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IFAC-PapersOnLine 48-18 (2015) 059–064

Feedback Control of Biological Rhythm in Crassulacean Acid Metabolism by CO2-Uptake Signal ⋆

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Abstract: The mechanism of endogenous circadian photosynthesis oscillations of plants performing crassulacean acid metabolism (CAM) is investigated in terms of a nonlinear theoretical model. Blasius et al. used throughout continuous time differential equations which adequately reflect the CAM dynamics. The model shows regular endogenous limit cycle oscillations that are stable for a wide range of temperatures in a manner that complies well with experimental data. We have recently presented four types of the feedback controllers for the phase shift of the CAM model of the single cell using the light intensity as an input. In this paper, we deal with the synchronization issues in the coupled cells with light intensity input. We show that the strong coupling causes the unsynchronization of the cells.

Keywords: Photosynthesis oscillation, limit cycle, nullcline, pulse control, synchronization.

1. INTRODUCTION

In plant, the circadian rhythms play important roles in gene expressions, photosynthesis, growth, and many other physiological processes. The plant circadian rhythm is composed of a large number of self-sustained cellular oscillations that synchronize each other. Precise and ecological control of the circadian rhythm provides a key technology for enhancing the plant growth in a closed cultivation system where light-dark cycles differ from the 24-h period (see Fukuda et al. (2013)). Climatic extremes threaten agricultural sustainability worldwide. Crassulacean acid metabolism (CAM) plants show a remarkable metabolic plasticity for modulating nocturnal and diurnal CO_2 uptake and have been identified as competitive biomass accumulators in comparison with many C_3 and C_4 crops. One approach to increase plant water-use efficiency is to introduce CAM into C_3 crops (see Borland et al. (2014)). Computational modeling of CAM accelerates the improvement of CAM crops in terms of biomass productivity and quality-related attributes (see Borland et al. (2013)). Blasius et al. (1999) investigated the mechanism of endogenous circadian photosynthesis oscillations of plants performing CAM in terms of a nonlinear theoretical model. They used throughout continuous time differential equations which modes adequately reflect the CAM dynamics. By incorporating results from both a complementary and a continuous membrane model, a detailed description of the molecular malate transport in and out of the vacuole through the tonoplast membrane was achieved. Their analysis showed that the membrane effectively acts as a hysteresis switch regulating the oscillations. It thus provided a molecular basis for the circadian clock. The model showed regular endogenous limit cycle oscillations that were stable for a wide range of temperatures, in a manner that complies well with experimental data. The nonlinear dynamical model of CAM is discussed from the control theoretical viewpoint. The state-variables of the nonlinear dynamic equations are an internal CO_2 concentration, a malate concentration in the cytoplasm, a malate concentration in the vacuole, and an order of the tonoplast membrane. The input variables are an external CO_2 concentration, a light intensity and a temperature.

We have recently presented a dynamic estimator of the tonoplast order and a fuzzy identifier of the nonlinear function in the dynamics of the tonoplast order (see Matsuo et al. (2013)). Moreover, we proposed the feedback controller by controlling the external CO_2 concentration and the light intensity (see Sakamoto et al. (2013)). Thought these estimator and controller require the state variables except for the order of the tonoplast membrane, they are not measurable directly.

To begin with, we propose the reconstruction method of the internal CO_2 concentration using the CO_2 uptake from outside, because the CO_2 uptake can be determined the CO_2 exchange which is measured using a CO_2 analyzer and an incubator (see Fukuda et al. (2004)). Next, we present a feedback controller and a feedforward controller with a pulse signal to shift the phase of the CAM model using the light intensity as an input. These controller allows to control the time and process of budding and unfolding of blossoms. For healthy growth of a plant, it is essential to maintain synchronized activities of the cellular oscillators so as to sustain the stable rhythm (see Fukuda et al. (2013)). Finally, we investigate the synchronization phenomena of two cells with different initial values by using the feedforward pulse signal of

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⋆ This work is partially supported by the Grant-in-Aid for Scientific Research (25420445), Japan Society for the Promotion of Science.

10.1016/j.ifacol.2015.11.011

the light intensity. The simulation results are given to examine the performance of the proposed controllers using MATLAB/Simulink.

2. THE MINIMAL CAM MODEL

The CAM model that we will use has been studied by Blasius and Beck (see Blasius et al. (1999); Beck et al. (2001)) and here we only outline the minimal CAM model. The model can be characterized by the major reactant pools of CAM that generate the carbon flow during the circadian cycle as shown in Fig.1. The pool concentrations are the following:

- internal CO_2 concentration, w;
- malate concentration in the cytoplasm, x;
- malate concentration in the vacuole, y; and
- z is a variable that describes the ordering of the lipid molecules in the tonoplast membrane.

