Exploitative Competition in a Chemostat for Two Complementary, and Possibly Inhibitory, Resources

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ABSTRACT

A model of the chemostat involving two populations of microorganisms competing for two complementary, growth-limiting substrates is considered. Instead of assuming the familiar Michaelis-Menten kinetics for nutrient uptake, a general class of functions is used which includes all monotone increasing uptake functions, but which also allows uptake functions that describe inhibition by the substrate at high concentrations. Graphical techniques are developed to analyze the model. In the case of monotone kinetics the results are similar to those of Hsu, Cheng, and Hubbell [16], who study this problem assuming Michaelis-Menten kinetics. For monotone kinetics, all dynamics are trivial in the sense that all solutions approach equilibria. However, when at least one of the competitors is inhibited by high concentrations of the substrate, one can easily construct examples for which there is a stable periodic solution. Surprisingly, if the substrates are inhibitory at high concentrations, there are examples for which coexistence is possible but neither competitor can survive in the absence of its rival.

1. INTRODUCTION

The classical theory of ecological competition and predator-prey relationships was originated by Lotka [20] and Volterra [36]. This approach is appealing because of its generality and its simplicity. The competition equations studied are basically an extension of the logistic model of single-species growth that dates back to Verhulst [35]. The classical theory is an attempt to describe population dynamics without being specific about which resources are limiting and how these limiting resources are utilized by the

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[†] Deceased. Geoffrey Butler passed away 13 July 1986. He supervised my doctoral studies and during that time he became a very dear friend.

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different competitors. These models are usually phenomenological rather than predictive, since it is very difficult to measure the critical parameters used in the theory independently of actually observing the populations in competition. One way to overcome these defects is to develop a more mechanistic, resource-based theory of ecological interactions, and such an approach is currently being taken by many researchers. Some of the pioneering work can be attributed to Monod [24] and Holling [15]. Though this approach may result in mathematical models that are less general and more difficult to analyze, the resulting models are often predictive, since parameters can frequently be measured independently of the competition (see e.g. Hansen and Hubbell [13]). Mathematical modeling of population interactions in a chemostat is certainly an example of this resource-based approach and is the approach taken in this paper.

When there is competition for two or more resources, it becomes necessary to consider how the resources, once consumed, interact to promote growth. Leon and Tumpson [19] and Rapport [27] use consumer needs to provide a criterion to classify resources. They classify resources as perfectly complementary, perfectly substitutable, or imperfectly substitutable.

Perfectly complementary resources are sources of different essential substances which must be taken together because each substance fulfils a different function with respect to growth. For example, a carbon source and a nitrogen source might be complementary for a bacterium. Perfectly substitutable resources, on the other hand, are alternative sources of an essential substance or of essential substances that fulfil the same function. The intermediate case is called imperfectly substitutable.

In this paper we shall restrict our attention exclusively to two perfectly complementary resources S and R. In this context we shall say that a population is S-limited (R-limited) if its per capita consumption rate of R (S) is independent of the concentration of R (S) and depends only on the concentration of S (R).

Models of microbial growth on perfectly complementary resources (with experimental justification) have been published in [4, 28, 30]. Leon and Tumpson [19] seem to be the first to have modeled exploitative competition for perfectly complementary resources. They assume that each competitor's functional response is a strictly monotone function of resource concentration. In the two-resource, two-competitor case they derive conditions for the existence of a locally asymptotically stable interior critical point and hence conditions for the coexistence of two competitors.

Hsu, Cheng, and Hubbell [16] derive a model for exploitative competition in a chemostat between two populations for two perfectly complementary resources. They assume that consumption of the resources follows Holling Type II, or equivalently Michaelis-Menten kinetics, generalized to the two-resource situation. They give a complete global analysis of their model. They conclude that "each of the four outcomes of classical Lotka-Volterra two-species competition theory has multiple mechanistic origins in terms of consumer resource interactions." They also give biological conditions based on parameters in their model that predict the competitive outcome. Their results are also summarized in a survey paper by Waltman et al. [37]. For other related work see [4, 11, 26, 34].

The content of this paper is organized as follows. In Section 2 we consider the model of Hsu et al. [16]. We point out that their derivation and their arguments apply for any functional responses that are strictly monotone functions of resource concentration. We also give an alternative method of obtaining their results which we shall find useful in Section 3.

In Section 3, we modify the model considered in Section 2 by allowing a more general class of functions to describe consumption and conversion rates, as was done in Butler and Wolkowicz [9] and Wolkowicz [38]. Again this class will allow us to consider substrates that are growth-limiting at low concentrations as well as at overly high concentrations. Inhibition of growth by high concentrations of substrate is particularly important when microorganisms are used for biological waste decomposition or for water purification (see [1, 2, 5, 6, 39]). After presenting some preliminary results, we develop graphical criteria that characterize the set of critical points and show under what circumstances the model permits trivial dynamics only. These graphical criteria are based on the methods developed in Section 2 as well as some concepts from linear programming. Surprisingly enough, using these graphical criteria, we are able to show that the model predicts that there are cases in which in the absence of a rival each population definitely dies out, whereas when both competitors are present there is a possibility of coexistence. Thus, in some sense the rivals are cooperating. We then show by means of an example that even if we allow only one resource to be inhibitory to only one of the competitors at high concentrations, the model permits an orbitally asymptotically stable periodic orbit. Hence the model predicts that under certain conditions coexistence of the competitors with concentrations in sustained oscillation is possible. In this same example, there is also an unstable periodic orbit associated with a locally asymptotically stable critical point. Thus, there can be initial-condition-dependent regions of coexistence. In each case, the existence of the periodic orbit is obtained through a Hopf bifurcation. Since the analysis of stability involves computations that would be extremely tedious, they were done using the symbol manipulation language REDUCE 2. The algorithm used is based on the work of Marsden and McCracken [22]. The REDUCE 2 program is general enough to be adapted for use to determine whether or not there is a Hopf bifurcation and, if there is, to determine the stability of the bifurcating periodic orbit, in the case of most systems of two-first-order, autonomous, ordinary differential equations. The program and an explanation of how to adapt it can be found in

Appendix 3 of Wolkowicz [38] along with the program results. We summarize the key steps in the bifurcation analyses for our examples in Appendix 1 of this paper. To illustrate the examples we use computer graphics to generate phase-plane portraits. The equations are solved numerically by means of the IMSL double-precision algorithm DGEAR.

We conclude the paper with a discussion in which we summarize the results and then discuss the difference in dynamics between monotone and nonmonotone kinetics.

Some auxiliary results appear in Appendix 2 of this paper. The linear analysis is standard and can be found in Appendix 2 of Wolkowicz [38].

2. THE MODEL—MONOTONE KINETICS

We consider the following model of exploitative competition in a chemostat between two populations of microorganisms for two purely complementary resources:

$$\begin{aligned} S'(t) &= [S^0 - S(t)]D - \sum_{i=1}^{2} \frac{x_i(t)}{y_{Si}} f_i(S(t),R(t)), \\ R'(t) &= [R^0 - R(t)]D - \sum_{i=1}^{2} \frac{x_i(t)}{y_{Ri}} f_i(S(t),R(t)), \\ x_i'(t) &= x_i(t)[-D + f_i(S(t),R(t))], \qquad i=1,2, \\ S(0) &= S_0 \geqslant 0, \qquad R(0) = R_0 \geqslant 0, \qquad x_i(0) = x_{i0} > 0, \quad i=1,2, \end{aligned} \tag{2.1}$$

where

$$f_i(S(t),R(t)) = \min(p_i(S(t), q_i(R(t))), \qquad i=1,2.$$

Here, $S(t)$ and $R(t)$ denote the concentrations of the two nonreproducing, complementary resources at time t, and $x_i(t)$ denotes the concentration of the ith population of microorganisms at time t. The function $p_i(S(t))$ $[q_i(R(t))]$ represents the per capita growth rate of the ith population when resource S is limiting [resource R is limiting], and so $f_i(S(t),R(t))$ is the function that represents the rate of conversion of nutrient to biomass for the ith population. We take the minimum here because the resources are purely complementary. We are therefore assuming that growth rates adjust instantaneously to changes in the resource concentration. The consumption rate of nutrient is also assumed to be proportional to the rate of conversion to biomass. Thus, $f_i(S,R)/y_{Si}$ $[f_i(S,R)/y_{Ri}]$ represents the consumption rate of resource S [resource R] by the ith species, where y_{Si} and y_{Ri} are the growth yield factors. It is assumed that the yield factor y_{Si} has the same value whether S is the rate-limiting nutrient or not. The same is assumed for

y_{Ri}. If only one feed bottle is used, then S^0 and R^0 denote the concentrations of resources S and R respectively in the feed bottle, and D denotes the input rate from the feed bottle containing the resources to the growth chamber, as well as the washout rate of nutrients, microorganisms, and by-products from the growth chamber to the collection vessel. Thus the volume in the growth chamber remains constant. Here we are assuming, therefore, that the input rate of resource and the dilution rate are constant and that there is perfect mixing in the growth vessel, so that nutrient and microorganisms are removed in proportion to their concentration. We are also assuming that individual death rates of either population are insignificant compared to the dilution rate D.

