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Full Length Research Paper

Global dynamic of a mathematical model of competition in the chemostat

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The purpose of this paper is to offer a complete global analysis of the behavior of solutions of either the variable - yield two microbial growths, limited by a single scare nutrient, or of competition between two microbial populations for a single limiting nutrient. Basically, we confirm that the variable - yield models make the same predictions concerning the growth of a single population and concerning by out come of competition between two microbial populations, as the simpler constant - yield models.

Key words: Chemostat, global stability, population dynamics, and equilibria.

INTRODUCTION

The classical mathematical models of growth and competition of microbial populations on a single limiting substrate in continuous culture, also called the chemostat, occupy a central place in ecological modeling (Hsu, 1978). The parameters of the model can be measured by growing the organisms separately in either batch or continuous culture. A rigorous, global description of the dynamics exhibited by the model equations were carried out in (Monod, 1950), and letter, in more generality in (Tilman, 1982). These mathematical results became more widely known to ecologists through the work of Tillman, particularly the monograph (Tilman 1982). More recent mathematical results and extensions of the classical model can be found in (Hsu, 1978).

In the classical model of the chemostat, discussed-in (Cunningham and Nisbet, 1980), it is assumed that the nutrient uptake rate is proportional to the reproductive rate. The constant of proportionality, which converts units of nutrient to units of organism, is called the yield constant. As a consequence of the assumed constant value of the yield, the classical model is sometimes referred to as the "constant yield" model.

In phyloplankton ecology, it has long been known that the yield is not constant and that it can vary depending on the growth rate (Droop, 1973). This led to the formulation of the variable - yield model, also called the variable – internal stores model (Grover, 1991), and the Caperon - Droop model (Hsu et al., 1977). This model effectively decouples specific growth rate from external nutrient concentration by introducing an intracellular store of nutrient. The specific growth rate is hypothesized to depend on a quantity, called the cell quota, which may be viewed as the average amount of stored nutrient in each cell of the particular organism in the chemostat.

The purpose of this paper is to give a mathematical analysis of the variable - yield model. Essentially, we confirm that the variable - yield models make the same predictions concerning the growth of a single population, and concerning to outcome of competition between two microbial populations.

In this paper, the variable - yield model of single – population growth is derived and analyzed, also, the competition model is formulated and its equilibrium solutions identified. The conservation principle is introduced, local stability properties of the equilibrium solutions are also determined.

The model

The variable - yield model of growth of a single population in the chemostat is derived and analyzed.

Let S(t) denote the free nutrient in the chemostat at time t, and two populations, with densities x_1 and x_2 competing for a single nutrient, with concentration *S*, in the chemostat. Competition occurs in the sense that each population consumes nutrient, thereby making it unavailable for its competitor. The average amount of stored per individual of population x_1 is denoted by y_1

and for population x_2 is denoted by y_2. The chemostat is fed medium, with nutrient concentration S°, at volumetric flow rate *D*. There is a compensating outflow, also at rate *D*, of the well - stirred contents of the chemostat. Assuming for convenience that the chemostat has unit volume, we have the following equations

$$S' = D\left(S^o - S\right) - x_1 e^{-\theta y_1}\rho_1\left(S\right) - x_2 e^{-\theta y_2}\rho_2\left(S\right),$$

$$x_1' = x_1\left(\mu_1\left(y_1\right) - D\right),$$

$$y_1' = e^{-\theta y_1}\rho_1\left(S\right) - \mu_1\left(y_1\right)y_1, \qquad (2.1)$$

$$x_2' = x_2\left(\mu_2\left(y_2\right) - D\right),$$

$$y_2' = e^{-\theta y_2}\rho_2(S) - \mu_2\left(y_2\right)y_2$$

The functions $\mu_1(y_1), \mu_2(y_2), \rho_1(S), \rho_2(S)$ are, respectively, the per capita growth rate and the per capita uptake rate of population x_i. The term $e^{-\theta y_i}$, $i = 1,2$ represents the effect of the inhibitor, this form having been used by Lenski and Hattingh (1986). We assume that μ_i is defined and continuously differentiable for $y_i \geq p_i$, where $p_i \geq 0$ and satisfies

$$\mu_i\left(y\right) \geq 0,$$
$$\mu_i'(y) > 0, \qquad (2.2)$$
$$\mu_i(p_i) = 0,$$

Observe that (2.2) imply that $y_i' \geq 0$, if $y_i = p_i$, and therefore the interval of y_i value, $\left[p_i, \infty\right]$ is positively invariant under the dynamics of (2.1). Biologically relevant initial values for (2.1) are:

$$x_i(0) > 0 \quad , \quad y_i(0) \geq p_i \quad , \quad S(0) \geq 0 .$$

We will repeatedly use the fact, a consequence of (2.2) that for a fixed value of S, $e^{-\theta y_i}\rho_i\left(S\right) - y_i\left(y_i\right)\mu_i$ is strictly decreasing in y_i, for $y_i \geq p_i$. Also note that $y_i\mu_i\left(y_i\right)$ increases without bound, as y_i increases.

