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Comparing the Effects of Interactive and Noninteractive Complementary Nutrients on Growth in a Chemostat

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ABSTRACT

We compare the effects of interactive and noninteractive complementary nutrients on the growth of an organism in the chemostat. We also compare these two situations to the case when the nutrients are substitutable. In previous studies, complementary nutrients have been assumed to be noninteractive. However, more recent research indicates that some complementary nutrient relationships are interactive. We show that interactive complementary and substitutable nutrients can lead to higher population densities than do noninteractive complementary nutrients. We numerically illustrate that if the washout rate is high, an organism can persist at higher densities when the complementary nutrients are interactive than when they are noninteractive, which can result in the extinction of the organism. Finally, we present an example by making a small adjustment to the model that leads to a single nutrient model with an intermediate metabolite of the original substrate as the nutrient for the organism.

Keywords: Chemostat; Growth; Dual Substrate; Complementary Nutrients; Substitutable Nutrients

1. Introduction

We consider a basic, resource-based model of growth in the chemostat. Such models have applications in ecology to model a simple lake and in biotechnology to model the commercial bio-reactor. Experimental verification of the match between theory and experiment in the chemostat can be found in [1]. Basic growth in the chemostat is described by the dimensionless system

$$\begin{aligned} \frac{dS}{dt} &= (S^{(0)} - S)D - \frac{x}{y_S} f(S), S(0) \geq 0 \\ \frac{dx}{dt} &= (f(S) - D)x, x(0) \geq 0. \end{aligned} \quad (1)$$

For a detailed discussion of growth in the chemostat and a description of the constants $S^{(0)}$ (input of the nutrient), y_S (yield constant), and D (dilution (washout) rate), see Smith and Waltman [2].

Two nutrients are complementary if they meet different needs for an organism. For example, ammonia provides nitrogen while glucose provides carbon [3] (building blocks of protein). Similarly, two nutrients are substitutable if they meet the same needs for an organism. For example, glucose, galactose, maltose, ribose, arabinose, and fructose all provide energy (sugar) [4].

See Stroot *et al.* [5], for a recent study of *Acinetobac-*

ter spp. bacteria in an activated sludge bioreactor system using the noninteractive Monod model for multiple nutrients.

However, other research [3,4,6-9] indicates that a model of interactive multiple limiting nutrients may be more appropriate for some situations. Of particular interest, Lendenmann and Egli [4] discuss several growth models appropriate for substitutable interactive nutrients and compare them to the growth of *E. coli* with sugar nutrients glucose, galactose, maltose, ribose, arabinose, and fructose. Whang *et al.* [9] perform a similar study using bacteria from the wastewater of a food-processing plant. On the other hand, Bapat *et al.* [10] use a Monod model to study the growth of *A. mediterranei* S699 with multiple interactive complementary nutrients. Champagne *et al.* [11] form a model of cometabolism with two interactive complementary nutrients in a well-mixed system. Bae and Rittmann [12] develop a dual-limiting model, compare the results to experimental data, and observe that they agree, which provides further evidence that a multiple nutrient limiting model might be more appropriate in some situations than a single nutrient limiting model. From [12], having an accurate kinetic model for dual limitation is essential for a proper design of treatment operations such as in bioremediation or contaminated groundwater... Dual limitation also can be

critical for predicting the fate of pollutants in certain natural environments, such as a deep lake or an ocean...

To consider a single organism's growth in the chemostat for two nutrients, we study the dimensionless system

$$\begin{aligned} \frac{dS_1}{dt} &= (S_1^{(0)} - S_1)D - \frac{x}{y_1} f(S_1, S_2), S_1(0) \geq 0 \\ \frac{dS_2}{dt} &= (S_2^{(0)} - S_2)D - \frac{x}{y_2} f(S_1, S_2), S_2(0) \geq 0 \quad (2) \\ \frac{dx}{dt} &= (f(S_1, S_2) - D)x, x(0) \geq 0. \end{aligned}$$

If the nutrients are complementary and noninteractive and assuming Monod (or Michaelis-Menten) kinetics typical choices of f take the following forms. When assuming that the nutrients are noninteractive, one of the nutrients is the limiting nutrient. If the nutrients are complementary and noninteractive, we take f to be

$$f(S_1, S_2) = \min\left(\frac{m_1 S_1}{K_1 + S_1}, \frac{m_2 S_2}{K_2 + S_2}\right), \quad (3)$$

The biological meaning of (3) is that one of S_1 or S_2 is the limiting nutrient, which is appropriate in modeling many situations [3]. If the nutrients are complementary and interactive, f has the form

$$f(S_1, S_2) = \frac{m_1 S_1}{K_1 + S_1} \frac{m_2 S_2}{K_2 + S_2}. \quad (4)$$

Finally, if the nutrients are supplementary, f has the form

$$f(S_1, S_2) = \frac{m_1 S_1}{K_1 + S_1} + \frac{m_2 S_2}{K_2 + S_2}. \quad (5)$$

and the constants are described in **Table 1**. (Refer to [13-

15] or [16]).