If the experimenter prefers to use two separate feed bottles, each containing only one resource, and input from each feed bottle to the growth chamber at different rates, say rate D_S from the bottle containing resource S and rate D_R from the bottle containing resource R, then $D = D_S + D_R$, $S^0 = (\bar{S}^0 D_S)/(D_S + D_R)$, and $R^0 = (\bar{R}^0 D_R)/(D_S + D_R)$, where $\bar{S}^0$ and $\bar{R}^0$ represent the concentrations of resources S and R, respectively, in each separate feed bottle. Here, D still represents the dilution rate.

We make the following assumptions concerning the functions p_i and q_i in our model:

$$p_i, q_i : \mathbb{R}_+ \to \mathbb{R}_+; \tag{2.2}$$

$$p_i, q_i \text{ are continuously differentiable;} \tag{2.3}$$

$$p_i(0) = 0, \qquad q_i(0) = 0, \tag{2.4}$$

that is, if there is no nutrient, there is no uptake. Due to the assumption (2.3), the functions $f_i(S, R)$ satisfy a Lipschitz condition in S and R on any compact subset of $\mathbb{R}_+ \times \mathbb{R}_+$, and so we have uniqueness of initial-value problems and continuous dependence on initial conditions and parameters for the system (2.1).

In this section we shall also assume that

$$p_i'(S) > 0 \quad \text{for } S > 0 \quad \text{and} \quad q_i'(R) > 0 \quad \text{for } R > 0, \tag{2.5}$$

that is, that the kinetics are strictly monotone.

This is precisely model III of Leon and Tumpson [19], adapted to a chemostat in which individual death rates are assumed insignificant compared to the dilution rate. The model applies when the functions p_i and q_i assume the form of the usual prototypes for monotone functional responses, e.g. Holling Type I (or Lotka-Volterra kinetics), Holling Type II (or Michaelis-Menten kinetics) and Holling Type III (or multiple saturation dynamics). In the case that all the p_i's and q_i's satisfy Michaelis-Menten dynamics, the model is precisely the one studied by Hsu, Cheng, and Hubbell [16].

By means of a linear analysis, Leon and Tumpson [19] proved that "Necessary and sufficient conditions for stable coexistence of two species engaged in exploitative competition for complementary resources" (at an asymptotically stable equilibrium) "are that each species must at equilibrium consume a greater fraction of the net rate of supply of its limiting resource than of the net rate of supply of its competitor's limiting resource."

Hsu et al. [16], on the other hand, do a complete global analysis of the model. We summarize their results here. Although they assume the functions p_i and q_i, $i=1,2$, all satisfy Michaelis-Menten kinetics, their proofs are also valid for strictly monotone functions. However, we give alternative proofs for some of their results. The methods we employ will be useful in a subsequent section where we relax the assumption (2.5) in order to allow resources that are inhibitory at high concentrations, as we did in [9]. Some of the ideas to be used in these proofs are similar to ones used in the proofs in [9].

We begin by stating some preliminary results. Just as in [9] (the proofs are similar as well), the system is as well behaved as one would expect from the biological problem. More precisely, solutions of (2.1) are positive and bounded. Furthermore, the polygonal set

$$\mathcal{M}=\left\{(S,R,x_1,x_2)\in\mathbf{R}_+^4 : S+\frac{x_1}{y_{S1}}+\frac{x_2}{y_{S2}}=S^0 \right.$$
$$\left. \text{and } R+\frac{x_1}{y_{R1}}+\frac{x_2}{y_{R2}}=R^0\right\} \tag{2.6}$$

is a global attractor for (2.1), and on $\mathcal{M}$ solutions satisfy

$$\begin{aligned} S'(t)+\sum_{i=1}^{2}\frac{x_i'(t)}{y_{Si}}&=0,\\ R'(t)+\sum_{i=1}^{2}\frac{x_i'(t)}{y_{Ri}}&=0. \end{aligned} \tag{2.7}$$

At this point we introduce some useful notation:

$$p_i(\lambda_{Si})=D \text{ and } q_i(\lambda_{Ri})=D, \qquad i=1,2. \tag{2.8}$$

Thus λ_{Si} and λ_{Ri} represent the breakeven concentrations for resource S and R respectively, when that resource is limiting. By the assumption (2.5), these concentrations are uniquely defined extended positive real numbers, provided we assume that $\lambda_{Si}=+\infty$ if $p_i(S)<D$ for all $S\geqslant 0$ (similarly, $\lambda_{Ri}=+\infty$ if $q_i(R)<D$ for all $R\geqslant 0$).

Following Hsu et al. [16], we define

$$C_i = y_{Si}/y_{Ri}, \qquad i = 1,2. \tag{2.9a}$$

Since the units of $1/y_{Si}$ are (units of S consumed)/(unit of population i produced), C_i represents the invariant ratio in which R and S are consumed by population i.

Let

$$T_i = \frac{R^0 - \lambda_{Ri}}{S^0 - \lambda_{Si}}, \qquad i = 1,2, \tag{2.9b}$$

and

$$T^* = \frac{R^0 - \lambda_{R2}}{S^0 - \lambda_{S1}} \quad \text{and} \quad T_* = \frac{R^0 - \lambda_{R1}}{S^0 - \lambda_{S2}}. \tag{2.10}$$

As Hsu et al. [16] explain, by comparing T_i and C_i we can determine whether population i is S-limited or R-limited. T_i represents the ratio in which resources R and S are externally regenerated under steady-state consumption pressure from population i in the absence of its competitor. Therefore $T_i > C_i$ implies that population i is S-limited because S is regenerating at a steady-state rate slower than R with respect to the required consumption ratio of population i. Similarly $T_i < C_i$ implies that population i is R-limited.

T^* (T_*) represents the ratio of the steady-state regeneration rate of R when x_2 (x_1) is alone to that of S when x_1 (x_2) is alone.

To avoid critical points for which the associated matrix of the linearization (the Jacobian) has any real root equal to zero, if the parameters are finite, we assume that

$$\begin{aligned} &\lambda_{S1} \text{ and } \lambda_{S2} \text{ are distinct from each other and from } S^0, \\ &\lambda_{R1} \text{ and } \lambda_{R2} \text{ are distinct from each other and from } R^0, \end{aligned} \tag{2.11}$$

and

$$T_* \text{ and } T^* \text{ are distinct from } C_1 \text{ and } C_2. \tag{2.12}$$

To ensure that the critical points are all isolated we assume that

$$C_1 \neq C_2. \tag{2.13}$$

So that we can assume that the vector field is continuously differentiable at and in some neighborhood of each critical point, we assume that

$$\text{if} \quad (\bar{S}, \bar{R}, \bar{x}_1, \bar{x}_2) \text{ is a critical point,}$$
$$\text{then} \quad p_i(\bar{S}) \neq q_i(\bar{R}), \quad i = 1,2. \tag{2.14}$$

This assumption implies that

$$T_i \neq C_i, \qquad i = 1,2. \tag{2.15}$$

Table 1 contains notation for the possible critical points of (2.1). In Table 2 we summarize criteria that ensure that these critical points lie in the nonnegative cone, as well as criteria that guarantee their local asymptotic stability. The linear analysis is standard and can be found in Appendix A2.A of [38].