In general (2.1) have at most three steady state solutions. One of these, which we label E_o, corresponds to the absence of both competitors. It is given by:

$$E_o = \left(x_1, y_1, x_2, y_2, S\right) = \left(0, y_1^o, 0, y_2^o, S^o\right)$$

at it always exists, y_i^0 is the unique solution of

$$e^{-\theta y_i}\rho_i\left(S\right) - y_i\mu_i\left(y_i\right) = 0$$

The two other possible steady states labeled E_1 and E_2 correspond to the presence of one population and the absence of the other.
For example

$$E_1 = \left(\hat{x}_1, \hat{y}_1, 0, \hat{y}_2, \hat{S}\right)$$

Where

$$\mu_1\left(\hat{y}_1\right) = D, \qquad (2.3)$$

$$e^{-\theta\hat{y}_1}\rho_1\left(\hat{S}\right) = D\left(\hat{y}_1\right),$$

$$\hat{x}_1 = \frac{S^o - \hat{S}}{\hat{y}_1},$$

$$e^{-\theta\hat{y}_2}\rho_2\left(\hat{S}\right) = \hat{y}_2\mu_2\left(\hat{y}_2\right).$$

Examination of (2.3) reveals that E_1 exists; $y_i \geq p_i$, and x_1 positive, iff

(i) $\mu_1\left(\hat{y}_1\right) = D$ has a solution $y_1 = \hat{y}_1$, and (2.4)

(ii) $e^{-\theta\hat{y}_1}\rho_1\left(\hat{S}\right) > D\,\hat{y}_1$

(2.4) says that the population x_1 can achieve a steady state population provided that:
(a) D is not too large.
(b) $S^o > \hat{S}$.
An analogous steady state in which only population x_2 is present is given by

$$E_2 = \left(0, \tilde{y}_1, \tilde{x}_2, \tilde{y}_2, \tilde{S}\right)$$

Where

$$\mu_2\left(\tilde{y}_2\right) = D,$$

$$e^{-\theta\tilde{y}_2}\rho_2\left(\tilde{S}\right) = D\,\tilde{y}_2, \quad (2.5)$$

$$\tilde{x}_2 = \frac{S^0 - \tilde{S}}{\tilde{y}_2},$$

$$e^{-\theta \tilde{y}_1} \rho_1 \left(\tilde{S}\right) = \tilde{y}_1 \mu \left(\tilde{y}_1\right)$$

E_2 exists iff

(i) $\mu_2 \left(\tilde{y}_2\right) = D$ has a solution $y_2 = \tilde{y}_2$, and

(ii) $e^{-\theta \tilde{y}_2} \rho_2 \left(\tilde{S}\right) > D \quad \tilde{y}_2$ (2.6)

A steady state of (2.1) is called nondegenerate provided the Jacobian matrix of the vector field determined by (2.1) at the steady state in nonsingular.

It is possible, but highly unlikely, that there exist steady states with both x_1 and x_2 present. This can happen iff both (2.4), (2.6) are satisfied and

$$\tilde{S} = \hat{S} \qquad (2.7)$$

In order to simplify the statement of the main result, it will be assumed that if both (2.4), (2.6) hold, then

$$\tilde{S} < \hat{S} \qquad (2.8)$$

Theorem 2.1

Assume that the steady states of (2.1) are nondegenerate, then the following assertion hold

If (2.4) and (2.6) do not hold, then E_o is the only steady state and every solution of (2.1) satisfies

$$\left(x_1(t), y_1(t), x_2(t), y_2(t), S(t)\right) \to E_o \quad as \quad t \to \infty$$

If (2.4) holds and (2.6) does not hold then E_o and E_1 are the only steady states and every solution which $x_1(0) > 0$, satisfies

$$\left(x_1(t), y_1(t), x_2(t), y_2(t), S(t)\right) \to E_1 \quad as \quad t \to \infty$$