2. Growth in the Chemostat

Using Thieme's results from 1992 [17], we show that System (2) is asymptotic to a single nonlinear equation.

$$\text{Let } \Sigma_1 = S_1^{(0)} - S_1 - \frac{1}{y_1}x \text{ and } \Sigma_2 = S_2^{(0)} - S_2 - \frac{1}{y_2}x$$

Then, $\Sigma_1' = -D\Sigma_1$ and $\Sigma_2' = -D\Sigma_2$ so System (2) can be rewritten as

$$\begin{aligned} \frac{d\Sigma_1}{dt} &= -D\Sigma_1 \\ \frac{d\Sigma_2}{dt} &= -D\Sigma_2 \end{aligned} \quad (6)$$

$$\frac{dx}{dt} = \left(f\left(S_1^{(0)} - \frac{1}{y_1}x - \Sigma_1, S_2^{(0)} - \frac{1}{y_2}x - \Sigma_2 \right) - D \right) x$$

Because the solutions of $\Sigma_1' = -D\Sigma_1$ and $\Sigma_2' = -D\Sigma_2$ are $\Sigma_1 = C_1 e^{-Dt} \rightarrow 0$ as $t \rightarrow \infty$ and $\Sigma_2 = C_2 e^{-Dt} \rightarrow 0$ as $t \rightarrow \infty$, in the limit as $t \rightarrow \infty$, System (6) is asymptotic to the equation

$$\frac{dx}{dt} = \left(f\left(S_1^{(0)} - \frac{1}{y_1}x, S_2^{(0)} - \frac{1}{y_2}x \right) - D \right) x \quad (7)$$

Depending on whether the nutrients are complementary (noninteractive or interactive) or substitutable and assuming Monod (or Michaelis-Menten) kinetics typical choices of f take the forms given by Equations (3)-(5). For all three situations, $x = 0$ is a boundary rest point. If f is given by (4), we have the additional rest points: as the Equation (8)

Similarly, if f is given by (5), we obtain the additional rest points: as the Equation (9)

$$\begin{aligned} x = \frac{1}{2(D - m_1 m_2)} & \left[D(K_1 + S_1^{(0)})y_1 + D(K_2 + S_2^{(0)})y_2 - m_1 m_2 (S_1^{(0)}y_1 + S_2^{(0)}y_2) \right. \\ & \pm \left(-4(D - m_1 m_2) \left(-m_1 m_2 S_1^{(0)} S_2^{(0)} + D(K_1 + S_1^{(0)})(K_2 + S_2^{(0)}) \right) y_1 y_2 \right. \\ & \left. \left. + \left(m_1 m_2 (S_1^{(0)}y_1 + S_2^{(0)}y_2) - D \left((K_1 + S_1^{(0)})y_1 + (K_2 + S_2^{(0)})y_2 \right) \right)^2 \right)^{1/2} \right] \end{aligned} \quad (8)$$

$$\begin{aligned} x = \frac{1}{2} & \left[K_1 y_1 + S_1^{(0)} y_1 + K_2 y_2 + S_2^{(0)} y_2 + \frac{K_1 m_1 y_1 + K_2 m_2 y_2}{D - m_1 - m_2} \right. \\ & \pm \frac{1}{D - m_1 - m_2} \left(-4(D - m_1 - m_2) \left(-K_2 m_1 S_1^{(0)} - (K_1 m_2 + (m_1 + m_2) S_1^{(0)}) S_2^{(0)} \right) \right. \\ & + D(K_1 + S_1^{(0)})(K_2 + S_2^{(0)})y_1 y_2 + (K_1 m_2 y_1 + (m_1 + m_2) S_1^{(0)} y_1 \\ & \left. \left. + K_2 m_1 + (m_1 + m_2) S_2^{(0)} y_2 - D(K_1 + S_1^{(0)})y_1 + (K_2 + S_2^{(0)})y_2 \right) \right)^2 \right] \end{aligned} \quad (9)$$

Numerical results using f given by (3) (noninteractive complementary), (4) (interactive complementary), and (5) (substitutable) using the parameter values given in **Table 2** are illustrated in **Figure 1**. In the figure, we can observe that substitutable nutrients lead to higher population densities than do complementary nutrients, which is not surprising. However, the differences in the densities from noninteractive and interactive nutrients are more surprising. When the nutrients are interactive, Rows 1 and 2 show that there can be a second (unstable) equilibrium population density. The stable population density is attained more quickly when the nutrients are interactive than when they are noninteractive. Finally, the stable

population density is generally higher when the nutrients are interactive than when they are noninteractive.

In fact, the population densities can be quite large as illustrated in **Figure 2**. Consider the values listed in Row 2 of **Table 2** (corresponding to Row 2 of **Figure 1**). In **Figure 2**, we increase D (the washout rate) from $D = 0.25$ to $D = 0.75$ (row 1), $D = 1.25$ (row 2), and $D = 1.75$ (row 3). Observe that as D increases, interactive complementary nutrients lead to higher population densities than do noninteractive complementary nutrients. In fact, when the washout rate is sufficiently high, extinction occurs when the nutrients are noninteractive complementary while stable persistence occurs when the nutri-

