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 scarce 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 the outcome 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 phytoplankton 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

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

$$x'_1 = x_1 \left(\mu_1 \left(y_1\right) - D\right),$$

$$y'_1 = e^{-\theta y_1} \rho_1(S) - \mu_1 \left(y_1\right) y_1,$$  \hspace{1cm} (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 $\mu_i(y_i), \mu_2(y_2), \rho_1(S), \rho_2(S)$ 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 $\mu_i$ is defined and continuously differentiable for $y_i \geq p_i$, where $p_i \geq 0$ and satisfies

$$\mu_i \left(y\right) \geq 0,$$

$$\mu'_i \left(y\right) > 0,$$  \hspace{1cm} (2.2)

$$\mu_i \left(p\right) = 0.$$  

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:

$$x_i(0) > 0 \hspace{0.5cm} , \hspace{0.5cm} y_i(0) \geq p_i \hspace{0.5cm} , \hspace{0.5cm} S(0) \geq 0.$$  

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, $y_1^o$ is the unique solution of

$$e^{-\theta y_1} \rho_1 \left(S\right) - y_1 \mu_1 \left(y_1\right) = 0.$$  

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

$$E_j = \left(x_j, y_j, 0, y_2, S\right)$$

Where

$$\mu_j \left(y_j\right) = D, \hspace{1cm} (2.3)$$

$$e^{-\theta y_j} \rho_j \left(S\right) = D \left(y_j\right),$$

$$\hat{x}_j = \frac{S^o - S}{y_j},$$

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

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

(i) $\mu_j \left(y_j\right) = D$ has a solution $y_j = \hat{x}_j$, and  \hspace{1cm} (2.4)

(ii) $e^{-\theta y_j} \rho_2 \left(S\right) > D \hat{x}_j.$  

(2.4) says that the population $x_j$ 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

$$E_2 = \left(0, y_1^o, x_2, y_2^o, S^o\right)$$

Where

$$\mu_2 \left(y_2^o\right) = D, \hspace{1cm} (2.5)$$

$$e^{-\theta y_2^o} \rho_2 \left(S^o\right) = D \left(y_2^o\right),$$

$$\hat{x}_2 = \frac{S^o - S}{y_2^o}.$$
\[ e^{-\theta \frac{1}{2}} \rho_1(S) = \tilde{y} \rho_1 \]

\( E_2 \) exists iff

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

(ii) \( e^{-\theta \frac{1}{2}} \rho_2(S) > D \quad \tilde{y} \) (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 is nonsingular.

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

\[ S \leq \tilde{S} \quad \text{(2.7)} \]

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

\[ S \leq \tilde{S} \quad \text{(2.8)} \]

**Theorem 2.1**

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

(2.4) and (2.6) do not hold, then \( E_0 \) is the only steady state and every solution of (2.1) satisfies

\[ (x_1(t), y_1(t), x_2(t), y_2(t), S(t)) \rightarrow E_o \quad \text{as} \quad t \rightarrow \infty \]

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

\[ (x_1(t), y_1(t), x_2(t), y_2(t), S(t)) \rightarrow E_1 \quad \text{as} \quad t \rightarrow \infty \]

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 \( x_2(0) > 0 \), satisfies

\[ (x_1(t), y_1(t), x_2(t), y_2(t), S(t)) \rightarrow E_2 \quad \text{as} \quad t \rightarrow \infty \]

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 \( x_0(0) > 0 \), satisfies

\[ (x_1(t), y_1(t), x_2(t), y_2(t), S(t)) \rightarrow E_2 \quad \text{as} \quad t \rightarrow \infty \]

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

\[ \mu_i(y_i^0) \neq 0, \quad i = 1, 2 \]

For the second (Third) assertion, only the single condition, \( \mu_2(y_2^0) \neq D \quad \mu_i(y_i^0) \neq D \) 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

\[ \mu_i(y_i) = \hat{y}_i e^{-\theta \frac{1}{2}} \rho_i(S) \]

\[ \mu_2(y_2) = \hat{y}_2 e^{-\theta \frac{1}{2}} \rho_2(S) \]