If (2.6) holds and (2.4) does not hold, then E_o and E_2 are the only steady states and every solution for which $x_0(0) > 0$, satisfies

$$\left(x_1(t), y_1(t), x_2(t), y_2(t), S(t)\right) \to E_2 \quad as \quad t \to \infty$$

If (2.4) and (2.6) hold, then E_o, E_1 and E_2 exist and if (2.8) holds, then every solution for which $x_2(0) > 0$, satisfies

$$\left(x_1(t), y_1(t), x_2(t), y_2(t), S(t)\right) \to E_2 \quad as \quad t \to \infty$$

Proof: For the First assertion of the Theorem, nondegeneracy holds for E_o iff

$$\mu_i \left(y_i^o\right) \neq 0, \quad i = 1, 2$$

For the second (Third) assertion, only the single condition, $\mu_2 \left(y_2^0\right) \neq D \quad \left(\mu_1 \left(y_1^0\right) \neq D\right)$ is needed to insure that the nondegeneracy assumption hold for both steady states.

Consider the case that both E_1 and E_2 exist. Drop from (2.1) the equations for y_i, $i = 1, 2$ and substitute

$$\mu_1(y_1) = \hat{y}_1^{-1} e^{-\theta \hat{y}_1} \rho_1(S).$$

$$\mu_2(y_2) = \hat{y}_2^{-1} e^{-\theta \hat{y}_2} \rho_2(S)$$

in the equations for x_i, $i = 1, 2$. Replace y_i by the equilibrium values $\hat{y}_1$ and $\hat{y}_2$ in the equation for *S*. This results the system

$$x_1' = x_1\left(\hat{y}_1^{-1} e^{-\theta \hat{y}_1} \rho_1(S) - D\right),$$

$$x_2' = x_2\left(\hat{y}_2^{-1} e^{-\theta \hat{y}_2} \rho_2(S) - D\right), \qquad (2.9)$$

$$S' = D\left(S^o - S\right) - x_1 \; e^{-\theta \hat{y}_1} \; \rho_1(S) - x_2 \; e^{-\theta \tilde{y}_2} \rho_2(S)$$

Which can be viewed as the constant yield model corresponding to (2.1)?

The system (2.1) becomes

$$x_i' = x_i\left(\mu_i(y_i) - 1\right),$$

$$y_i' = e^{-\theta y_i} \rho_i(S) - y_i \mu_i(y_i) \qquad (2.10)$$

$$S' = 1 - S - \sum_{i=1}^{2} x_i e^{-\theta y_i} \rho_i(S)$$

With $\bar{t} = Dt,\ \bar{S} = S \big/ S^0,\ \bar{y}_i = y_i \big/ y_i^*,\ \bar{x}_i = x_i\, y_i^* \big/ S^o,\ y_i^*$ are arbitrarily chosen representative values of the variables y_i and

$$\bar{\mu}_i(\bar{y}_i) = D^{-1} \mu_i\left(y_i^* \, \bar{y}_i\right),$$

$$\bar{\rho}_i\left(\bar{S}, \bar{y}_i\right) \equiv \left(D\, y_i^*\right)^{-1} \rho_i\left(S^o \bar{S}, y_i^* \, \bar{y}_i\right)$$

Let $\Sigma = S + y_1 x_1 + y_2 x_2$, Σ consists of unbounded free nutrient plus stored nutrient and it satisfies:

$$\Sigma' = 1 - \Sigma \qquad (2.11)$$

Therefore, all solutions of (2.10) asymptotically approach the surface

$$S + y_1 x_1 + y_2 x_2 = 1 \qquad (2.12)$$

i.e. $\quad \Sigma(t) \to 1 \quad as \quad t \to \infty$

Consequently as a first step in the analysis of (2.10), we consider the restriction of (2.10) to the exponentially attracting invariant subset given by (2.12). Dropping S from (2.10), we obtain the system.

$$x_1' = x_1(\mu_1(y_1) - 1),$$

$$y_1' = e^{-\theta y_1} \rho_1 (1 - y_1 x_1 - x_2 y_2) - y_1 \mu_1(y_1), \qquad (2.13)$$

$$x_2' = x_2(\mu_2(y_2) - 1),$$

$$y_2' = e^{-\theta y_2} \rho_2 (1 - y_1 x_1 - x_2 y_2) - y_2 \mu_2(y_2)$$

The biologically relevant domain for (2.13) is

$$\Gamma = \{(x_1, y_1, x_2, y_2) \in R_+^4;\ x_1 y_1 + x_2 y_2 \le 1,\ \ y_1 \ge p_i,\ \ i = 1,2\}$$

The equilibria

Consider the system (2.13) in the region Γ. The steady state E_o is given by

$$E_0 = (0, y_1^0, 0, y_2^0)$$

Where y_i^0 are uniquely determined by $e^{-\theta y_i^0} \rho_i(1) = y_i^0 \mu_i(y_i^0), \quad i = 1,2$.