In Table 3 we provide a summary of all the possible biological outcomes along with the competition criteria that yield each outcome. To prove the results summarized in Table 3 we proceed as follows. First we note that since

TABLE 1

Notation for the Critical Points[a] of (2.1)

Symbol	Critical point[b]
E_{S^0,R^0}	$= (S^0, R^0, 0, 0)$
$E_{\lambda_{S1},*}$	$= \left(\lambda_{S1}, R^0 - C_1(S^0 - \lambda_{S1}), y_{S1}(S^0 - \lambda_{S1}), 0\right)$
$E_{*,\lambda_{R1}}$	$= \left(S^0 - \dfrac{R^0 - \lambda_{R1}}{C_1}, \lambda_{R1}, y_{R1}(R^0 - \lambda_{R1}), 0\right)$
$E_{\lambda_{S2},*}$	$= \left(\lambda_{S2}, R^0 - C_2(S^0 - \lambda_{S2}), 0, y_{S2}(S^0 - \lambda_{S2})\right)$
$E_{*,\lambda_{R2}}$	$= \left(S^0 - \dfrac{R^0 - \lambda_{R2}}{C_2}, \lambda_{R2}, 0, y_{R2}(R^0 - \lambda_{R2})\right)$
$E_{\lambda_{S1},\lambda_{R2}}$	$= (\lambda_{S1}, \lambda_{R2}, x_1^*, x_2^*)$ where $x_1^* = y_{S1} y_{R1} \left(\dfrac{y_{S2}(S^0 - \lambda_{S1}) - y_{R2}(R^0 - \lambda_{R2})}{y_{R1} y_{S2} - y_{S1} y_{R2}} \right)$ $x_2^* = y_{S2} y_{R2} \left(\dfrac{y_{R1}(R^0 - \lambda_{R2}) - y_{S1}(S^0 - \lambda_{S1})}{y_{R1} y_{S2} - y_{S1} y_{R2}} \right)$
$E_{\lambda_{S2},\lambda_{R1}}$	$= (\lambda_{S2}, \lambda_{R1}, \hat{x}_1, \hat{x}_2)$ where $\hat{x}_1 = y_{S1} y_{R1} \left(\dfrac{y_{S2}(S^0 - \lambda_{S2}) - y_{R2}(R^0 - \lambda_{R1})}{y_{R1} y_{S2} - y_{S1} y_{R2}} \right)$ $\hat{x}_2 = y_{S2} y_{R2} \left(\dfrac{y_{R1}(R^0 - \lambda_{R1}) - y_{S1}(S^0 - \lambda_{S2})}{y_{R1} y_{S2} - y_{S1} y_{R2}} \right)$

[a] Under the assumption (2.13), i.e. $C_1 \neq C_2$.

[b] Provided it lies in $\mathbf{R}^4_+$.

TABLE 2

Summary of the Local Stability Analysis of (2.1)[a]

Critical point	Criteria for existence	Criteria for asymptotic stability
E_{S^0,R^0}	Always exists	$\lambda_{S1} > S^0$ or $\lambda_{R1} > R^0$ and $\lambda_{S2} > S^0$ or $\lambda_{R2} > R^0$
$E_{\lambda_{S1},*}$	$\lambda_{S1} < S^0$ and $T_1 > C_1$	$\lambda_{S1} < \lambda_{S2}$ or $T^* < C_1$
$E_{*,\lambda_{R1}}$	$\lambda_{R1} < R^0$, $\lambda_{S1} < S^0$, and $T_1 < C_1$	$\lambda_{R1} < \lambda_{R2}$ or $T_* > C_1$ and $\lambda_{S2} < S^0$
$E_{\lambda_{S2},*}$	$\lambda_{S2} < S^0$ and $T_2 > C_2$	$\lambda_{S1} > \lambda_{S2}$ or $T_* < C_2$
$E_{*,\lambda_{R2}}$	$\lambda_{R2} < R^0$, $\lambda_{S2} < S^0$, and $T_2 < C_2$	$\lambda_{R1} > \lambda_{R2}$ or $T_* > C_2$ and $\lambda_{S1} < S^0$
$E_{\lambda_{S1},\lambda_{R2}}$	$\lambda_{S1} > \lambda_{S2}$ and $\lambda_{R1} < \lambda_{R2}$ and $\left(\begin{array}{l} C_1 < T^* < C_2 \text{ and } \lambda_{S1} < S^0 \\ \text{or} \\ C_1 > T^* > C_2 \text{ and } \lambda_{S1} < S^0 \end{array}\right)$	$\left.\begin{array}{l} \\ \\ \\ \end{array}\right\} C_1 < C_2$
$E_{\lambda_{S2},\lambda_{R1}}$	$\lambda_{S1} < \lambda_{S2}$ and $\lambda_{R1} > {}_{R2}$ and $\left(\begin{array}{l} C_1 < T_* < C_2 \text{ and } \lambda_{S2} < S^0 \\ \text{or} \\ C_1 > T_* > C_2 \text{ and } \lambda_{S2} < S^0 \end{array}\right)$	$\left.\begin{array}{l} \\ \\ \\ \end{array}\right\} C_1 > C_2$

[a] Exploitative competition between two populations for two complementary resources; monotone functional responses.

$\mathcal{M}$ is globally attracting and all solutions are bounded, the omega-limit set of any solution of (2.1) lies entirely in $\mathcal{M}$. We shall show that the dynamics of (2.1) restricted to $\mathcal{M}$ are trivial (i.e. all trajectories with initial conditions in $\mathcal{M}$ approach some equilibrium in the limit). Next we shall appeal to the local-analysis results and do a phase-plane analysis in (x_1, x_2) space to eliminate saddle connections, and hence shall show that all solutions of (2.1) asymptotically approach equilibria. Finally, we shall consider the location of the stable manifolds of certain critical points to show that no solution with initial conditions in the positive cone can converge to that critical point.

That the dynamics of (2.1) restricted to $\mathcal{M}$ are trivial follows from Hirsch's results [14] on competitive systems adapted to monotone Lipschitzian functions rather than C^1 functions, since (2.1) restricted to $\mathcal{M}$ is

TABLE 3

Classification of Competitive Outcomes of (2.1)[a]

	Biological Outcome	Competition criteria
1.	Both populations die out: (a) ⇒ population 1 dies out; (b) ⇒ population 2 dies out: Competitive-independent extinction.	(a) $\lambda_{S1} > S^0$ or $\lambda_{R1} > R^0$ and (b) $\lambda_{S2} > S^0$ or $\lambda_{R2} > R^0$
2.	Population 1 always wins. Population 2 dies out.	$\lambda_{S1} < S^0$ and $\lambda_{R1} < R^0$ and $\left(\begin{array}{l} \lambda_{S1} < \lambda_{S2} \text{ and } \lambda_{R1} < \lambda_{R2} \\ \text{or} \\ \lambda_{S1} < \lambda_{S2}, \lambda_{R1} > \lambda_{R2} \text{ and } T_* > C_1, C_2 \\ \text{or} \\ \lambda_{S1} > \lambda_{S2}, \lambda_{R1} < \lambda_{R2} \text{ and } T^* < C_1, C_2 \\ \text{or} \\ \lambda_{S2} > S^0 \\ \text{or} \\ \lambda_{R2} > R^0 \end{array}\right)$
3.	Population 2 always wins. Population 1 dies out.	$\lambda_{S2} < S^0$ and $\lambda_{R2} < R^0$ and $\left(\begin{array}{l} \lambda_{S1} > \lambda_{S2} \text{ and } \lambda_{R1} > \lambda_{R2}, \\ \text{or} \\ \lambda_{S1} < \lambda_{S2}, \lambda_{R1} > \lambda_{R2}, \text{ and } T_* < C_1, C_2 \\ \text{or} \\ \lambda_{S1} > \lambda_{S2}, \lambda_{R1} < \lambda_{R2}, \text{ and } T^* > C_1, C_2 \\ \text{or} \\ \lambda_{S1} > S^0 \\ \text{or} \\ \lambda_{R1} > R^0 \end{array}\right)$
4.	Populations 1 and 2 coexist at a positive equilibrium.	$\lambda_{S_i} < S^0$ and $\lambda_{R_i} < R^0$, $i = 1,2$ and $\left(\begin{array}{l} \lambda_{S1} < \lambda_{S2}, \lambda_{R1} > \lambda_{R2}, \text{ and } C_1 > T_* > C_2 \\ \text{or} \\ \lambda_{S1} > \lambda_{S2}, \lambda_{R1} < \lambda_{R2}, \text{ and } C_1 < T^* < C_2 \end{array}\right)$
5.	One population wins and the other dies out. Initial concentrations determine the outcome. Coexistence only for solutions with initial conditions on the separatrix (a set of measure zero).	$\lambda_{S_i} < S^0$ and $\lambda_{R_i} < R^0$, $i = 1,2$ and $\left(\begin{array}{l} \lambda_{S1} < \lambda_{S2}, \lambda_{R1} > \lambda_{R2}, \text{ and } C_1 < T_* < C_2 \\ \text{or} \\ \lambda_{S1} > \lambda_{S2}, \lambda_{R1} < \lambda_{R2}, \text{ and } C_1 > T^* > C_2 \end{array}\right)$

[a] Exploitative competition between two populations for two complementary resources; monotone functional responses.

equivalent to the system

$$x_i'(t) = x_i(t)\left[-D + f_i\left(S^0 - \frac{x_1(t)}{y_{S1}} - \frac{x_2(t)}{y_{S2}},\ R^0 - \frac{x_1(t)}{y_{R1}} - \frac{x_2(t)}{y_{2R}}\right)\right], \qquad i=1,2,$$

$$x_{i0} > 0, \quad i=1,2, \qquad \frac{x_{10}}{y_{S1}} + \frac{x_{20}}{y_{S2}} \leqslant S^0, \qquad \frac{x_{10}}{y_{R1}} + \frac{x_{20}}{y_{R2}} \leqslant R^0, \tag{2.16}$$

coupled with

$$S(t) = S^0 - \frac{x_1(t)}{y_{S1}} - \frac{x_2(t)}{y_{S2}}, \qquad R(t) = R^0 - \frac{x_1(t)}{y_{R1}} - \frac{x_2(t)}{y_{R2}}, \tag{2.17}$$

and (2.16) is a two-dimensional competitive system. Hirsch's results for two-dimensional competitive systems depend on Kamke's comparison theorem, which requires only monotone behavior with respect to the appropriate variables. Viewing the system this way, it is not surprising that the biological outcomes of the two-resource model can be compared with the outcomes of the classical model of Verhulst [35] for two-species competition with constant carrying capacity. These outcomes with corresponding competitive criteria are compared in Table 4.2 of Waltman, Hubbell, and Hsu [37].

