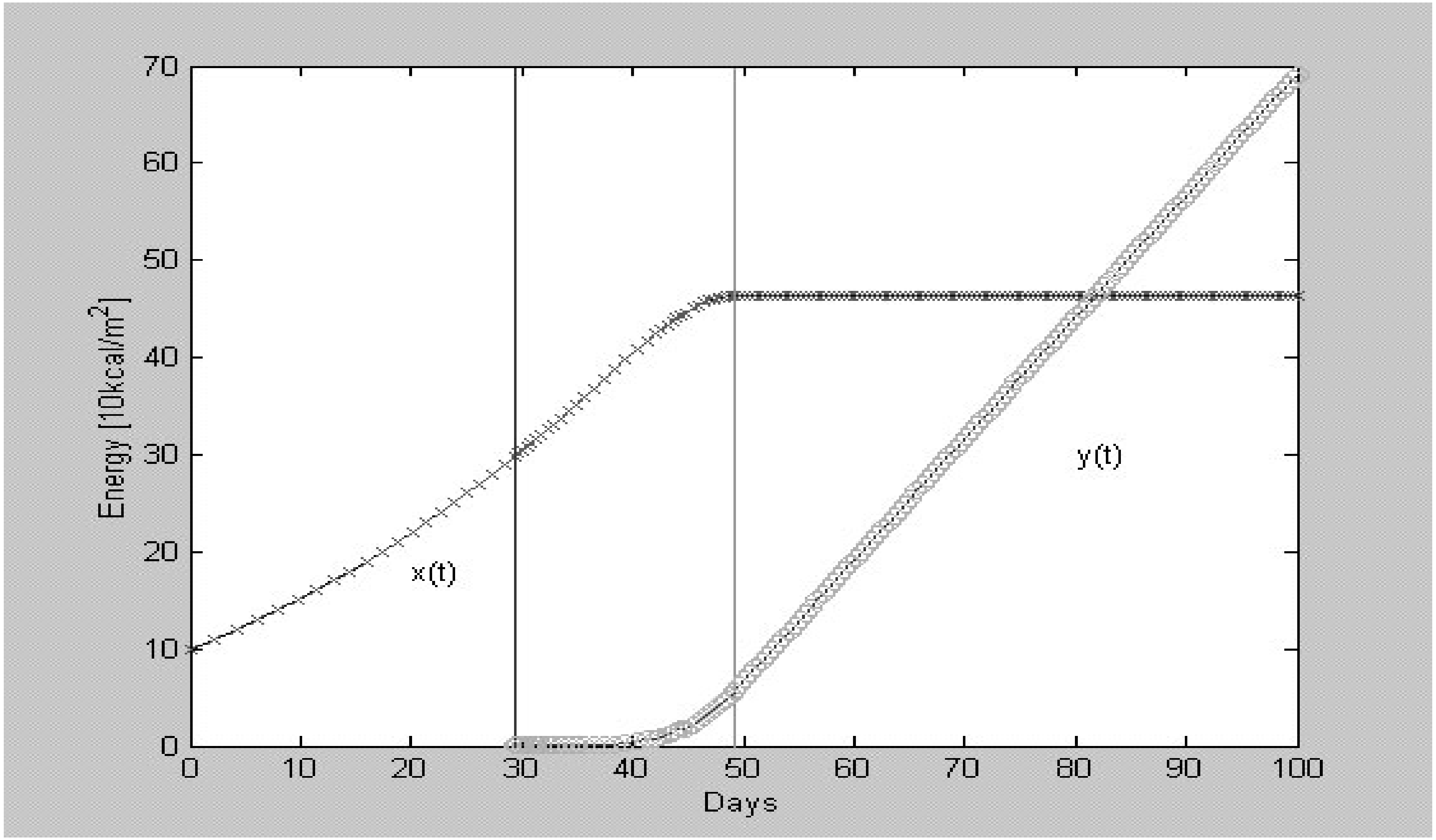
Numerical methods

- E.g. by the *shooting method*:
  - guess $p_x(0)$ and $p_y(0)$
  - integrate equations until $t=T$
  - check that transversality conditions $p_x(T)=0$ and $p_y(T)=1$ are satisfied
- In the paper a smarter taylor-made method is suggested.