The steady state E_1 is given by

$$E_1 = (\hat{x}_1, \hat{y}_1, 0, \hat{y}_2)$$

provided that $\mu_1(y_1) = 1$ has a solution $\hat{y}_1 > 0$ and $e^{-\theta \hat{y}_1} \rho_1(1) > \hat{y}_1$.

We say that E_1 exists if these two conditions are satisfied. Then

$$\mu_1(\hat{y}_1) = 1,$$

$$e^{-\theta \hat{y}_1} \rho_1 (1 - \hat{y}_1 \hat{x}_1) = \hat{y}_1, \qquad (3.1)$$

$$e^{-\theta \hat{y}_2} \rho_2 (1 - \hat{y}_1 \ \hat{x}_1) = \hat{y}_2 \ \ \mu_2(\hat{y}_2).$$

The first equation determines $\hat{y}_1$ uniquely, the second equation determines $\hat{x}_1$ uniquely, and the third determines $\hat{y}_2$ uniquely, by the monotonicity properties (2.2) and (2.3).

Similarly, the steady state E_2 is given by

$$E_2 = (0, \tilde{y}_1, \tilde{x}_2, \tilde{y}_2)$$

provided that $\mu_2(y_2) = 1$ has a solution $\tilde{y}_2 > 0$ and $e^{-\theta \tilde{y}_2} \rho(1) > \tilde{y}_2$.

We say that E_2 exists if these two conditions are satisfied. Then

$$\mu_2(\tilde{y}_2) = 1,$$

$$e^{-\theta \tilde{y}_2} \rho_2 (1 - \tilde{x}_2 \tilde{y}_2) = \tilde{y}_2, \qquad (3.2)$$

$$e^{-\theta \tilde{y}_1} \rho_1 (1 - \tilde{x}_2 \tilde{y}_2) = \tilde{y}_1 \ \ \mu_1(\tilde{y}_1)$$

We assume that if both E_1 and E_2 exist then

$$\tilde{S} = 1 - \tilde{x}_2 \tilde{y}_2 < 1 - \hat{x}_1 \hat{y}_1 = \hat{S} \qquad (3.3)$$

(3.3) can be assumed without loss of generality if $\tilde{S} \ne \hat{S}$. If (3.3) holds, then E_o, E_1 and E_2 are the only possible steady state of (2.13).

The stability of the rest points is determined by the linearization at these points. The variational matrix for (2.13) takes the form.

$$J = \begin{bmatrix} \mu_1(y_1) - 1 & x_1 \mu_1'(y_1) & 0 & 0 \\ -y_1 e^{-\theta y_1} \rho_1' (1 - x_1 y_1 - x_2 y_2) & -x_1 e^{-\theta y_1} \rho_1' - \theta \rho_1 e^{-\theta y_1} - \mu_1 - y_1 \mu_1' & -y_2 \rho_1' e^{-\theta y_1} & -x_2 \rho_1' e^{-\theta y_1} \\ 0 & 0 & \mu_2 - 1 & x_2 \mu_2' \\ -y_1 e^{-\theta y_2} \rho_2 & -x_1 \rho_2' e^{-\theta y_2} & -y_2 \rho_2' e^{-\theta y_2} & \begin{pmatrix} -x_2 \rho_2' e^{-\theta y_2} - \\ \rho_2 \theta e^{-\theta y_2} - \mu_2 \\ -y_2 \mu_2' \end{pmatrix} \end{bmatrix} \qquad (3.4)$$

The local stability of E_o is determined by the Jacobian matrix $J(x_1, y_1, x_2, y_2)$ at $E_0(0, y_1^o, 0, y_2^o)$ provided that $\mu_i(y_i^o) \ne 0,\ e^{-\theta y_1^o} \rho_i(1) = y_i^o \mu_1(y_i^o), i = 1,2$.