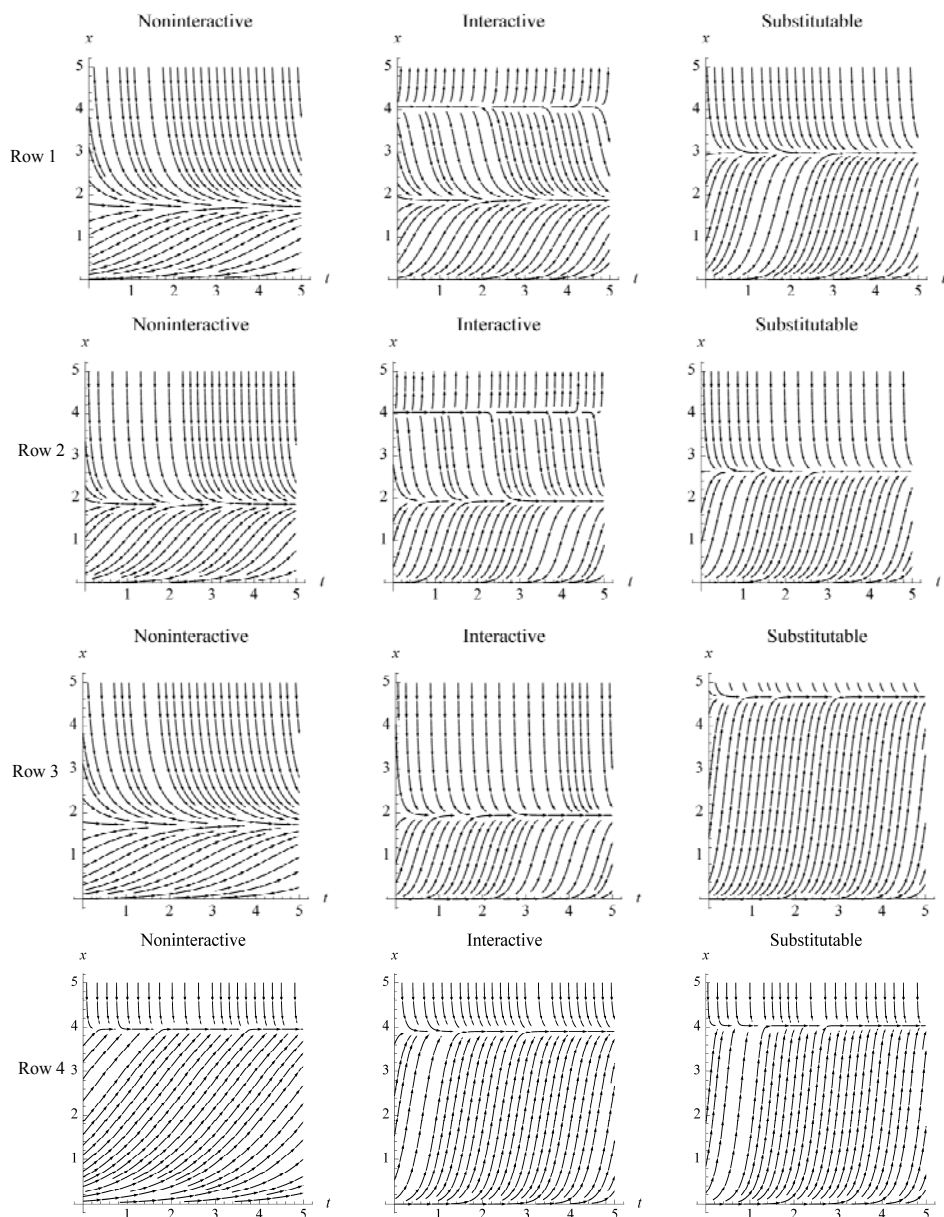


Figure 1. Modeling growth with noninteractive complementary, interactive complementary, and substitutable nutrients using the parameter values given in Table 2.