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

\[ x'_i = x_i \left( \hat{y}_i e^{-\theta \frac{1}{2}} \rho_i(S) - D \right), \]

\[ x'_2 = x_2 \left( \hat{y}_2 e^{-\theta \frac{1}{2}} \rho_2(S) - D \right), \quad \text{(2.9)} \]

\[ S' = D(S'' - S) - x_1 e^{-\theta \frac{1}{2}} \rho_1(S) - x_2 e^{-\theta \frac{1}{2}} \rho_2(S) \]

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

\[ x'_i = x_i \left( \mu_i(y_i) - 1 \right), \]

\[ y'_i = e^{-\theta \frac{1}{2}} \rho_i(S) - y_i \mu_i(y_i) \quad \text{(2.10)} \]

\[ S' = 1 - S - \sum_{i=1}^{2} x_i e^{-\theta \frac{1}{2}} \rho_i(S) \]

With \( \bar{t} = D t, \bar{S} = S/S', \bar{y}_i = y_i/y_i, \bar{x}_i = x_i/y_i/S', \bar{y}_i^* \) are arbitrarily chosen representative values of the variables \( y_i \) and

\[ \bar{\mu}(\bar{y}) = D^{-1} \mu \left( y_i \bar{y}_i \right), \]

\[ \bar{\rho}(\bar{S}, \bar{y}) = \left(D \bar{y}_i^* \right)^{-1} \rho \left( S'' \bar{S}, y_i^* \bar{y}_i \right) \]

Let \( \Sigma = S + y_1 x_1 + y_2 x_2 \), \( \Sigma \) consists of unbounded free nutrient plus stored nutrient and it satisfies:
\[ \Sigma' = 1 - \Sigma \quad (2.11) \]

Therefore, all solutions of (2.10) asymptotically approach the surface
\[ S + y_1x_1 + y_2x_2 = 1 \quad (2.12) \]
i.e. \( \Sigma(t) \to 1 \ as \ t \to \infty \)

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.
\[
\begin{align*}
x'_1 &= x_1(\mu_1(y_1) - 1), \\
y'_1 &= e^{-\theta y_1} \rho_1(1 - y_1x_1 - x_2y_2) - y_1\mu_1(y_1), \\
x'_2 &= x_2(\mu_2(y_2) - 1), \\
y'_2 &= e^{-\theta y_2} \rho_2(1 - y_1x_1 - x_2y_2) - y_2\mu_2(y_2)
\end{align*}
\]

The biologically relevant domain for (2.13) is
\[ \Gamma = \{(x_1,y_1,x_2,y_2) \in \mathbb{R}^4; x_1, y_1 + x_2 y_2 \leq 1, \ y_i \geq \rho_i, \ i = 1,2 \} \]

The equilibria

Consider the system (2.13) in the region \( \Gamma \). The steady state \( E_0 \) is given by
\[ E_0 = (0, y_1^0, 0, y_2^0) \]

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

The steady state \( E_1 \) is given by
\[ E_1 = (\hat{x}_1, \hat{y}_1, 0, \hat{y}_2) \]

provided that \( \mu_1(\hat{y}_1) = 1 \) 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
\[ \mu_1(\hat{y}_1) = 1, \]
\[ e^{-\theta \hat{y}_1} \rho_1(1 - \hat{y}_1, \hat{x}_1) = \hat{y}_1, \quad (3.1) \]

\[ e^{-\theta \hat{y}_2} \rho_2(1 - \hat{y}_2, \hat{x}_2) = \hat{y}_2 \mu_2(\hat{y}_2). \]

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
\[ E_2 = (0, y_1^0, \hat{y}_2, y_2^0) \]

provided that \( \mu_2(y_2) = 1 \) has a solution \( y_2^0 > 0 \) and \( e^{-\theta y_2} \rho_1(1) > y_2^0 \).

