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Stability of stationary solutions in models of the Calvin cycle

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ABSTRACT

In this paper results are obtained concerning the number of positive stationary solutions in simple models of the Calvin cycle of photosynthesis and the stability of these solutions. It is proved that there are open sets of parameters in the model of Zhu et al. (2009) for which there exist two positive stationary solutions. There are never more than two isolated positive stationary solutions but under certain explicit special conditions on the parameters there is a whole continuum of positive stationary solutions. It is also shown that in the set of parameter values for which two isolated positive stationary solutions exist there is an open subset where one of the solutions is asymptotically stable and the other is unstable. In related models derived from the work of Grimbs et al. (2011), for which it was known that more than one positive stationary solution exists, it is proved that there are parameter values for which one of these solutions is asymptotically stable and the other unstable. A key technical aspect of the proofs is to exploit the fact that there is a bifurcation where the centre manifold is one-dimensional.

1. Introduction

The Calvin cycle is an important part of photosynthesis and many mathematical models have been proposed to describe it [1,2]. These vary widely in the number of chemical species included and the kinetics chosen for the individual reactions. In what follows we concentrate on some of the simplest models with the aim of obtaining rigorous results on the number of stationary solutions of the models and their stability. It may be hoped that a deeper understanding of the simpler models will lead to new approaches to analysing the more comprehensive ones.

In [3] a model of the Calvin cycle was introduced which is a system of ordinary differential equations describing the concentrations of five substances. This level of biological detail is similar to that found in the standard textbook [4] on cell biology. Based on computer modelling the authors of [3] conclude that their system has only one steady state for fixed values of the parameters under certain biological restrictions.

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(A stationary solution of a system of ODE is one which is independent of time and a steady state is an alternative name for a stationary solution.) They explicitly exclude the case of non-isolated steady states from consideration. They do not make general statements about the stability of the steady states although some results of simulations included in the paper indicate the stability of the steady state considered. In what follows we prove that under certain explicit restrictions on the parameters of the system a continuum of positive steady states occurs. We also give a proof that when these restrictions are not satisfied there exist at most two positive steady states for each choice of the parameters. It is shown that there do exist open sets of parameters for which there are two positive steady states. This does not contradict the results of [3] since the biologically motivated fixed choice of Michaelis constants made there excludes the cases where more than one steady state is present in the model.

It is proved that there are parameters for which an asymptotically stable positive steady state exists. Thus for these parameters any solution which has the property that at some time the concentrations are sufficiently close to those in the steady state converges to the steady state at late times. There are also open regions in parameter space for which no positive steady state exists and regions for which the only positive steady state is unstable. The stability of the state where all concentrations are zero is also dependent on the parameters. Thus for some choices of parameters there are solutions for which all concentrations tend to zero at late times and for other choices of parameters no solutions of this kind exist. More detailed versions of these statements can be found in Theorems 1 and 2 in Section 2. It follows from Theorem 4 of [5] that there are runaway solutions of this model where all concentrations tend to infinity at late times.

In [6] the authors introduced what looks at first sight like a small modification of the model of [3] by rescaling two of the coefficients. It turns out, however, that this modifies the dynamics significantly. These authors considered different possibilities for the kinetics. The model of [6] with Michaelis–Menten kinetics is the main subject of Section 3. It was already known from [6,5] that this model has two positive steady states for certain choices of the parameters. However nothing had been proved about their stability. Here we show that there are parameters for which one of these steady states is stable and one unstable. It is also shown that this implies analogous statements for a more complicated model, also introduced in [6], where each basic reaction is described using a Michaelis–Menten scheme with a substrate, an enzyme and a substrate–enzyme complex. Details are given in Theorem 3.

Section 4 is concerned with equations derived from a model introduced in [6] where the concentration of ATP is included as an additional variable and the diffusion of ATP is taken into account. This leads to a system of reaction–diffusion equations. Setting the diffusion coefficient to zero in this model or restricting consideration to spatially homogeneous solutions gives rise to a system of ODE which was called the MAdh system in [5]. It was proved there that there are parameters for which this model has two positive steady states. However once again nothing was proved about the stability of these solutions. Here we show that for certain values of the parameters one of the steady states is stable and the other unstable. Details are in Theorem 4. The last section contains a summary of the results of the paper and an outlook on possible future developments.

2. The model of Zhu et al.

This section is concerned with a model of the Calvin cycle introduced by Zhu et al. [3]. The basic system of equations is

$$\frac{dx_{\mathrm{RuBP}}}{dt} = v_5 - v_1, \tag{1}$$

$$\frac{dx_{\mathrm{PGA}}}{dt} = 2v_1 - v_2 - v_6, \tag{2}$$

$$\frac{dx_{\mathrm{DPGA}}}{dt} = v_2 - v_3, \tag{3}$$