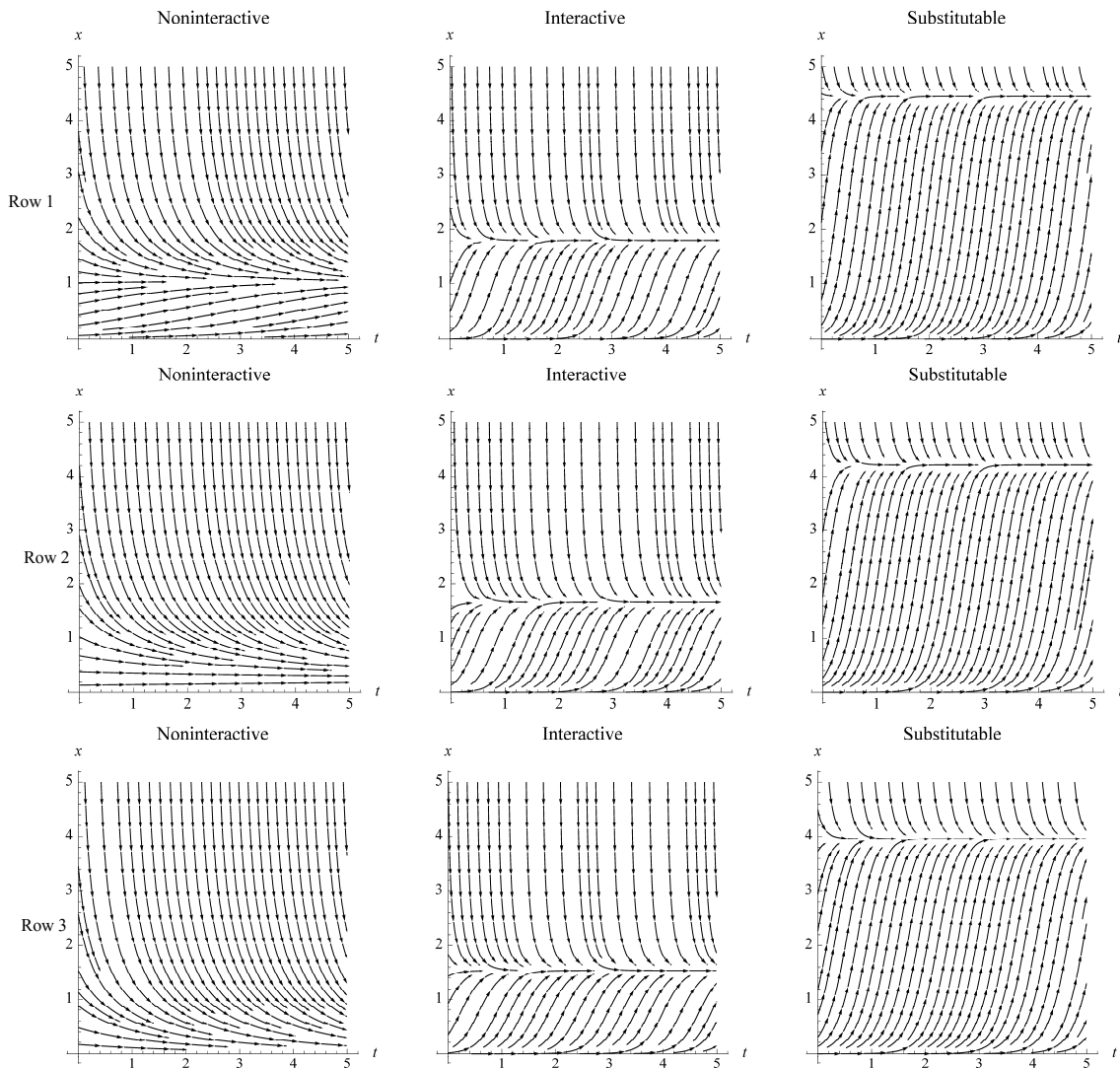


Figure 2. Row 1: $D = 0.75$; Row 2: $D = 1.25$; Row 3: $D = 1.75$.

Table 1. Descriptions of the constants in Equations (2)-(5).

$S_1^{(0)}, S_2^{(0)}$	Input concentration of the nutrients S_1 and S_2
D	Dilution (washout) rate of chemostat
m_1, m_2	Maximal growth rate of i th competitor
K_1, K_2	Michaelis-Menten (half-saturation) constants
y_1, y_2	Yield constants
$f(S_1, S_2)$	Growth rate

Entes are interactive and complementary.

3. An Intermediate Metabolite

A particularly interesting situation occurs when one substance degrades to a nutrient for the growth of an organism. Specifically, Sanchez *et al.* [18], study the particular

situation in which phenol degrades to an intermediate metabolite that is then the primary nutrient for the organism (bacterium *Pseudomonas putida* Q5). This situation is particularly interesting because a “harmful” substance degrades to a state in which it is a nutrient for the organism under consideration that is growing in the chemostat, rendered harmless, and eliminated. To model this situation, System (2) is adjusted to

$$\begin{aligned} \frac{dS_1}{dt} &= (S_1^{(0)} - S_1)D - \frac{x}{y_1} f_1(S_1, S_2), S_1(0) \geq 0 \\ \frac{dS_2}{dt} &= -DS_2 - \frac{x}{y_1} f_1(S_1, S_2) - f_2(S_2)x, S_2(0) \geq 0 \quad (10) \\ \frac{dx}{dt} &= (f_2(S_2) - D)x, x(0) \geq 0, \end{aligned}$$

where $a > 0$ is a positive constant. Sanchez *et al.* [18], successfully fit a model of the form of System (10) using

$$f_1(S_1, S_2) = \frac{m_1 S_1}{K_{1a} + S_1^p} \frac{S_2}{K_{1b} + S_1^n}, \quad (11)$$

where

$$p = p_1 + \left(1 + e^{-(S_2 + p_2)}\right)^{-1}$$

and

$$n = n_1 + \left(1 + e^{-(S_2 + n_2)}\right)^{-1}$$

and $f_2 = a \cdot S_2$ to data obtained from their study of bacterium *Pseudomonas putida* Q5. With $p = n = 1$ and $m_1 = m_1 m_2$ (Notation in Equations (3)-(5).) and $f_2 = a \cdot S_2$, (11) is the same as (4).