We say that \( E_2 \) exists if these two conditions are satisfied. Then
\[ \mu_2(y_2^0) = 1, \]
\[ e^{-\theta y_2} \rho_2(1 - y_2^0, \hat{y}_2) = y_2^0, \quad (3.2) \]

\[ e^{-\theta y_2} \rho_1(1 - y_2^0, y_2^0) = y_2^0 \mu_1(y_2^0) \]

We assume that if both \( E_1 \) and \( E_2 \) exist then
\[ \hat{y}_1 - y_2^0 < 1 - \hat{x}_1, \hat{y}_1 = \hat{S} \quad (3.3) \]

(3.3) can be assumed without loss of generality if \( \hat{S} \neq \tilde{S} \). If (3.3) holds, then \( E_0, E_1 \) and \( E_2 \) are the only possible steady state of (2.13).

The stability of the rest points is determined by the Jacobian matrix \( J(x_1, y_1, x_2, y_2) \) at \( E_0(0, y_1^0, 0, y_2^0) \) provided that
\[ \mu_i(y_i^0) \neq 0, \quad e^{-\theta y_i^0} \rho_i(1) = y_i^0 \mu_i(y_i^0), i = 1,2. \]

\[
J = \begin{bmatrix}
-\gamma e^{-\theta y_1} \rho_1(y_1) & -\gamma e^{-\theta y_1} \rho_1(y_1) & 0 & 0 \\
\gamma e^{-\theta y_1} \rho_1(y_1) & 0 & 0 & 0 \\
0 & -\gamma e^{-\theta y_2} \rho_2(y_2) & 0 & 0 \\
0 & 0 & -\gamma e^{-\theta y_2} \rho_2(y_2) & 0 \\
\end{bmatrix}
\]

(3.4)

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

\[
J_{i,0} = \begin{bmatrix}
\rho_1(y_1) & 0 & 0 & 0 \\
0 & \rho_1(y_1) & 0 & 0 \\
0 & 0 & \rho_2(y_2) & 0 \\
0 & 0 & 0 & \rho_2(y_2) \\
\end{bmatrix}
\]

(3.5)
It is easy that \( J_0 \) has eigen values as the form
\[
\lambda_{i, 2} = \mu_i - 1, \quad \lambda_{i, 3} = -\theta \mu_i y_i - \mu_i - y_i, \quad i = 1, 2
\]  
(3.6)

With \( \mu_i^n = \mu_i \left( y_i^n \right) \).

\( \lambda_{i, 2} \) are negative and the sign of \( \lambda_i \), \( i = 1, 2 \) determines the stability of \( E_0 \) and then \( E_0 \) is locally asymptotically stable if \( \mu_i^n - 1 < 0 \), \( i = 1, 2 \).

The local stability of \( E_1 \) determined by the Jacobian matrix \( J_1 \) at \( E_1 \left( \hat{x}_1, \hat{y}_1, 0, \hat{y}_2 \right) \) provided that \( \mu_i \left( \hat{y}_i \right) = 1 \) has a solution \( \hat{y}_1 > 0 \) and \( e^{-\theta \hat{y}_i} \rho_i \left( 1 \right) > \hat{y}_1 \). We say that \( E_1 \) exists if these two conditions are satisfied. Then
\[
\mu_i \left( \hat{y}_i \right) = 1, \quad i = 1, 2
\]  
(3.7)

\[
e^{-\theta \hat{y}_i} \rho_i \left( 1 - \hat{x}_i \hat{y}_i \right) = \hat{y}_1, \quad \mu_2 \left( \hat{y}_2 \right)
\]

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 \( J_1 \) at \( E_1 \) is
\[
J_1 = \begin{bmatrix}
-\lambda_1 & -\lambda_2 & 0 \\
0 & -\lambda_3 & 0 \\
0 & 0 & -\lambda_4
\end{bmatrix}
\]  
(3.8)