$$J_0 = J\Big|_{E_0(0, y_1^o, 0, y_2^o)} \begin{bmatrix} \mu_1(y_1^o) - 1 & 0 & 0 & 0 \\ e^{-\theta y_1^o} \rho_1'(1) y_1^o & \left(-\theta e^{-\theta y_1^o} \rho_1'(1) - \mu_1(y_1^o) - y_1^o - \mu_1'^o\right) & \left(-y_2^o e^{-\theta y_1^0} \rho_1'(1)\right) & 0 \\ 0 & 0 & \left(\mu_2(y_2^0) - 1\right) & 0 \\ e^{-\theta y_2^o} \rho_2'(1) y_1^o & 0 & -y_2^o \rho_2'(1) e^{-\theta y_2^0} & \begin{pmatrix} -\theta_0 \rho_2(1) e^{-\theta y_2^o} \\ -y_2^o \mu_2'^o - \mu_2^o \end{pmatrix} \end{bmatrix}$$

(3.5)

It is easy that J_0 has eigen values as the form

$$\lambda_{1,2,} = \mu_i^o - 1 \quad , \quad \lambda_{3,4} = -\theta \mu_i^o \, y_i^o - \mu_i^o - y_i^o \, \mu_i'^o \;\; , \; i = 1,2$$
(3.6)

With $\mu_i^o = \mu_i\left(y_i^o\right)$.

$\lambda_{3,4}$ are negative and the sign of λ_i , $i = 1,2$ determines the stability of E_o and then E_o is locally asymptotically stable if $\mu_i^o - 1 < 0$, $i = 1,2$.
The local stability of E_1 determined by the Jacobian matrix J at $E_1(\hat{x}_1, \hat{y}_1, 0, \hat{y}_2)$ provided that $\mu_1(\hat{y}_1) = 1$ has a solution $\hat{y}_1 > 0$ and $e^{-\theta \hat{y}_1}\rho_1(1) > \hat{y}_1$. We say that E_1 exists if these two conditions are satisfied. Then

$$\mu_1(\hat{y}_1) = 1,$$

$$e^{-\theta \hat{y}_1}\rho_1\left(1 - \hat{x}_1 \hat{y}_1\right) = \hat{y}_1 , \qquad (3.7)$$

$$e^{-\theta \hat{y}_2}\rho_2\left(1 - \hat{x}_1 \hat{y}_1\right) = \hat{y}_2 \quad \mu_2\left(\hat{y}_2\right)$$

The first equation determines $\hat{y}_1$ uniquely, the second determines $\hat{x}_1$ uniquely, and the third determines $\hat{y}_2$ uniquely, by the monotonicity properties (2.2) and (2.3).
The Jacobian matrix J at E_1 is

$$J_1 = J\big|_{E_1(\hat{x}_1, \hat{y}_1, 0, \hat{y}_2)} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ -\hat{y}_1 e^{-\theta \hat{y}_1}\rho_1'(1 - x_1 y_1) & \begin{bmatrix} -\hat{x}_1 e^{-\theta \hat{y}_1}\rho_1'(1 - \hat{x}_1\hat{y}_1) \\ -\theta\rho_1(1 - \hat{x}_1\hat{y}_1) - 1 \end{bmatrix} & \left(-\hat{y}_2\rho_1'(1 - \hat{x}_1\hat{y}_1)\right)e^{-\theta y_1} & 0 \\ 0 & 0 & \mu_2(\hat{y}_2) - 1 & 0 \\ -\hat{y}_2 e^{-\theta \hat{y}_2}\rho_2'(1 - x_1 y_1) & -\hat{x}_1\rho_2'(1 - \hat{x}_1\hat{y}_1)e^{-\theta \hat{y}_2} & -\hat{y}_2\rho_2' \; e^{-\theta \hat{y}_2} & \begin{bmatrix} -\hat{\rho}_2\theta \; e^{-\theta \hat{y}_2} - \hat{\mu}_2 \\ -\hat{y}_2 - \hat{\mu}' \end{bmatrix}_2 \end{bmatrix}$$
(3.8)

J_1 has eigen values as the form

$$\lambda_1 = 0 \quad , \quad \lambda_2 = -1 - \theta\hat{\rho}_1 - \hat{x}_1 e^{-\theta \hat{y}_1}\hat{\rho}_1' \qquad \lambda_3 = \hat{\mu}_2 - 1$$
and
$$\lambda_4 = -\hat{\mu}_2 - \hat{y}_2 - \hat{\mu}_2' - \hat{\rho}_2 \;\; \theta \;\; e^{-\theta \hat{y}_2} \qquad (3.9)$$

With $\hat{\rho}_1 = \rho_1(1 - \hat{x}_1 \hat{y}_1)$, $\hat{\mu}_i = \mu_i(\hat{y}_i)$, $i = 1,2$