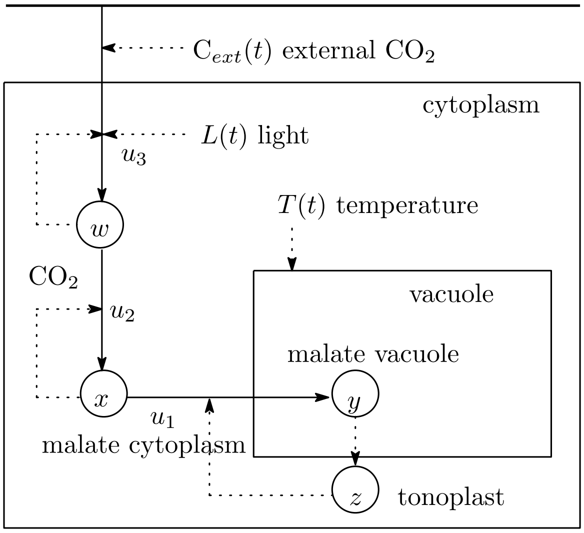

Fig. 1. Flow diagram of the CAM model showing as dynamic variables (encircled) three reactant pools (internal CO_2 concentration, w; malate concentration in the cytoplasm, x; and in the vacuole, y) and the order of the tonoplast, z, within a CAM cell.

These are the dynamic variables of the cyclic process. They are connected by the flows, u_1, u_2, u_3, during the gain and loss terms of the metabolites. The model depends on three external control parameters: temperature, T, light intensity, L, and external CO_2 concentration, C_{ext}. The dynamics are characterized by a set of four coupled, nonlinear differential equations of first order in time:

$$\left.\begin{aligned} \epsilon\dot{w} &= -u_2 + u_3 \\ \epsilon\dot{x} &= -u_1 + u_2 \\ \dot{y} &= u_1 \\ \tau\dot{z} &= g(z,T) - y \end{aligned}\right\} \tag{1}$$

where the function $g(z,T)$ is the thermodynamic equilibrium value of malate concentration in the vacuole ,y, and is a third-order nonlinear function depends on the temperature, T (see Blasius et al. (1999)). The temperature-dependent z-null cline, $y = g(z,T)$, corresponds to the hysteretic behavior of the phase diagram in the membrane model shown in Fig.2(seeNeff et al. (1998)). The constant, τ, is the time-constant for relaxation into thermal equilibrium. The smallest parameter $\epsilon \ll 1$ reflects the volume ratio of cytoplasm to vacuole, which is typically of the order of 1/100 in CAM plants (see Blasius et al. (1999)). The flows $u_i, i = 1, 2, 3$ involve modeling of the metabolic reactions and comprise the whole structure of the carbon circulation in CAM. They are described by the following equations:

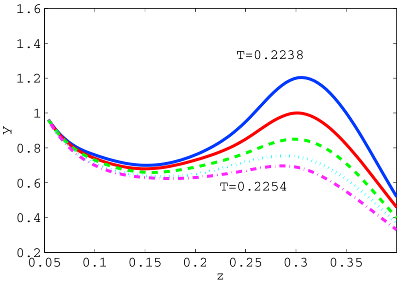

Fig. 2. The nonlinear function $y = g(z,T)$ when $T =$ 0.2238, 0.2244, 0.2246, 0.2250, 0.2254.

$$\left.\begin{aligned} u_1 &= cx - \frac{y}{z} \\ u_2 &= \frac{w}{x} - x \\ u_3 &= J_{\mathrm{CO}_2} - C_{\mathrm{CO}_2} + R_{\mathrm{CO}_2} \\ J_{\mathrm{CO}_2} &= c_J \frac{(C_{\mathrm{ext}}(t) - w)}{\exp(\alpha w)} \\ C_{\mathrm{CO}_2} &= L(t)w \\ R_{\mathrm{CO}_2} &= c_R \frac{L_K}{L(t) + L_K} \frac{w_1}{w + w_1} \end{aligned}\right\} \tag{2}$$

The meaning of each variable is the following:

J_{CO_2} : CO_2 uptake from outside

C_{CO_2} : CO_2 consumption by photosynthesis, which is directly proportional to the external control parameter light intensity, $L(t)$

R_{CO_2} : CO_2 production by respiration.

Blasius *et al.* calculated the dynamic behavior using the dimensionless variables with the parameters (see Blasius et al. (1999)): $C_{\mathrm{ext}} = 1$, $L(t) = 1$, $T = 0.2238, 0.2242, 0.2246, 0.2250, 0.2254$, $c = 5.5$, $c_J = 1$, $c_R = 1$, $\varepsilon = 0.001$, $\tau = 0.35$, $\alpha = 1.5$, $w_1 = 0.1$, $L_K = 0.5$, $R = 0.1$. Using these parameters, we perform the computer simulation by MATLAB/Simulink. The initial conditions of the states are given as $w(0) = 0.4, x(0) = 0.62, y(0) = 0.56, z(0) = 0.2$. The nonlinear function $g(z,T)$ is approximated via the third-order spline interpolation from the figure shown in the reference(see Blasius et al. (1999)). Figure 3 shows the dynamic responses of the state variables when $T = 0.2242$. Blasius *et al.* have shown the influence of temperature as an external control parameter (see Blasius et al. (1999)). With increasing temperature the steady state malate level decreases, until at the critical temperature, the system undergoes supercritical Hopf bifurcation, and the stable fixed point changes into unstable one surrounded by a small-amplitude limit cycle (see Blasius et al. (1999)).