We use a more elementary approach, one similar to the approach used in [9], to show that the dynamics are trivial. This approach also gives more information about the behavior of solutions on the polygonal set $\mathscr{M}$, and will be employed when we consider nonmonotone uptake functions in a later section.

We shall require the following notation:

$$B_i = \{(S,R) : S > \lambda_{Si} \text{ and } R > \lambda_{Ri}\}, \qquad i=1,2. \tag{2.18}$$

$$Q = \bigcup_{i=1}^{2} B_i. \tag{2.19}$$

$$K = \bigcap_{i=1}^{2} B_i. \tag{2.20}$$

Therefore,

$$\begin{aligned} f_i(S,R) &> D && \text{if } (S,R) \in B_i, \\ f_i(S,R) &< D && \text{if } (S,R) \notin \operatorname{cl} B_i, \\ f_i(S,R) &= D && \text{if } (S,R) \in \partial B_i. \end{aligned}$$

Here Q can be thought of as an analogue of the Q defined in [9], and parts (i) and (ii) of the following lemma can be viewed as an analogue of Lemma 4.4 of [9]. The lemma is illustrated in Figure 1.

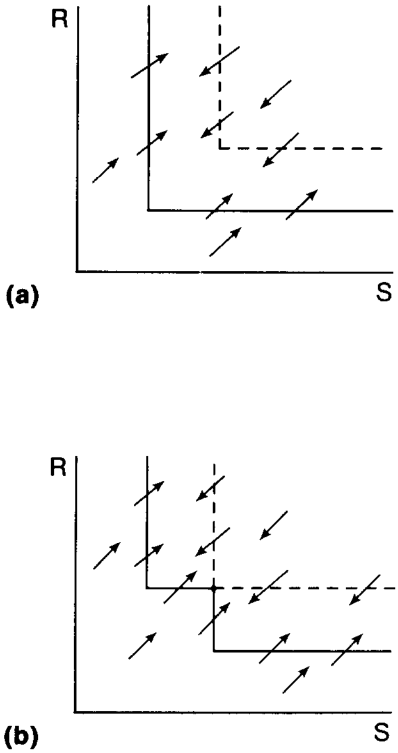

FIG. 1. Dynamics on $\mathcal{M}$ are trivial: (a) ($\lambda_{S1} < \lambda_{S2}$ and $\lambda_{R1} < \lambda_{R2}$) or ($\lambda_{S1} > \lambda_{S2}$ and $\lambda_{R1} > \lambda_{R2}$); (b) ($\lambda_{S1} < \lambda_{S2}$ and $\lambda_{R1} > \lambda_{R2}$) or ($\lambda_{S1} > \lambda_{S2}$ and $\lambda_{R1} < \lambda_{R2}$)— ∂Q; --- ∂K.

LEMMA 2.1

Let $(S(t), R(t), x_1(t), x_2(t))$ *be a solution of* (2.1) *with initial conditions restricted to* $\mathcal{M}$. (*Note that this still implies that* $x_{i0} > 0$, $i = 1, 2$.)

(i) *If there exists* $\tau \geqslant 0$ *with* $(S(\tau), R(\tau)) \in \partial Q \setminus \partial K$, *then* $S'(\tau) > 0$ *and* $R'(\tau) > 0$.

(ii) *If there exists* $\tau \geqslant 0$ *with* $(S(\tau), R(\tau)) \in \partial Q \cap \partial K$, *then* $(S(\tau), R(\tau), x_1(\tau), x_2(\tau))$ *is an equilibrium for* (2.1) *and so* $S'(\tau) = 0 = R'(\tau)$.

(iii) *If there exists* $\tau \geqslant 0$ *with* $(S(\tau), R(\tau)) \in \partial K \setminus \partial Q$, *then* $S'(\tau) < 0$ *and* $R'(\tau) < 0$.

(iv) *If there exists* $\tau \geqslant 0$ *with* $(S(\tau), R(\tau)) \in \mathbf{R}_+^2 \setminus \mathrm{cl}\, Q$, *then* $S'(\tau) > 0$ *and* $R'(\tau) > 0$.

(v) *If there exists* $\tau \geqslant 0$ *with* $(S(\tau), R(\tau)) \in K$, *then* $S'(\tau) < 0$ *and* $R'(\tau) < 0$.

Proof. (i): If $(S(\tau), R(\tau)) \in \partial Q \setminus \partial K$, then since $x_i'(t) = x_i(t)[-D + f_i(S(t), R(t))]$, $i = 1,2$, either $x_1'(\tau) = 0$ and $x_2'(\tau) < 0$ or $x_1'(\tau) < 0$ and $x_2'(\tau) = 0$. The result follows by (2.7).

(ii): If $(S(\tau), R(\tau)) \in \partial Q \cap \partial K$, then $x_1'(\tau) = x_2'(\tau) = 0$. By (2.7) and (2.13) it follows that $S'(\tau) = R'(\tau) = 0$ and we are at an equilibrium.

(iii), (iv), and (v) are proved similarly. ■

The next lemma is the analogue of Lemma 4.5 of [9] and is also illustrated in Figure 1. It follows immediately from Lemma 2.1.

LEMMA 2.2

Let $(S(t), R(t), x_1(t), x_2(t))$ *be a solution of* (2.1) *with initial conditions in* $\mathscr{M}$. *For all sufficiently large t precisely one of the following holds*:

(i) $(S(t), R(t)) \in \mathbb{R}^2_+ \setminus \mathrm{cl}\, Q$,
(ii) $(S(t), R(t)) \in K$,
(iii) $(S(t), R(t)) \in Q \setminus \mathrm{cl}\, K$, *or*
(iv) $(S(t), R(t)) \in \partial Q \cap \partial K$.

THEOREM 2.3

The dynamics of (2.1) *with initial conditions restricted to* $\mathscr{M}$ *are trivial.*

Proof. Let $\gamma(t) = (S(t), R(t), x_1(t), x_2(t))$ be a solution of (2.1) with initial conditions in $\mathscr{M}$. Then for all sufficiently large t precisely one of the options of Lemma 2.2 holds. Recall that on $\mathscr{M}$

$$S(t) + \frac{x_1(t)}{y_{S1}} + \frac{x_2(t)}{y_{S2}} = S^0, \qquad R(t) + \frac{x_1(t)}{y_{R1}} + \frac{x_2(t)}{y_{R2}} = R^0. \tag{2.21}$$

If option (i) holds, i.e. $(S(t), R(t)) \in \mathbb{R}^2_+ \setminus \mathrm{cl}\, Q$ for all large t, then $x_1'(t) < 0$ and $x_2'(t) < 0$ for all large t, since $x_i'(t) = x_i(t)[-D + f_i(S(t), R(t))]$, $x_i(t) > 0$ for all $t \geqslant 0$, and $S(t) < \min(\lambda_{S1}, \lambda_{S2})$ and $R(t) < \min(\lambda_{R1}, \lambda_{R2})$ for all large t. Since solutions are bounded, the monotonicity of $x_1(t)$ and $x_2(t)$ for large t implies convergence, and hence by (2.21) $S(t)$ and $R(t)$ also converge.

If option (ii) or (iii) holds the proof is similar.