\( J_1 \) has eigen values as the form
\[
\lambda_1 = 0, \quad \lambda_2 = -1 - \theta \hat{x}_1 - \hat{x}_1 \hat{y}_1, \quad \lambda_3 = \hat{y}_2 - 1
\]
and
\[
\lambda_4 = -\hat{y}_2 - \hat{y}_2 - \hat{y}_2 - \theta e^{-\theta \hat{y}_2}
\]  
(3.9)

With \( \hat{\mu}_i = \rho_i \left( 1 - \hat{x}_i \right) \), \( \hat{\mu}_i = \mu_i \left( \hat{y}_i \right) \), \( i = 1, 2 \)

It is easy to see that \( \lambda_2, \lambda_4 \) are negative real parts and \( \lambda_1 = 0 \) is zero; then the sign of \( \lambda_3 = \hat{\mu}_2 - 1 \) determines the stability of \( E_1 \) 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 \( \lambda_2 = \mu_i \left( \hat{y}_2 \right) - 1 \) of the Jacobian \( J \) at \( E_2 \left( 0, \hat{y}_1, \hat{y}_2, \hat{y}_2 \right) \) with the following equations uniquely
\[
\mu_i \left( \hat{y}_i \right) - 1 \neq 0, \quad \hat{y}_i = 0
\]  
(3.10)

\[
e^{-\theta \hat{y}_i} \rho_i \left( 1 - \hat{x}_i \hat{y}_i \right) = \beta_i \hat{y}_i
\]  
(3.11)

Let \( \rho_i \left( 1 - \hat{x}_i \hat{y}_i \right) = \beta_i \), \( \mu_i \left( \hat{y}_i \right) = \beta_i \)

\( J_2 \) has eigen values
\[
\lambda_1 = \beta_i - 1, \quad \lambda_2 = 0
\]
\[
\lambda_3 = -\theta \beta_i e^{-\theta \hat{y}_i} \beta_i - \beta_i e^{\theta \hat{y}_i} < 0
\]  
(3.12)

\[
\lambda_4 = -\hat{x}_2 \beta_i e^{-\hat{x}_2} \beta_i - \theta e^{-\theta \hat{y}_2} \beta_i - 1 < 0
\]
and the sign of \( \lambda_4 \) determines the stability of \( E_2 \).

**Theorem 3.1**

\( E_0 \) is locally asymptotically stable if both \( \mu_i \left( y_i^n \right) < 1 \), \( i = 1, 2 \), and unstable if \( \mu_i \left( y_i^n \right) > 1 \) for some \( i \). Furthermore, \( \mu_i \left( y_i^n \right) > 0 \) iff \( E_1 \) exists.

**Proof:** The first assertion has already been noted. If \( \mu_i \left( y_i^n \right) > 1 \) then, by our assumptions about \( \mu_i \), \( \hat{y}_1 \) exists that \( \mu_i \left( \hat{y}_1 \right) = 1 \) and \( \hat{y}_1 < y_i^n \). Therefore
\[
\rho_i \left( 1 - e^{-\theta y_i^n} \mu_i \left( y_i^n \right) > y_i^n \right) \hat{y}_1
\]

This implies that \( E_1 \) exists. Conversely if \( E_1 \) exists, then
\[
e^{\theta \hat{y}_i} \rho_i \left( 1 - \hat{y}_i \right) = \hat{y}_i \mu_i \left( \hat{y}_i \right) > 0 \]
\[
\hat{y}_i \mu_i \left( y_i^n \right) - e^{\theta \hat{y}_i} \rho_i \left( 1 \right) = 0 > \hat{y}_i \mu_i \left( \hat{y}_i \right) - e^{\theta \hat{y}_i} \rho_i \left( 1 \right)
\]
Therefore \( y_0^* > \hat{y}_1 \) by monotonically if \( y_0 = y_1 e^{-\alpha y_1} \rho_1(1) \), and consequently

\[
\mu_1(y_0^*) > \mu_1(\hat{y}_1) = 1
\]

**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 \( S_{E_1} = 1 - x_1^* y_1^* < 1 - x_1^* y_1^* = S \), 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 \( \hat{y}_2 \) of \( \mu_2(y_2) = 1 \). By monotonicity of \( \mu_2 \) it follows that \( \hat{y}_2 \geq \hat{y}_1 \).