Although we cannot reduce System (10) to a single equation as with System (2), we can reduce it to a system of two equations. To do so, let $\Sigma = S_1^{(0)} - S_1 - S_2 - x$. Then, $\Sigma' = -D\Sigma$ and System (10) can be rewritten as

$$\begin{aligned} \frac{d\Sigma}{dt} &= -D\Sigma \\ \frac{dS_2}{dt} &= -DS_2 - \frac{x}{y_1} f_1(S_1^{(0)} - S_2 - x - \Sigma, S_2) - f_2(S_2)x, \\ \frac{dx}{dt} &= (f_2(S_2) - D)x. \end{aligned} \quad (12)$$

Because the solution of $\Sigma' = -D\Sigma$ is $\Sigma = Ce^{-Dt} \rightarrow 0$ as $t \rightarrow \infty$, in the limit as $t \rightarrow \infty$, System (12) is asymptotic to the system

$$\begin{aligned} \frac{dS_2}{dt} &= -DS_2 - \frac{x}{y_1} f_1(S_1^{(0)} - S_2 - x, S_2) - f_2(S_2)x, \\ \frac{dx}{dt} &= (f_2(S_2) - D)x. \end{aligned} \quad (13)$$

For the problem to be biologically meaningful, the feasible region is

$$\begin{aligned} x^* &= \left((D - m_2) \left(K_2 m_1 \left(-m_2 S_1^{(0)} + D(K_2 + S_1^{(0)}) \right) \right. \right. \\ &\quad \left. \left. + (D(K_{1b} - K_2) - K_{1b} m_2) \left(-m_2 (K_{1a} + S_1^{(0)}) + D(K_{1a} + 2K_2 + S_1^{(0)}) \right) \right) y_1 \right) \\ &\pm \left[(D - m_2)^2 K_2^2 m_1^2 \left(m_2 S_1^{(0)} - D(K_2 + S_1^{(0)}) \right)^2 \right. \\ &\quad \left. + 2K_2 m_1 (D - m_2) (D(-K_{1b} + K_2) + K_{1b} m_2) \left(m_2 S_1^{(0)} - (K_{1a} + S_1^{(0)}) \right) \right. \\ &\quad \left. + D \left(K_{1a} (K_2 - S_1^{(0)}) - S_1^{(0)} (K_2 + S_1^{(0)}) \right) \right] y_1 \\ &\quad \left. + (D - m_2)^2 (D(-K_{1b} + K_2) + K_{1b} m_2)^2 (K_{1a} + S_1^{(0)})^2 y_1^2 \right) \Bigg/ \left(2(D - m_2)^2 (K_{1b} (D - m_2) y_1) \right. \\ &\quad \left. + K_2 (m_1 - D y_1) \right)^{1/2} \end{aligned}$$

$$\Omega = \left\{ (x, S_2) \mid x \geq 0, S_2 \geq 0, S_1^{(0)} - S_2 - x \geq 0 \right\}. \quad (14)$$

Assuming Monod kinetics, we now assume that f_1 takes the form given by (11) and that $n = p = 1$ and that $f_2(S_2) = m_2 S_2 / (K_2 + m_2 S_2)$.

The rest points of System (13) are $E_{0_2} = (0, 0)$ and potentially two interior rest points of the form

$$E_I = \left(x^*, DK_2 / (m_2 - D) \right),$$

where

Evaluated at E_{0_2} , the Jacobian has eigenvalues $\lambda_{1,2} = -D$, so E_{0_2} is always stable.

If we eliminated S_2 rather than S_1 , the limiting system is

$$\begin{aligned} \frac{dS_1}{dt} &= (S_1^{(0)} - S_1) D - \frac{x}{y_1} f_1(S_1, S_1^{(0)} - S_1 - x) \\ \frac{dx}{dt} &= \left(f_2(S_1^{(0)} - S_1 - x) - D \right) x \end{aligned} \quad (15)$$

with feasible region

$$\Omega = \left\{ (x, S_1) \mid x \geq 0, S_1 \geq 0, S_1^{(0)} - S_1 - x \geq 0 \right\}. \quad (16)$$

Again, assuming that f_1 takes the form given by (11) and that $n = p = 1$ and that $f_2(S_2) = m_2 S_2 / (K_2 + S_2)$, we find that System (15) has rest points $E_{0_1} = (0, S_1^{(0)})$

Table 2. Parameter values used for Figure 1.

	D	$S_1^{(0)}$	y_1	m_1	K_1	$S_2^{(0)}$	y_2	m_2	K_2
1.	0.25	4	1	6	4	2	1	7	4
2.	0.25	4	1	6	4	2	1	7	8
3.	0.25	4	2	6	1	2	1	7	8
4.	0.25	4	1	6	1	2	3	7	8

and potentially two interior rest points of the form $E_I = (x^*, S_1^*)$, where and

Evaluated at E_{0_2} , the Jacobian has eigenvalues $\lambda_{1,2} = -D$, so E_{0_2} is always stable.

Finally, if we had eliminated x rather than S_1 or S_2 , the limiting system is

$$\begin{aligned} \frac{dS_1}{dt} &= (S_1^{(0)} - S_1)D - \frac{S_1^{(0)} - S_1 - S_2}{y_1} f_1(S_1, S_2) \\ \frac{dS_2}{dt} &= -DS_2 + \frac{S_1^{(0)} - S_1 - S_2}{y_1} f_1(S_1, S_2) \\ &\quad - f_2(S_2)(S_1^{(0)} - S_1 - S_2) \end{aligned} \tag{17}$$