It is easy to see that λ_2, λ_4 are negative real parts and $\lambda_1 = 0$ is zero; then the sign of $\lambda_3 = \hat{\mu}_2 - 1$ determines the stability of $\hat{E}_1$ and it is stable if $\hat{\mu}_2 - 1 < 0$. A parallel analysis shows that the stability of E_2, if it exists, is determine by the eigen value $\lambda_2 = \mu_1(\tilde{y}_1) - 1$ of the Jacobian J at $E_2\left(0, \tilde{y}_1, \tilde{x}_2, \tilde{y}_2\right)$ with the following equations uniquely

$$\mu_1(\tilde{y}_1) - 1 \neq 0 \qquad , \qquad \tilde{x}_1 = 0 \; ,$$

$$\mu_2(\tilde{y}_2) = 1 , \qquad (3.10)$$

$$e^{-\theta \tilde{y}_1}\rho_1\left(1 - \tilde{x}_2 \tilde{y}_2\right) = \tilde{\mu}_1 \tilde{y}_1 ,$$

$$e^{-\theta \tilde{y}_2}\rho_2\left(1 - \tilde{x}_2 \tilde{y}_2\right) = \tilde{y}_2$$

The Jacobian J at E_2 as the form

$$J_2 = J\big|_{E_2(0, \tilde{y}_1, \tilde{x}_2, \tilde{y}_2)} = \begin{bmatrix} \mu_1(\tilde{y}_1) - 1 & 0 & 0 & 0 \\ -\tilde{y}_1 e^{-\theta \hat{y}_1}\rho_1'(1 - \tilde{x}_2\tilde{y}_2) & -\theta\tilde{\rho}_1 e^{-\theta \tilde{y}_1} - \tilde{\mu}_1 - \tilde{y}_1\tilde{\mu}_1' & -\tilde{y}_2\tilde{\rho}_1' e^{-\theta \tilde{y}_1} & -\tilde{x}_2\tilde{\rho}_1' e^{-\theta \tilde{y}_1} \\ 0 & 0 & 0 & 0 \\ -\tilde{y}_1 e^{-\theta \tilde{y}_2}\rho_2'(1 - \tilde{x}_2\tilde{y}_2) & 0 & -\tilde{y}_2\tilde{\rho}_2' e^{-\theta \tilde{y}_2} & -\tilde{x}_2\tilde{\rho}_2' e^{-\theta \tilde{y}_2} - 1 - \tilde{\rho}_2\theta e^{-\theta \tilde{y}_2} \end{bmatrix}$$
(3.11)

Let $\rho_i'\left(1 - \tilde{x}_2 \;\; \tilde{y}_2\right) = \tilde{\rho}_i'$, $\mu_i\left(\tilde{y}_i\right) = \tilde{\mu}_i$

J_2 has eigen values

$$\lambda_1 = \tilde{\mu}_1 - 1 \qquad , \quad \lambda_2 = 0$$

$$\lambda_3 = -\theta\tilde{\rho}_1 e^{-\theta \tilde{y}_1} - \tilde{\mu}_1 - \tilde{y}_1\tilde{\mu}_1' < 0 \qquad (3.12)$$

$$\lambda_4 = -\tilde{x}_2\tilde{\rho}_2' \;\; e^{-\theta \tilde{y}_2} - \tilde{\rho}_2\theta e^{-\theta \tilde{y}_2} - 1 < 0$$

and the sign of λ_i determines the stability of E_2.

Theorem 3.1

E_o is locally asymptotically stable if both $\mu_i\left(y_i^o\right) < 1, \;\; i = 1,2$, and unstable if $\mu_i\left(y_i^o\right) > 1$ for some *i*. Furthermore, $\mu_i\left(y_i^o\right) > 0$ iff E_i exists.
Proof: The first assertion has already been noted. If $\mu_1\left(y_1^o\right) > 1$ then, by our assumptions about μ_i, $\hat{y}_1$ exists that $\mu_1(\hat{y}_1) = 1$ and $\hat{y}_1 < y_1^o$. Therefore

$$\rho_1(1)e^{-\theta y_1^o} = y_1^o \, \mu_1\left(y_1^o\right) > y_1^o > \hat{y}_1$$