If option (iv) holds the result follows by Lemma 2.1(ii). ■

Next we consider the system (2.16)–(2.17). This system is equivalent to the system (2.1) with initial conditions restricted to $\mathscr{M}$. We do a phase-plane

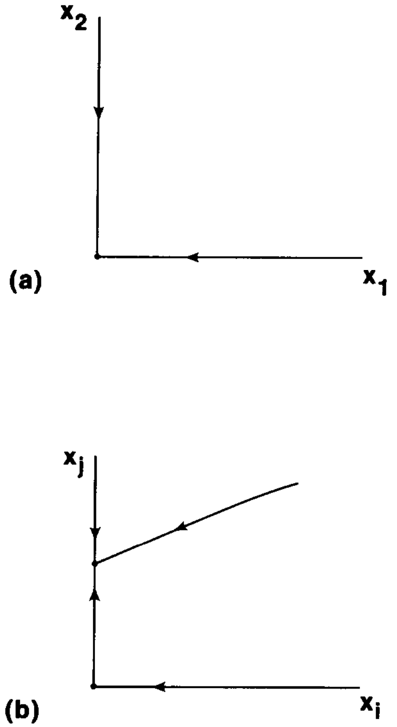

FIG. 2. Competition-independent extinction. (a) $\lambda_{S_i} > S^0$ and $\lambda_{R_i} > R^0$, $i = 1,2$; each population dies out even in the absence of its competitor. (b) $\lambda_{S_i} > S^0$ or $\lambda_{R_i} > R^0$, $i = 1$ or 2; $\lambda_{S_j} < S^0$ and $\lambda_{R_j} < R^0$, $j = 1$ or 2, $j \neq i$; population x_i dies out even in the absence of its competitor.

analysis of (2.16) in (x_1, x_2) space based on the information summarized in Table 2 in order to show that no saddle connections are possible and hence the dynamics of (2.1) are trivial.

If we allow $\lambda_{S_i} > S^0$ or $\lambda_{R_i} > R^0$ for $i = 1$ or 2, then there is no equilibrium for which the concentration of x_i is positive and hence there is competition-independent extinction of x_i. See Figure 2(a),(b). Figure 2(a) corresponds to the first biological outcome of Table 3. Figure 2(b) corresponds to the second and third biological outcomes.

If we assume that $\lambda_{S_i} < S^0$ and $\lambda_{R_i} < R^0$, $i = 1,2$, then (since we are assuming $C_1 \neq C_2$) there are only four basic pictures [see Figure 3(a)–(d)]. On $\mathcal{M}$ Figure 3(a) corresponds to the second biological outcome of Table 3, Figure 3(b) to the third, Figure 3(c) to the fourth, and Figure 3(d) to the fifth. Clearly there are no saddle connections. We have therefore proved

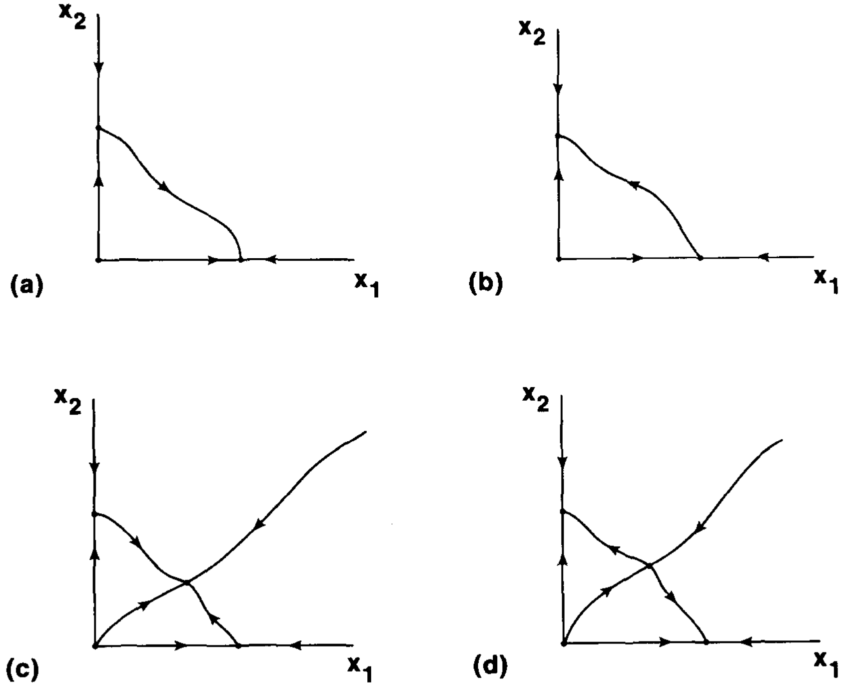

FIG. 3. Phase portraits in (x_1, x_2) space for (2.1), assuming $\lambda_{S_i} < S^0$ and $\lambda_{R_i} < R^0$, $i = 1, 2$. (a) Population 1 always wins. (b) Population 2 always wins. (c) Populations 1 and 2 coexist at a globally asymptotically stable interior equilibrium. (d) Initial concentrations determine the outcome: one population wins, the other dies out, except for solutions with initial conditions on the separatrix.

THEOREM 2.4

The dynamics of (2.1) *are trivial.*

Finally we note that by considering the location of the stable manifolds of the critical points on $\partial \mathbf{R}^4_+$ it follows that for the particular parameter ranges described in Table 3, solutions of (2.1) (i.e. solutions with initial conditions in the positive cone) have the same type of asymptotic behavior as solutions with initial conditions in the relative interior of $\mathcal{M}$. Hence we have shown that Table 3 applies globally.

3. THE MODEL—GENERAL KINETICS

In the previous section we restricted our attention to monotone kinetics. However, certain substrates may be growth-limiting at low concentrations as well as growth-inhibiting at high concentrations; for example, there is inhibition of *Nitrobacter* by nitrite and of *Nitrosomonas* by ammonia [17]. Such inhibition results in nonmonotone uptake functions. For specific models of inhibitory kinetics the reader is referred to [1, 5, 39]. Inhibition by high concentrations is often seen when microorganisms are used for biological waste decomposition or for water purification.

We continue to study exploitative competition for two purely complementary resources. We now allow the resources to be inhibitory at high concentrations. We make the same basic assumptions we made for the model (2.1) of the previous section and use the same notation. In particular, as in the previous section, we assume that growth rates adjust instantaneously to changes in resource concentration, that the functions $p_i(S)$ $[q_i(R)]$ represent the per capita growth rate of the ith population when resource S [resource R] is limiting, and that resource consumption rates and growth rates are proportional. Recall that for complementary resources S and R, a population is considered S-limited if its per capita consumption rate is independent of the concentration of R and is considered R-limited if its per capita consumption rate is independent of the concentration of S. In the context of the model (3.1) below, a population can be limited by a resource either because that resource is in short supply or because it is overabundant.

The model we study in this section is

$$\begin{aligned}
S'(t) &= [S^0 - S(t)]\,D - \sum_{i=1}^{2} \frac{x_i(t)}{y_{Si}} f_i(S(t), R(t)),\\
R'(t) &= [R^0 - R(t)]\,D - \sum_{i=1}^{2} \frac{x_i(t)}{y_{Ri}} f_i(S(t), R(t)),\\
x_i'(t) &= x_i(t)[-D + f_i(S(t), R(t))], \qquad i = 1,2,\\
S(0) &= S_0 \geqslant 0, \qquad R(0) = R_0 \geqslant 0,\\
x_i(0) &= x_{i0} > 0, \qquad i = 1,2,
\end{aligned} \tag{3.1}$$

where

$$f_i(S(t), R(t)) = \min(p_i(S(t)), q_i(R(t))), \qquad i = 1,2,$$

and p_i and q_i satisfy the assumptions (2.2)–(2.4). It is the same as the model (2.1) with the important exception that we no longer require p_i and q_i to be monotone. Instead we make the following assumption:

> There exist uniquely defined extended positive real numbers λ_{Si}, λ_{Ri}, μ_{Si}, and μ_{Ri}, $i=1,2$, with $\lambda_{Si} \leqslant \mu_{Si}$ and $\lambda_{Ri} \leqslant \mu_{Ri}$ such that
>
> $$\begin{aligned} p_i(S) &< D \quad \text{if} \quad S \notin [\lambda_{Si}, \mu_{Si}], \\ p_i(S) &> D \quad \text{if} \quad S \in (\lambda_{Si}, \mu_{Si}), \\ q_i(R) &< D \quad \text{if} \quad R \notin [\lambda_{Ri}, \mu_{Ri}], \\ q_i(R) &> D \quad \text{if} \quad R \in (\lambda_{Ri}, \mu_{Ri}). \end{aligned} \tag{3.2}$$