$$\begin{aligned} x^* &= \frac{1}{\left(2(D - m_2)(K_{1b}(D - m_2)y_1 + K_2(m_1 - Dy_1))\right)} \\ &\quad \times \left[K_2 m_1 \left(-m_2 S_1^{(0)} + D(K_2 + S_1^{(0)}) \right) + (D(K_{1b} - K_2) - K_{1b} m_2) \left(-m_2 (K_{1a} + S_1^{(0)}) + D(K_{1a} + 2K_2 + S_1^{(0)}) \right) y_1 \right. \\ &\quad \pm \left(K_2^2 m_1^2 \left(m_2 S_1^{(0)} - D(K_2 + S_1^{(0)}) \right)^2 \right. \\ &\quad \left. + 2K_2 m_1 (D - m_2) (D(-K_{1b} + K_2) + K_{1b} m_2) \left(m_2 S_1^{(0)} (K_{1a} + S_1^{(0)}) \right. \right. \\ &\quad \left. \left. + D(K_{1a} (K_2 - S_1^{(0)}) - S_1^{(0)} (K_2 + S_1^{(0)})) \right) y_1 \right. \\ &\quad \left. + (D - m_2)^2 (D(-K_{1b} + K_2) + K_{1b} m_2) \times (K_{1a} + S_1^{(0)})^2 y_1^2 \right]^{1/2} \end{aligned}$$

$$\begin{aligned} S_1^* &= \frac{1}{\left(2(D - m_2)(K_{1b}(D - m_2)y_1 + K_2(m_1 - Dy_1))\right)} \\ &\quad \times \left[K_2 m_1 \left(-m_2 S_1^{(0)} + D(K_2 + S_1^{(0)}) \right) + (-D + m_2) (D(-K_{1b} + K_2) + K_{1b} m_2) (-K_{1a} + S_1^{(0)}) y_1 \right. \\ &\quad \mp \left(K_2^2 m_1^2 \left(m_2 S_1^{(0)} - D(K_2 + S_1^{(0)}) \right)^2 \right. \\ &\quad \left. + 2K_2 m_1 (D - m_2) (D(-K_{1b} + K_2) + K_{1b} m_2) \left(m_2 S_1^{(0)} (K_{1a} + S_1^{(0)}) + D(K_{1a} (K_2 - S_1^{(0)}) - S_1^{(0)} (K_2 + S_1^{(0)})) \right) y_1 \right. \\ &\quad \left. + (D - m_2)^2 (D(-K_{1b} + K_2) + K_{1b} m_2)^2 \times (K_{1a} + S_1^{(0)})^2 y_1^2 \right] \end{aligned}$$

$$\begin{aligned} S_1^* &= \frac{1}{\left(2(D - m_2)(K_{1b}(D - m_2)y_1 + K_2(m_1 - Dy_1))\right)} \\ &\quad \times \left[K_2 m_1 \left(-m_2 S_1^{(0)} + D(K_2 + S_1^{(0)}) \right) + (-D + m_2) (D(-K_{1b} + K_2) + K_{1b} m_2) (-K_{1a} + S_1^{(0)}) y_1 \right. \\ &\quad \pm \left(K_2^2 m_1^2 \left(m_2 S_1^{(0)} - D(K_2 + S_1^{(0)}) \right)^2 \right. \\ &\quad \left. + 2K_2 m_1 (D - m_2) (D(-K_{1b} + K_2) + K_{1b} m_2) \left(m_2 S_1^{(0)} (K_{1a} + S_1^{(0)}) + D(K_{1a} (K_2 - S_1^{(0)}) - S_1^{(0)} (K_2 + S_1^{(0)})) \right) y_1 \right. \\ &\quad \left. + (D - m_2)^2 (D(-K_{1b} + K_2) + K_{1b} m_2)^2 \times (K_{1a} + S_1^{(0)})^2 y_1^2 \right]^{1/2} \end{aligned}$$

with feasible region

$$\Omega = \{(S_1, S_2) \mid S_1 \geq 0, S_2 \geq 0, S_1^{(0)} - S_1 - S_2 \geq 0\}. \tag{18}$$

Using the same assumptions regarding f_1 and f_2 and made previously, the rest points of System (17) are $E_{0_3} = (S_1^*, S_2^*) = (S_1^{(0)}, 0)$ and potentially two interior rest points of the form

$$E_I = (x^*, S_1^*) \quad E_I = (S_1^*, DK_2 / (m_2 - D)),$$

where

Figure 3 shows the behavior of Systems (13), (15), and (17) using the parameter values in **Table 3**. In all three cases, the plots indicate that all solutions tend to $(x, S_1, S_2) = (0, S_1^{(0)}, 0)$ as $t \rightarrow \infty$. However, in the first