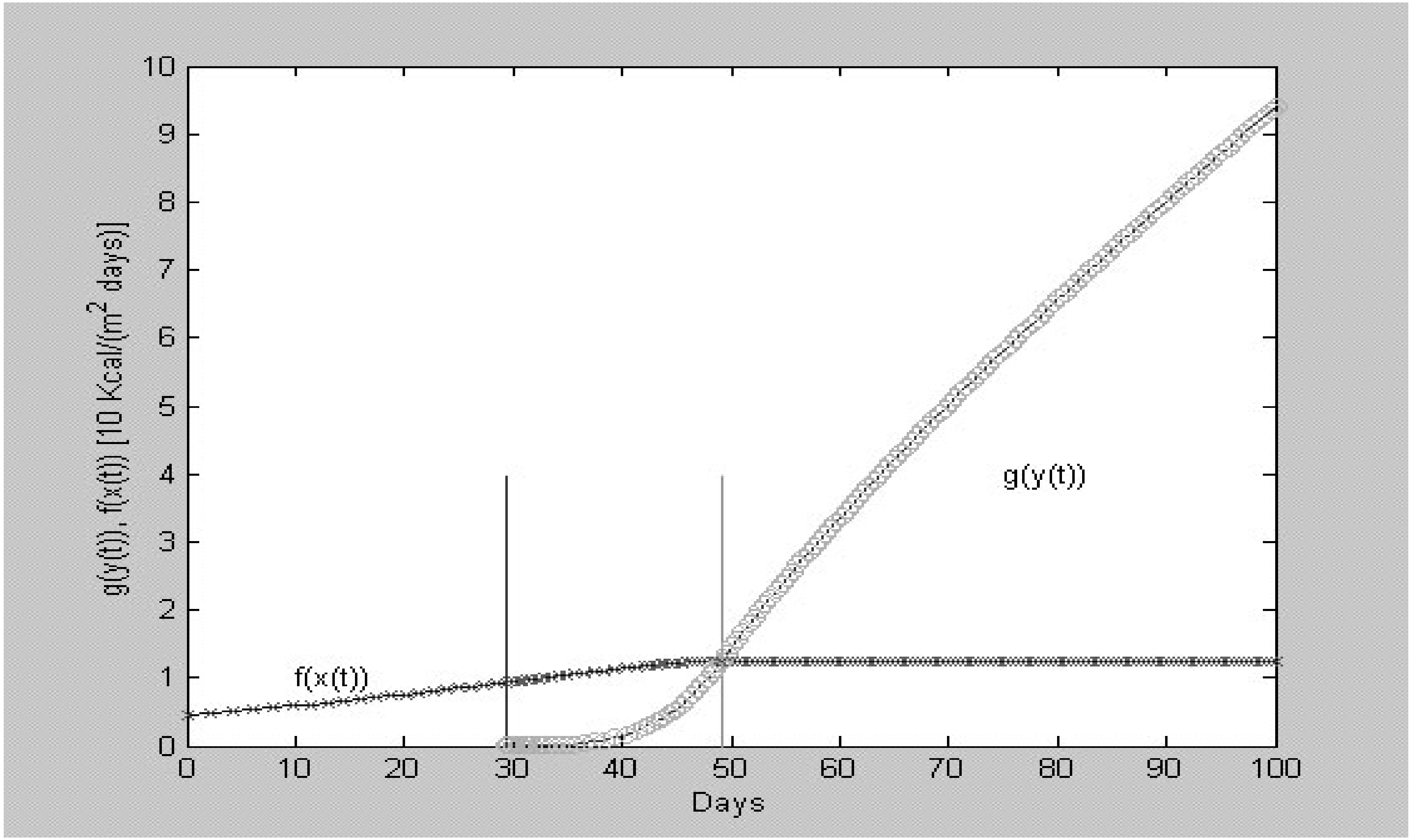
The optimal solution

- T_1=29.4 days, T_2=49.15 days, T=100 days
- $y(T_2)$ = 55.6 kcal/m^2 **$y(T)$=691.7 kcal/m^2**
- $x(T_1)$ =298.4 kcal/m^2 $x(T_2)$ =463.4 kcal/m^2
- $p_x(T_1)$=1.34 $\perp$