We make the following generic assumptions:

$$\begin{gathered} \text{If} \quad \lambda_{Si}\ [\lambda_{Ri}, \mu_{Si}, \mu_{Ri}] \text{ is finite,} \quad \text{then} \\ p_i'(\lambda_{Si}) \neq 0 \quad \left[q_i'(\lambda_{Ri}) \neq 0, \quad p_i'(\mu_{Si}) \neq 0, \quad q_i'(\mu_{Ri}) \notin 0\right]. \end{gathered} \tag{3.3}$$

If the parameters are finite, we assume

λ_{S1}, λ_{S2}, μ_{S1}, and μ_{S2} are distinct from each other and from S^0, (3.4a)

λ_{R1}, λ_{R2}, μ_{R1}, and μ_{R2} are distinct from each other and from R^0. (3.4b)

If $(\bar{S}, \bar{R}, \bar{x}_1, \bar{x}_2)$ is a critical point, then $p_i(\bar{S}) \notin q_i(\bar{R}), i=1,2$. (3.5)

We shall also require the following notation:

$$\mathscr{B}_i = \{(S,R) : \lambda_{Si} < S < \mu_{Si} \text{ and } \lambda_{Ri} < R < \mu_{Ri}\}, \qquad i=1,2. \tag{3.6}$$

$$\mathscr{Q} = \bigcup_{i=1}^{2} \mathscr{B}_i. \tag{3.7}$$

$$\mathscr{K} = \bigcap_{i=1}^{2} \mathscr{B}_i. \tag{3.8}$$

Therefore,

$$\begin{aligned} f_i(S,R) &> D \quad \text{if} \quad (S,R) \in \mathscr{B}_i, \\ f_i(S,R) &< D \quad \text{if} \quad (S,R) \notin \operatorname{cl} \mathscr{B}_i, \\ f_i(S,R) &= D \quad \text{if} \quad (S,R) \in \partial \mathscr{B}_i. \end{aligned}$$

Again, as one expects from the biology, solutions of (3.1) are positive and bounded. (The proof is similar to the proof of Theorem 3.1 in [9].) Also, the polygonal set

$$\mathscr{M} = \left\{(S,R,x_1,x_2) \in \mathbf{R}_+^4 : S + \frac{x_1}{y_{S1}} + \frac{x_2}{y_{S2}} = S^0 \text{ and } R + \frac{x_1}{y_{R1}} + \frac{x_2}{y_{R2}} = R^0\right\} \tag{3.9}$$

TABLE 4

Notation for (3.1)

$C_i = y_{Si}/y_{Ri}$, $i=1,2$		
$T_i = \dfrac{R^0 - \lambda_{Ri}}{S^0 - \lambda_{Si}}$, $i=1,2$,	$T^* = \dfrac{R^0 - \lambda_{R2}}{S^0 - \lambda_{S1}}$	$T_* = \dfrac{R^0 - \lambda_{R1}}{S^0 - \lambda_{S2}}$
$V_i = \dfrac{R^0 - \mu_{Ri}}{S^0 - \mu_{Si}}$, $i=1,2$,	$V^* = \dfrac{R^0 - \mu_{R2}}{S^0 - \mu_{S1}}$,	$V_* = \dfrac{R^0 - \mu_{R1}}{S^0 - \mu_{S2}}$
$U_i = \dfrac{R^0 - \lambda_{Ri}}{S^0 - \mu_{Si}}$, $i=1,2$,	$U^* = \dfrac{R^0 - \lambda_{R2}}{S^0 - \mu_{S1}}$,	$U_* = \dfrac{R^0 - \lambda_{R1}}{S^0 - \mu_{S2}}$
$W_i = \dfrac{R^0 - \mu_{Ri}}{S^0 - \lambda_{Si}}$, $i=1,2$,	$W^* = \dfrac{R^0 - \mu_{R2}}{S^0 - \lambda_{S1}}$,	$W_* = \dfrac{R^0 - \mu_{R1}}{S^0 - \lambda_{S2}}$

is a global attractor for (3.1), and, as in Section 2, on $\mathcal{M}$ solutions satisfy

$$\begin{aligned} S'(t) + \sum_{i=1}^{2} \frac{x_i'(t)}{y_{Si}} &= 0 \\ R'(t) + \sum_{i=1}^{2} \frac{x_i'(t)}{y_{Ri}} &= 0. \end{aligned} \tag{3.10}$$

However, even if at high concentrations, only one resource is inhibitory to only one of the competitors, Lemma 2.2 need not hold, and the dynamics need not be trivial. For example, the existence of a nontrivial, orbitally asymptotically stable periodic orbit for the model (3.1) is possible. In this case the concentrations of the resources and of the competitors oscillate indefinitely.

Before we consider examples that illustrate this oscillatory behavior, we give a table of useful notation (Table 4), a table of notation for the critical points (Table 5), and a table summarizing criteria for the existence and stability of these critical points (Table 6). We then give sufficient conditions that guarantee that the dynamics of (3.1) are trivial.

To ensure that the vector field at, and in a neighborhood of, each critical point is C^1, we make the assumption (3.5). In terms of the notation in Table 4, that assumption implies that

$$T_i,\ W_i,\ V_i \text{ and } U_i \text{ are all distinct from } C_i, \qquad i=1,2. \tag{3.11}$$

We also assume that

$$C_1 \neq C_2 \tag{3.12}$$

TABLE 5

Notation for the Critical Points of (3.1)

Notation	Critical point[a]
$E_{\mu_{S1},*}$	$=\left(\mu_{S1}, R^0 - C_1\left(S^0-\mu_{S1}\right), y_{S1}\left(S^0-\mu_{S1}\right), 0\right)$
$E_{*,\mu_{R1}}$	$=\left(S^0-\dfrac{R^0-\mu_{R1}}{C_1}, \mu_{R1}, y_{R1}\left(R^0-\mu_{R1}\right), 0\right)$
$E_{\mu_{S2},*}$	$=\left(\mu_{S2}, R^0 - C_2\left(S^0-\mu_{S2}\right), 0, y_{S2}\left(S^0-\mu_{S2}\right)\right)$
$E_{*,\mu_{R2}}$	$=\left(S^0-\dfrac{R^0-\mu_{R2}}{C_2}, \mu_{R2}, 0, y_{R2}\left(R^0-\mu_{R2}\right)\right)$
$E_{\gamma,\eta}$	$=(\gamma, \eta, x_1^*, x_2^*)$
	where $x_1^* = y_{S1}y_{R1}\left(\dfrac{y_{S2}\left(S^0-\gamma\right)-y_{R2}\left(R^0-\eta\right)}{y_{R1}y_{S2}-y_{S1}y_{R2}}\right)$,
	$x_2^* = y_{S2}y_{R2}\left(\dfrac{y_{R1}\left(R^0-\eta\right)-y_{S1}\left(S^0-\gamma\right)}{y_{R1}y_{S2}-y_{S1}y_{R2}}\right)$,
	$(\gamma,\eta) = (\lambda_{S1},\lambda_{R2}), (\lambda_{S2},\lambda_{R1}), (\mu_{S1},\lambda_{R2}), (\mu_{S2},\lambda_{R1}),$ $(\lambda_{S1},\mu_{R2}), (\lambda_{S2},\mu_{R1}), (\mu_{S1},\mu_{R2}), (\mu_{S2},\mu_{R1})$

[a] Provided it lies in $\mathbf{R}_+^4$. The points E_{S^0,R^0}, $E_{\lambda_{S1},*}$, $E_{*,\lambda_{R1}}$, $E_{\lambda_{S2},*}$ and $E_{*,\lambda_{R2}}$ as defined Table 1 are also critical points of (3.1) provided they lie in $\mathbf{R}_+^4$.

and

$$T_*,\ T^*,\ W_*,\ W^*,\ V_*,\ V^*,\ U_*, \text{ and } U^* \text{ are distinct from } C_1 \text{ and } C_2. \tag{3.13}$$

This ensures that the critical points are isolated and, together with the assumptions (3.3) and (3.4), ensures that for each critical point, none of the eigenvalues of the associated matrix of the linearization equals zero.

Next we develop simple graphical criteria that, when satisfied, ensure that the dynamics are trivial. We adapt certain concepts and terminology frequently used in linear programming (see e.g. Luenberger [21]). We also apply the techniques used in Section 2. In particular, Lemma 2.1 (see below) also holds for the model (3.1) subject to considerations of feasibility, provided we replace Q by $\mathscr{Q}$ and K by $\mathscr{K}$.

We shall refer to $\mathscr{M}$ as the *feasible region*.