This implies that E_1 exists. Conversely if E_1 exists, then

$$e^{-\theta \hat{y}_1} \;\; \rho_1(1) > \hat{y}_1 = \hat{y}_1 \mu_1(\hat{y}_1) , \qquad \text{so}$$

$$y_1^o \mu_1\left(y_1^0\right) - e^{-\theta y_1^0}\rho_1(1) = 0 > \hat{y}_1\mu_1(\hat{y}_1) - e^{-\theta \hat{y}}\rho_1(1)$$

Therefore $y_1^0 > \hat{y}_1$ by monotonically if $y\,\mu_1(y) - e^{-\theta y}\,\rho_1(1)$, and consequently

$$\mu_1\left(y_1^0\right) > \mu_1(\hat{y}_1) = 1$$

Theorem 3.2

If E_1 exists and E_2 does not exist, then $\lambda_1 < 0$ and E_1 is locally asymptotically stable. Similarly, if E_2 and E_1 does not exist, then $\lambda_2 < 0$ and E_2 is locally asymptotically stable. If E_1 and E_2 exist and $\tilde{S} = 1 - \tilde{x}_2\tilde{y}_2 < 1 - \tilde{x}_1\tilde{y}_1 = \hat{S}$ hold, then $\lambda_1 > 0$ and $\lambda_2 < 0$, so E_1 is unstable and E_2 is locally asymptotically stable.

Proof: Suppose E_1 exists and E_2 does not and $\lambda_1 \geq 0$. Then $\mu_2(\hat{y}_2) \geq 1$, so there exists a unique solution $\tilde{y}_2$ of $\mu_2(y_2) = 1$. By monotonicity of μ_2 it follows that $\hat{y}_2 \geq \tilde{y}_2$.

Since

$$e^{-\theta \tilde{y}_2}\rho_2(1) > e^{-\theta \hat{y}_2}\rho_2(1 - \hat{x}_1\hat{y}_1) = \hat{y}_2\,\mu_2(\hat{y}_2) \geq \hat{y}_2 \geq \tilde{y}_2$$

we conclude that E_2 exists, contradicting our hypothesis. Therefore, $\lambda_1 < 0$ if E_1 exists and E_2 does not.

Suppose that E_1 and E_2 exists and $\tilde{S} = 1 - \tilde{x}_2\tilde{y}_2 < 1 - \hat{x}_1\hat{y}_1 = \hat{S}$, (2.13) holds.

Then

$$\tilde{y}_2\mu_2(\tilde{y}_2) - e^{-\theta\tilde{y}_2}\rho_2(\tilde{S}) = \tilde{y}_2 - e^{-\theta\tilde{y}_2}\rho_2(\tilde{S}) = 0$$
$$= \hat{y}_2\mu_2(\hat{y}_2) - e^{-\theta\tilde{y}_2}\rho_2(\hat{S}) < \hat{y}_2\mu_2(\hat{y}_2) - e^{-\theta\hat{y}_2}\rho_2(\tilde{S})$$

implying the $\tilde{y}_2 < \hat{y}_2$. Similar reasoning gives $\tilde{y}_1 < \hat{y}_1$. Therefore

$$\lambda_2 = \mu_1(\tilde{y}_1) - 1 < \mu_1(\hat{y}_1) - 1 = 0$$

and

$$\lambda_1 = \mu_2(\hat{y}_2) - 1 > \mu_2(\tilde{y}_2) - 1 = 0 .$$

In the next part, these local stability considerations will be shown to lead to corresponding global results. For this analysis, it will be important to approximate the one - dimensional unstable manifold of E_1 when both E_1 and E_2 exist and (2.13) holds. To this end, we provide information below on an eigenvector corresponding to the eigen value λ_2 of J_1.

Let $\underline{V} = (\underline{x}_1, \underline{y}_1, \underline{x}_2, \underline{y}_2)$ denote such an eigenvector. We find that:

$$\underline{x}_1 = \lambda_1^{-1}\,\hat{x}_1\,\underline{y}_1\,\mu_1(\hat{y}_1)$$

$$\left[\lambda_1^{-1}\,\hat{y}_1\frac{\partial\rho_1}{\partial s}\hat{x}_1\,\mu_1'(\hat{y}_1) + \lambda_1 + \hat{x}_1\frac{\partial\rho_1}{\partial s} + 1 + \hat{y}_1\,\mu_1'(\hat{y}_1) - \frac{\partial\rho_1}{\partial y_1}\right]\underline{y}_1 = -\hat{y}_2\frac{\partial\rho_1}{\partial s}$$