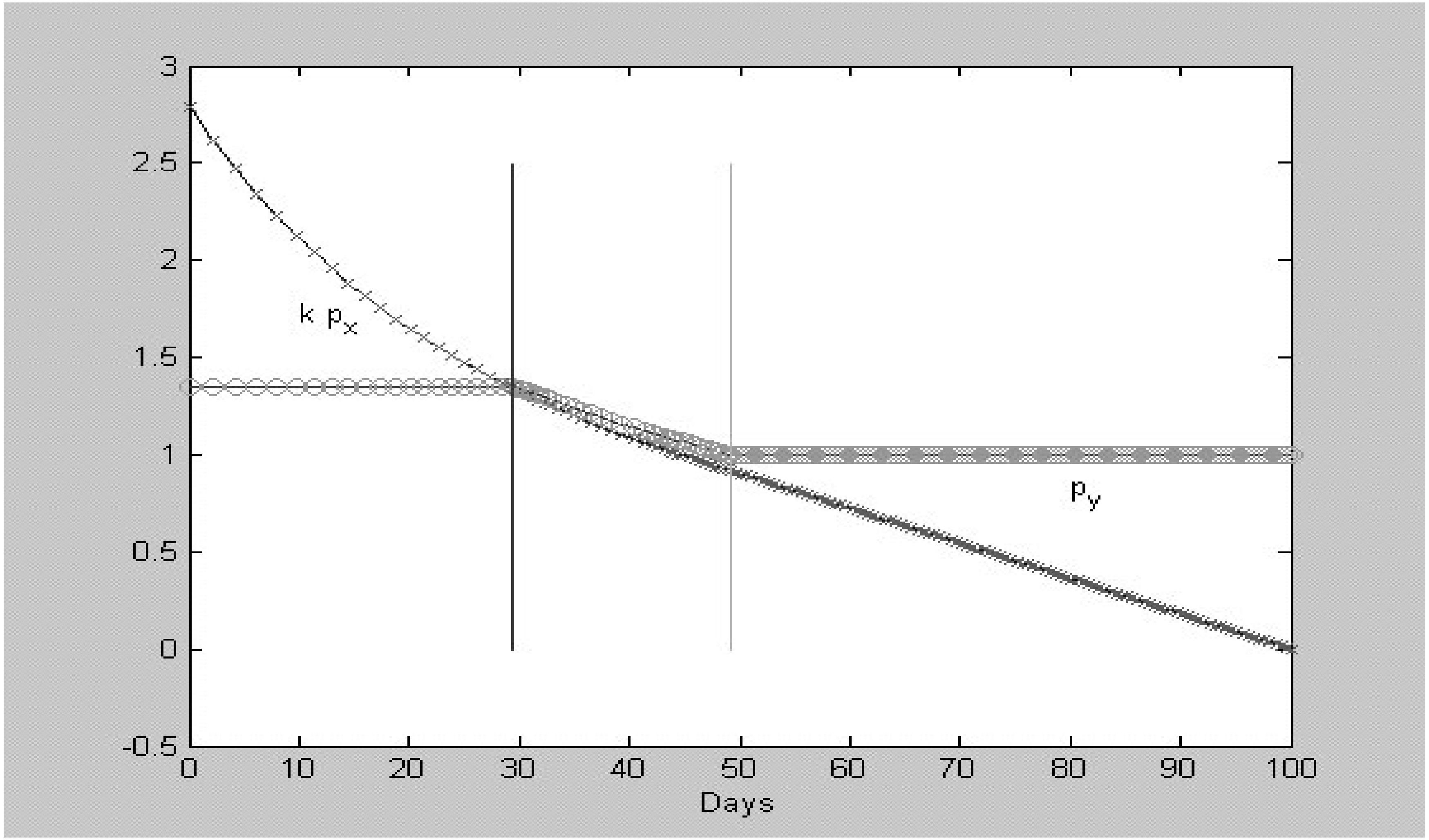
The optimal solution



The optimal solution



The optimal solution



Numerical experiments

- Increasing k or $T \Rightarrow$ delays T_1 and increases $T_2 - T_1$
- Decreasing $g(y) \Rightarrow$ advances T_1 and increases $T_2 - T_1$
- Increasing photosynthesis $\Rightarrow$ delays T_1 and increases $T_2 - T_1$
- Increasing temperature $\Rightarrow$ delays T_1 but decreases $T_2 - T_1$

Discussion

- The Modified Botanic Model is introduced.
- The correct solution of the optimal control problem using the KZ and MBM models are given:
  - Mixed state-control constraint
  - Pontryagin *et al*. (1966), Krotov and Gurman (1973)
- Numerical experiments are performed, but comparisons of MBM with botanical data remain.