DEFINITION 3.1

We define the *feasible region projected on* (S, R) *space*, which we denote by $\mathscr{F}$, as the set

$$\mathscr{F} = \left\{(S,R) \in \mathbf{R}_+^2 \colon S + \frac{x_1}{y_{S1}} + \frac{x_2}{y_{S2}} = S^0, \right.$$
$$\left. R + \frac{x_1}{y_{R1}} + \frac{x_2}{y_{R2}} = R^0,\ x_1 \geqslant 0,\ x_2 \geqslant 0 \right\}. \tag{3.14}$$

TABLE 6

Existence and Stability Criteria for Critical Points of (3.1)

Critical Point	Criteria for existence	Criteria for asymptotic stability
E_{S^0,R^0}	Always exists	$(\lambda_{S1} > S^0$ or $\lambda_{R1} > R^0$ or $\mu_{S1} < S^0$ or $\mu_{R1} < R^0)$ and $(\lambda_{S2} > S^0$ or $\lambda_{R2} > R^0$ or $\mu_{S2} < S^0$ or $\mu_{R2} < R^0)$
$E_{\lambda_{S1},*}$	$\lambda_{S1} < S^0$, $T_1 > C_1$ and $W_1 < C_1$	$\lambda_{S1} < \lambda_{S2}$ or $\lambda_{S1} > \mu_{S2}$ or $T^* < C_1$ or $W^* > C_1$
$E_{*,\lambda_{R1}}$	$\lambda_{R1} < R^0$, $\lambda_{S1} < S^0$, and $T_1 < C_1$ and if $\mu_{S1} < S^0$ then $C_1 < U_1$	$\lambda_{R1} < \lambda_{R2}$ or $\lambda_{R1} > \mu_{R2}$ or $(C_1 < T_*$ and $\lambda_{S2} < S^0)$ or $\lambda_{S2} > S^0$ or $(C_1 > U_*$ and $\mu_{S2} < S^0)$
$E_{\lambda_{S2},*}$	$\lambda_{S2} < S^0, T_2 > C_2$, and $W_2 < C_2$	$\lambda_{S2} < \lambda_{S1}$ or $\lambda_{S2} > \mu_{S1}$ or $T_* < C_2$ or $W_* > C_2$
$E_{*,\lambda_{R2}}$	$\lambda_{R2} < R^0, \lambda_{S2} < S^0$ and $T_2 < C_2$ and if $\mu_{S2} < S^0$ then $C_2 < U_2$	$\lambda_{R2} < \lambda_{R1}$ or $\lambda_{R2} > \mu_{R1}$ or $(C_2 < T^*$ and $\lambda_{S1} < S^0)$ or $\lambda_{S1} > S^0$ or $(C_2 > U^*$ and $\mu_{S1} < S^0)$
$E_{\mu_{S1},*}$	$\mu_{S1} < S^0, V_1 < C_1$, and $U_1 > C_1$	Always unstable
$E_{*,\mu_{R1}}$	$\mu_{R1} < R^0, \lambda_{S1} < S^0$, and $W_1 < C_1$ and if $\mu_{S1} < S^0$ then $C_1 < V_1$	Always unstable
$E_{\mu_{S2},*}$	$\mu_{S2} < S^0, V_2 < C_2$, and $U_2 > C_2$	Always unstable
$E_{*,\mu_{R2}}$	$\mu_{R2} < R^0$, $\lambda_{S2} < S^0$ and $W_2 < C_2$ and if $\mu_{S2} < S^0$ then $C_2 < V_2$	Always unstable
$E_{\lambda_{S1},\lambda_{R2}}$	$\lambda_{S2} < \lambda_{S1} < \mu_{S2}$ and $\lambda_{R1} < \lambda_{R2} < \mu_{R1} C_1 < C_2$ and $\left(\begin{array}{l} C_1 < T^* < C_2 \text{ and } \lambda_{S1} < S^0 \\ \text{or} \\ C_1 > T^* > C_2 \text{ and } \lambda_{S1} < S^0 \end{array}\right)$	
$E_{\lambda_{S2},\lambda_{R1}}$	$\lambda_{S1} < \lambda_{S2} < \mu_{S1}$ and $\lambda_{R2} < \lambda_{R1} < \mu_{R2} C_1 > C_2$ and $\left(\begin{array}{l} C_1 < T_* < C_2 \text{ and } \lambda_{S2} < S^0 \\ \text{or} \\ C_1 > T_* > C_2 \text{ and } \lambda_{S2} < S^0 \end{array}\right)$	

TABLE 6 *Continued*

Critical Point	Criteria for existence	Criteria for asymptotic stability
$E_{\mu_{S1},\lambda_{R2}}$	$\lambda_{S2} < \mu_{S1} < \mu_{S2}$ and $\lambda_{R1} < \lambda_{R2} < \mu_{R1}$ and $\left(\begin{array}{l} C_1 < U^* < C_2 \text{ and } \mu_{S1} < S^0 \\ \text{or} \\ C_1 > U^* > C_2 \text{ and } \mu_{S1} < S^0 \end{array}\right)$	[a]
$E_{\mu_{S2},\lambda_{R1}}$	$\lambda_{S1} < \mu_{S2} < \mu_{S1}$ and $\lambda_{R2} < \lambda_{R1} < \mu_{R2}$ and $\left(\begin{array}{l} C_1 < U_* < C_2 \text{ and } \mu_{S2} < S^0 \\ \text{or} \\ C_1 > U_* > C_2 \text{ and } \mu_{S2} < S^0 \end{array}\right)$	[a]
$E_{\lambda_{S1},\mu_{R2}}$	$\lambda_{S2} < \lambda_{S1} < \lambda_{S2}$ and $\lambda_{R1} < \mu_{R2} < \mu_{R1}$ and $\left(\begin{array}{l} C_1 < W^* < C_2 \text{ and } \lambda_{S1} < S^0 \\ \text{or} \\ C_1 > W^* > C_2 \text{ and } \lambda_{S1} < S^0 \end{array}\right)$	[a]
$E_{\lambda_{S2},\mu_{R1}}$	$\lambda_{S1} < \lambda_{S2} < \mu_{S1}$ and $\lambda_{R2} < \mu_{R1} < \mu_{R2}$ and $\left(\begin{array}{l} C_1 < W_* < C_2 \text{ and } \lambda_{S2} < S^0 \\ \text{or} \\ C_1 > W_* > C_2 \text{ and } \lambda_{S2} < S^0 \end{array}\right)$	[a]
$E_{\mu_{S1},\mu_{R2}}$	$\lambda_{S2} < \mu_{S1} < \mu_{S2}$ and $\lambda_{R1} < \mu_{R2} < \mu_{R1}$ and $\left(\begin{array}{l} C_1 < V^* < C_2 \text{ and } \mu_{S1} < S^0 \\ \text{or} \\ C_1 > V^* > C_2 \text{ and } \mu_{S1} < S^0 \end{array}\right)$	Always unstable[b]
$E_{\mu_{S2},\mu_{R1}}$	$\lambda_{S1} < \mu_{S2} < \mu_{S1}$ and $\lambda_{R2} < \mu_{R1} < \mu_{R2}$ and $\left(\begin{array}{l} C_1 < V_* < C_2 \text{ and } \mu_{S2} < S^0 \\ \text{or} \\ C_1 > V_* > C_2 \text{ and } \mu_{S2} < S^0 \end{array}\right)$	Always unstable[b]

[a] Stability depends on the sign of the real part of the roots of the characteristic equation

$$\xi^2 - \xi\left(x_1^*\frac{\partial f_1}{\partial x_1} + x_2^*\frac{\partial f_2}{\partial x_2}\right) + x_1^*x_2^*\left(\frac{\partial f_1}{\partial x_1}\frac{\partial f_2}{\partial x_2} - \frac{\partial f_1}{\partial x_2}\frac{\partial f_2}{\partial x_1}\right) = 0$$

evaluated at the critical point.

[b] By phase-plane analysis in (S, R) space using Lemma 2.1.

$\mathcal{F}$ is therefore the projection of $\mathcal{M}$ on (S, R) space. Since we are assuming $C_1 \neq C_2$, for each pair $(\hat{S}, \hat{R})$ with $\hat{S} \geqslant 0$ and $\hat{R} \geqslant 0$ there is at most one pair $(\hat{x}_1, \hat{x}_2)$ such that $(\hat{S}, \hat{R}, \hat{x}_1, \hat{x}_2) \in \mathcal{F}$.

We point out here that if $(S(t), R(t), x_1(t), x_2(t))$ is a solution of (3.1) with initial conditions in $\mathcal{M}$, then $(S(t), R(t)) \in \mathcal{F}$ for all $t \geqslant 0$. Thus Lemma 2.1 only applies to points $(S(\tau), R(\tau)) \in \mathcal{F}$, and therefore Figure 1 (in Section 2) is actually only valid for points in $\mathcal{F}$.