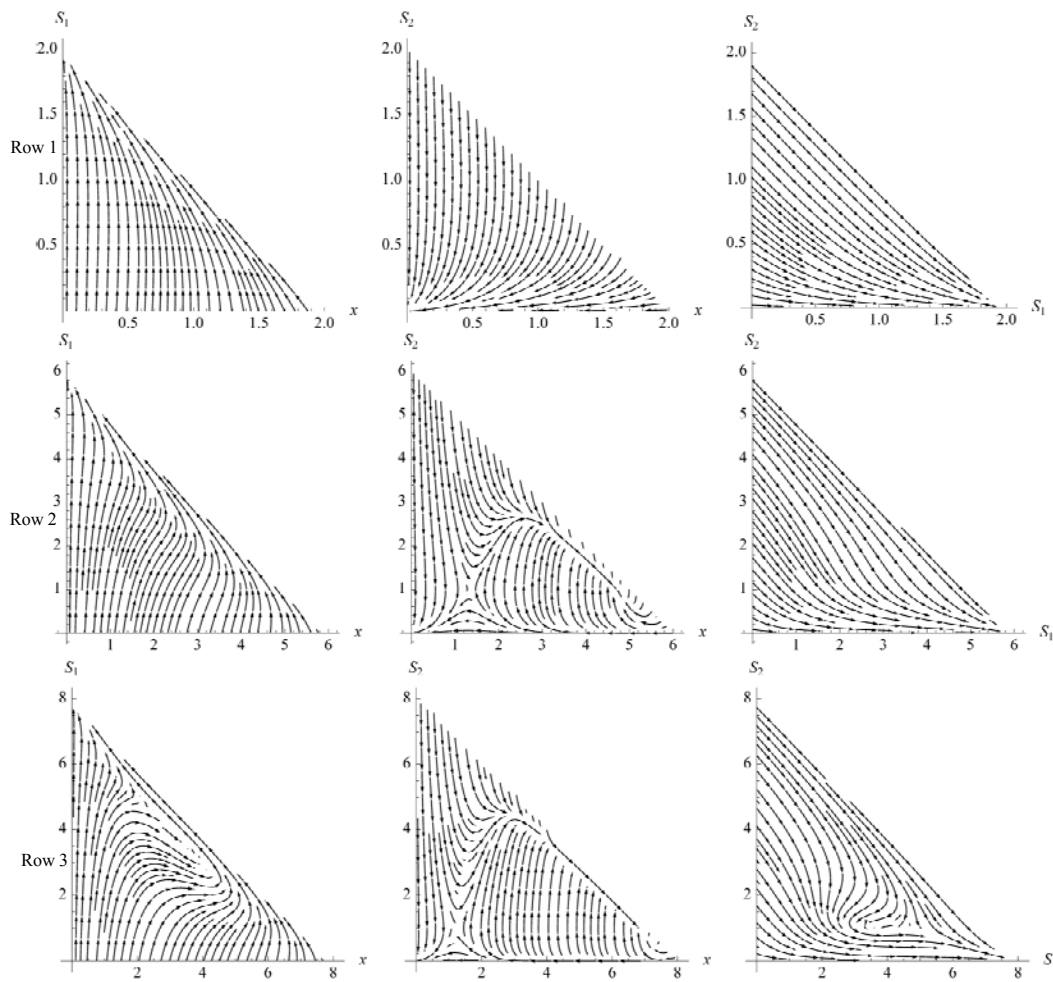


Figure 3. Modeling growth when the nutrient is an intermediate state of the substrate using the parameter values in Table 3.

Table 3. Parameter values used for Figure 3.

	D	$S_1^{(0)}$	y_1	m_1	K_{1a}	K_{1b}	m_2	K_2
1.	0.5	2	1	3	2	2	1	1
2.	0.5	6	1	3	2	2	1	1
3.	0.5	8	1	3	2	2	1	1

two cases there are no interior rest points. While in the third, when $S_1^{(0)}$ is increased to 8, (3,4), (3,1), and (4,1), respectively, are degenerate rest points. For each, one eigenvalue of the Jacobian evaluated at the rest point is $\lambda_1 = -0.0833$ and the other is $\lambda_2 = 0$.

More interesting behavior of the systems is illustrated in Figure 4 where we use the parameter values in Table 4. The figure illustrates that when $S_1^{(0)}$ (input concentration of the substrate), m_1 , or m_2 (growth rates) are increased, equilibrium states occur.

In all three situations, there is one unstable rest point, $(x, S_1, S_2) = (1.76, 7.24, 1)$, $(1.54, 9.46, 1)$, and $(0.260, 4.56, 0.143)$ as shown in Table 5. However, in the first

two rows of Table 5, $(x, S_1, S_2) = (6.23, 2.76, 1)$ and $(8.46, 2.54, 1)$ are stable spirals while in the third row, $(x, S_1, S_2) = (2.92, 1.93, 0.143)$ is an unstable spiral.

Thus, depending on the parameter values equilibrium states may be stable or unstable. Moreover, slight adjustments to the parameter values might make a stable state unstable and vice-versa.

4. Conclusions

In this paper, we have formed a model of growth in a chemostat with two interactive complementary nutrients. We have used numerical results to graphically illustrate differences in the behavior of systems modeling noninteractive complementary nutrients, interactive complementary nutrients, and substitutable nutrients. Not surprisingly, we have illustrated that substitutable nutrients lead to higher population densities than do complementary nutrients. We have illustrated some surprising differences in the behavior of systems modeling noninteractive complementary nutrients and interactive complementary nutrients. It is possible that if the nutrients are