Since

\[
e^{-\alpha y_1} \rho_1(1) > e^{-\alpha \hat{y}_1} \rho_2(1 - \hat{y}_1, \hat{y}_1) = \hat{y}_2 \mu_2(\hat{y}_2) \geq \hat{y}_2 \geq \hat{y}_1\]

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 \( E_2 \) exist and \( S_{E_1} = 1 - x_1^* y_1^* < 1 - x_1^* y_1^* = S \), (2.13) holds. Then

\[
y_1^* \mu_1(y_1^*) - e^{-\alpha y_1} \rho_1(S) = y_1^* \mu_1(\hat{y}_1^*) = \hat{y}_2 < y_1^* \mu_2(\hat{y}_2) < \hat{y}_2 = y_1^* \mu_1(\hat{y}_1^*) - e^{-\alpha y_1} \rho_1(S)
\]

implying the \( y_1^* < \hat{y}_2 \). Similar reasoning gives \( y_1^* < \hat{y}_1 \).

Therefore

\[
\lambda_2 = \mu_1(y_1^*) - 1 < \mu_1(\hat{y}_1) = 1
\]

and

\[
\lambda_1 = \mu_2(\hat{y}_2) - 1 > \mu_2(y_1^*) - 1 = 0
\]

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 \( E_i \) 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 eigenvalue \( \lambda_2 \) of \( J_i \).

Let \( V = \{(x_1, y_1, x_2, y_2)\} \) denote such an eigenvector. We find that:

\[
x_1 = \mu_1^{-1} \hat{x}_1, y_1 = \mu_1(\hat{y}_1)
\]

\[
\mu_2(\hat{y}_2) - 1 = 0
\]

\[
\lambda_2 = \mu_1(y_1^*) - 1 < \mu_1(\hat{y}_1) = 1
\]

\[
x_i = \frac{1}{\mu_1(y_1^*)} \hat{x}_i, u_i = \frac{1}{\mu_1(y_1^*)} \hat{u}_i
\]

\[
x_1 = \frac{1}{\mu_1(y_1^*)} \hat{x}_1, u_1 = \frac{1}{\mu_1(y_1^*)} \hat{u}_1
\]

\[
x_2 = \frac{1}{\mu_1(y_1^*)} \hat{x}_2, u_2 = \frac{1}{\mu_1(y_1^*)} \hat{u}_2
\]

\[
\xi = \{(x_1, u_1, x_2, u_2) \in R^4 | x_1 > 0, u_1 + u_2 \leq 1\}
\]

Which is positively invariant for (2.13).

We can see \( E_o = (0, 0, 0, 0) \), \( E_i = (\hat{x}_i, \hat{u}_i, 0, 0) \) and...
$E_2 = (0,0,\tilde{B_2},\tilde{E_2})$ as steady states of (3.13), where
$\tilde{u}_i = \hat{x}_i, \quad \hat{y}_i$ and $\tilde{B_2} = \hat{y}_2, \hat{x}_2$, provided, of course, that
they exist for (3.13).

By comparison result we obtain bounds on solutions of (3.13). If $(x_i, \mu_i, x_2, \mu_2)$ is a solution of (2.13) in $\xi$ then

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

$$u_i' \leq e^{-\rho_u^{u_i}} \rho_i (1-u_i)x_i - u_i, \quad i = 1, 2$$

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

$$\overline{x}_i = \tilde{x}_i \left( \mu_i \left( \frac{\overline{u}_i}{\tilde{x}_i} \right) - 1 \right)$$

$$\overline{u}_i = e^{-\rho_u^{\overline{u}_i}} \rho_i (1-\overline{u}_i)\overline{x}_i - \overline{u}_i, \quad i = 1, 2$$

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

$$x_i(t) \leq \overline{x}_i(t)$$

$$u_i(t) \leq \overline{u}_i(t), \quad t \geq 0, \quad i = 1, 2$$

We know that

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

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