$$\left[-\frac{\partial\rho_2}{\partial y_2} + \mu_2(\hat{y}_2) + \hat{y}_2\mu_2'(\hat{y}_2)\right]\underline{y}_2 = -\hat{y}_1\frac{\partial\rho_2}{\partial s}\underline{x}_1 - \hat{x}\frac{\partial\rho_2}{\partial s}\underline{y}_1 - \hat{y}_2\frac{\partial\rho_2}{\partial s}$$

$$\underline{x}_2 = 1$$

Where the argument of the partial derivatives of ρ_i is $(1 - \hat{x}_1\,\hat{y}_1)$. If $\lambda_1 > 0$, then

$$\underline{x}_i < 0\ ,\ \underline{y}_1 < 0\ ,\ \underline{x}_2 = 1 .$$

Theorem 3.3

If E_o is the only steady state, then all solutions tend to E_o as $t \to \infty$.

If E_o and E_1 are the only steady states, then all solutions with $x_1(0) > 0$ approach E_1 as $t \to \infty$.

(iii) If E_o and E_2 are the only steady states, then all solutions with $x_2(0) > 0$ approach E_2 as $t \to \infty$.

(iv) If E_o, E_1 and E_2 exists and (2.13) holds, then all solutions with $x_2(0) > 0$ approach E_2 as $t \to \infty$.

Proof: Let $u_1 = x_1 y_1$, $u_2 = x_2 y_2$.

In the new variables (x_1, μ_1, x_2, μ_2), system (2.13) taken the form

$$x_1' = x_1\left(\mu_1\left(\frac{u_1}{x_1}\right) - 1\right),$$

$$u_1' = e^{-\theta\frac{u_1}{x_1}}\rho_1(1 - u_1 - u_2)x_1 - u_1, \qquad (3.13)$$

$$x_2' = x_2\left(\mu_2\left(\frac{u_2}{x_2}\right) - 1\right),$$

$$u_2' = e^{-\theta\frac{\mu_2}{x_2}}\rho_2(1 - u_1 - u_2)x_2 - u_2$$

With $x_i > 0$ and

$$\zeta = \left\{(x_1, u_1, x_2, u_2) \in R_+^4 \mid x_i > 0\ , u_1 + u_2 \leq 1\right\} \qquad (3.14)$$

Which is positively invariant for (2.13),

We can see E_o = (0, 0, 0, 0), $E_1 = (\hat{x}_1, \hat{u}_1, 0, 0)$ and

$E_2 = (0, 0, \tilde{x}_2, \tilde{u}_2)$ as steady states of (3.13), where $\hat{u}_1 = \hat{x}_1 \ \hat{y}_1$ and $\tilde{u}_2 = \tilde{y}_2 \ \tilde{x}_2$, provided, of course, that they exist for (3.13).

By comparison result we obtain bounds on solutions of (3.13). If (x_1, μ_1, x_2, μ_2) is a solution of (2.13) in ξ then

$$x_i' = x_i \left(\mu_i \left(\frac{u_i}{x_i} \right) - 1 \right), \qquad (3.15)$$

$$u_i' \le e^{-\theta \frac{u_i}{x_i}} \rho_i (1 - u_i) x_i - u_i \ , \ i = 1, 2$$

Can be compared to the solutions $(\bar{x}_i, \bar{u}_i)$ of

$$\bar{x}_i' = \bar{x}_i \left(\mu_i \left(\frac{\bar{u}_i}{x_i} \right) - 1 \right)$$

$$\bar{u}_1' = e^{-\theta \frac{\bar{u}_i}{x_i'}} \rho_i (1 - \bar{u}_i) \bar{x}_i - \bar{u}_i \qquad , \qquad i = 1, 2$$

With $(x_i(0), u_i(0)) = (\bar{x}_i(0), \bar{u}_i(0))$, also

$$\begin{aligned} x_i(t) &\le \bar{x}_i(t) \\ u_i(t) &\le \bar{u}_i(t) \qquad , \qquad t \ge 0 \qquad , \qquad i = 1, 2 \end{aligned}$$

We know that

$$\lim_{t \to \infty} (\bar{x}_i(t), \bar{u}_i(t)) = \begin{cases} (0, 0) & \text{if } E_1 \text{ does not exists} \\ (\hat{x}_1, \hat{u}_1) & \text{if } i = 1, \ E_1 \text{ exists} \\ (\tilde{x}_2, \tilde{u}_2) & \text{if } i = 2 \text{ and } E_2 \text{ exists} \end{cases}$$

The last two equations imply the boundedness of solutions of (3.13) and imply the assertion of the theorem.

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