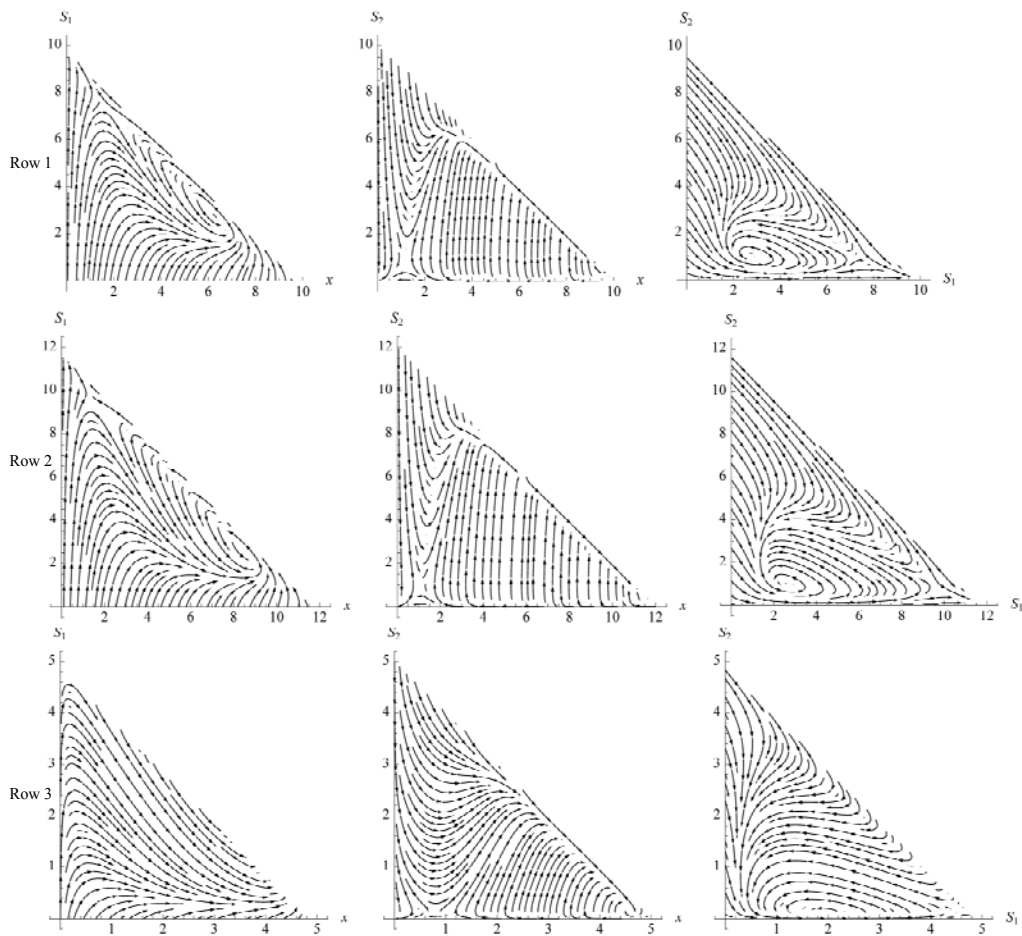


Figure 4. Modeling growth when the nutrient is an intermediate state of the substrate using the parameter values in Table 4.

Table 4. Parameter values used for Figure 4.

	D	$S_1^{(0)}$	y_1	m_1	K_{1a}	K_{1b}	m_2	K_2
1.	0.5	10	1	3	2	2	1	1
2.	0.5	12	1	3	2	2	1	1
3.	0.25	5	1	8	2	2	2	1

Table 5. Rest points and eigenvalues of Jacobian for Figure 4.

Row	$x-S_1$	$x-S_2$	S_1-S_2	Eigenvalues of Jacobian
1	(1.76,7.24)	(1.76,1)	(7.24,1)	-0.359, 0.298
	(6.23, 2.76)	(6.24,1)	(2.76,1)	$-0.983 \pm 0.850i$
2	(1.54,9.46)	(1.54,1)	(9.46,1)	-0.373, 0.311
	(8.46,2.54)	(8.46,1)	(2.54,1)	$-0.142 \pm 1.26i$
3	(0.260, 4.56)	(0.296, 0.143)	(4.56,1.43)	0.230, -0.224
	(2.92,1.93)	(2.92, 0.143)	(1.93,0.143)	$0.0401 \pm 0.919i$

interactive, the organism will attain a stable population density while if the nutrients are noninteractive, the organism will become extinct. The simulations indicate that interactive complementary nutrients frequently lead to higher population densities than do noninteractive complementary nutrients. This agrees with the experimental results of Whang *et al.* [9] that show that complementary substrates (glucose and peptone) significantly increased hydrogen production by anaerobic hydrogen-producing bacteria.

A slight adjustment to the system leads to a completely different interpretation of the model in which the nutrient is an intermediate byproduct of the substrate. The simulations indicate the equilibrium states are very sensitive to the parameter values and slight adjustments to them can cause a stable state to become unstable and vice versa. This agrees with the experimental results of Sanchez *et al.* [18], which illustrated that slight adjustments of the inlet concentration (corresponding to $S_1^{(0)}$) had major effects on the washout rate (when the limit as $t \rightarrow \infty$ converges to $(x, S_1, S_2) = (0, S_1^{(0)}, 0)$).

The Mathematica notebooks that the authors used to carry out many of the calculations as well as generate the

figures are available from the authors by sending an email request to Jim Braselton.

In future studies, we hope to examine how competitive relationships (competition, predator-prey, and so forth) are modeled under circumstances such as these.

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