Again adopting the terminology of linear programming, we give

DEFINITION 3.2

A *basic feasible solution of* $\mathcal{M}$ is a point $(S, R, x_1, x_2) \in \mathcal{M}$ with at least two components equal to zero.

DEFINITION 3.3

A *basic feasible solution of* $\mathcal{F}$ is a point (S, R) such that (S, R, x_1, x_2) is a basic feasible solution of $\mathcal{M}$.

We generate the $C_2^4 = 6$ possible basic feasible solutions of $\mathcal{M}$ and therefore of $\mathcal{F}$ in Appendix 2, and we summarize the results in Table 7.

It is well known from the theory of linear programming that $\mathcal{M}$ is precisely the closed convex hull of the set of all basic feasible solutions of $\mathcal{M}$, and so $\mathcal{F}$ is the closed convex hull of all basic feasible solutions of $\mathcal{F}$. See Figure 4 for examples of $\mathcal{F}$.

It is interesting to note that the feasible region depends only on the yield factors y_{Si} and y_{Ri} and the concentrations S^0 and R^0 of S and R in the feed bottle. Since S^0 and R^0 are easily controlled by the experimenter, the shape of the feasible region can be controlled, and as we shall see, this

TABLE 7

Basic Feasible Solutions

Basic feasible solutions		Criteria for existence
of $\mathcal{M}$	of $\mathcal{F}$	
$(S^0, R^0, 0, 0)$	(S^0, R^0)	Always exists
$(0, R^0 - C_1 S^0, y_{S1} S^0, 0)$	$(0, R^0 - C_1 S^0)$	$R^0/S^0 \geqslant C_1$
$(S^0 - R^0/C_1, 0, y_{R1}, 0)$	$(S^0 - R^0/C_1, 0)$	$R^0/S^0 \leqslant C_1$
$(0, R^0 - C_2 S^0, 0, y_{S2} S^0)$	$(0, R^0 - C_2 S^0)$	$R^0/S^0 \geqslant C_2$
$(S^0 - R^0/C_2, 0, y_{R2} R^0, 0)$	$(S^0 - R^0/C_2, 0)$	$R^0/S^0 \leqslant C_2$
$(0, 0, \Gamma, \Delta)$[a]	$(0,0)$	$C_1 \leqslant R^0/S^0 \leqslant C_2$ or $C_2 \leqslant R^0/S^0 \leqslant C_1$

[a] $\Gamma = y_{S1} y_{R1} (y_{S2} S^0 - y_{R2} R^0)/(y_{S2} y_{R1} - y_{S1} y_{R2})$, $\Delta = y_{S2} y_{R2} (y_{R1} R^0 - y_{S1} S^0)/(y_{S2} y_{R1} - y_{S1} y_{R2})$.

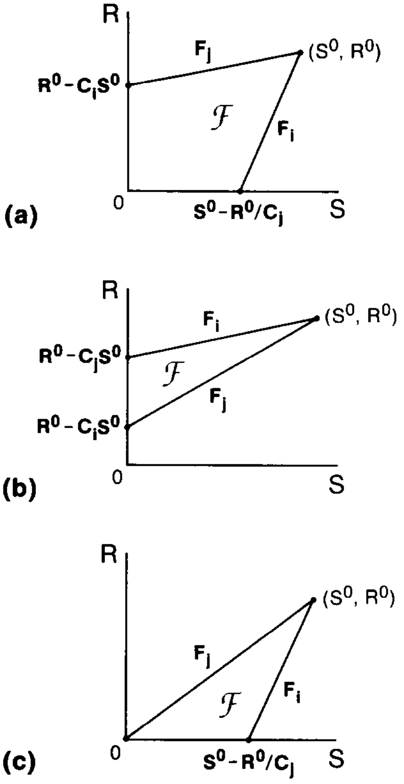

FIG. 4. Examples of the feasible region projected on (S, R) Space $\mathscr{F}$: (a) $C_i < R^0/S^0 < C_j$, $i=1$ or 2, $j=1$ or 2, $i \neq j$; (b) $R^0/S^0 > C_i > C_j$, $i=1$ or 2, $j=1$ or 2, $i \neq j$; (c) $C_i = R^0/S^0 < C_j$.

implies that the experimenter has a lot of control over which critical points lie in the feasible region.

Using this idea of the feasible region, we are able to determine graphically whether a critical point exists or not. In order to do this we need the following notation. For each $i = 1, 2$, that portion of $\partial \mathscr{F}$ which corresponds to the portion of $\partial \mathscr{M}$ along which $x_i = 0$ we call F_i. We also define

$$\mathscr{G} = \partial \mathscr{B}_1 \cap \partial \mathscr{B}_2 \cap \operatorname{int} \mathscr{F}. \tag{3.15}$$

LEMMA 3.4

(i) *The set of all critical points in* $\mathbb{R}_+^4$ *is the set of all points in* $\mathscr{M}$ *for which the projection onto* (S, R) *space belongs to the set* $(\partial \mathscr{B}_1 \cap F_2) \cup (\partial \mathscr{B}_2 \cap F_1) \cup \{(S^0, R^0)\} \cup \mathscr{G}$.

(ii) *The set of all interior critical points in* $\mathbb{R}_+^4$ *is the set of all points in* $\mathcal{M}$ *for which the projection onto* (S, R) *space belongs to the set* $\mathcal{G}$.

(iii) *The set of all boundary critical points in* $\mathbb{R}_+^4$ *is the set of all points in* $\mathcal{M}$ *for which the projection onto* (S, R) *space belongs to the set*

$$(\partial\mathcal{B}_1 \cap F_2) \cup (\partial\mathcal{B}_2 \cap F_1) \cup \{(S^0, R^0)\}.$$

Proof. The proof is obvious (and the result holds even if $C_1 = C_2$, in which case more than one point of $\mathcal{M}$ may correspond to a point in $\mathcal{F}$ and so the critical points will not be isolated). ■

The application of Lemma 3.4 is illustrated in Figure 5. Although in Table 6 we see that there are seventeen possible critical points, from this lemma it follows that for any particular example there can be no more than

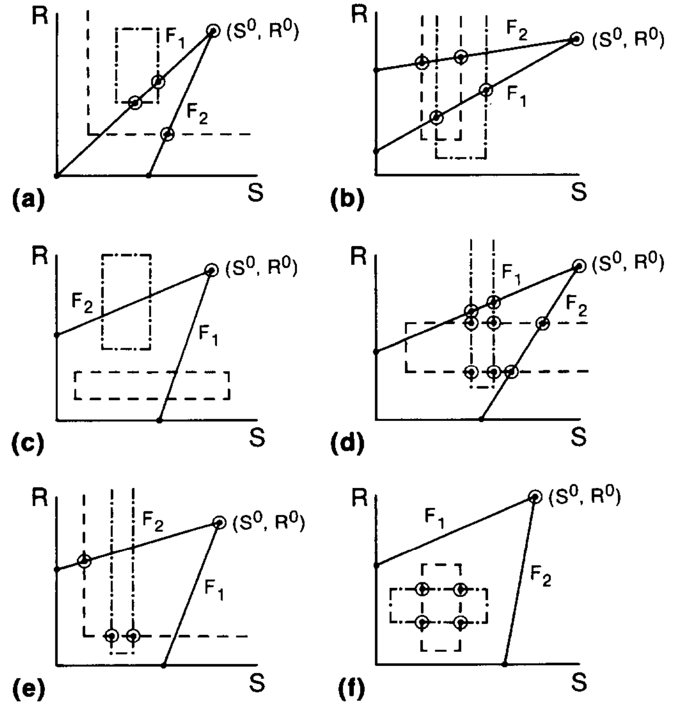

FIG. 5. Examples of the graphical method of determining critical points. ⊙ denotes a critical point. Dashed lines: $\partial\mathcal{B}_1$; dot-dash lines: $\partial\mathcal{B}_2$.

nine critical points [see Figure 5(d)] and even as few as one critical point (see Figure 5(c)].

We are now ready to give a sufficient condition that ensures that the dynamics of (3.1) are trivial.

THEOREM 3.5

If

$$\mathcal{G} \cap \{(\lambda_{S1}, \mu_{R2}), (\lambda_{S2}, \mu_{R1}), (\mu_{S1}, \lambda_{R2}), (\mu_{S2}, \lambda_{R1})\} = \varnothing, \tag{3.16}$$

then the dynamics of (3.1) *are trivial.*

[See Figure 5(a), (b), and (c) for examples of when this theorem applies. Note also that at most two of the for points in the braces in (3.16) can intersect $\mathcal{G}$ in any particular example.]

Proof. By the generic assumptions (3.3)–(3.5) and (3.11)–(3.13) it follows that the critical points are isolated, the vector field is C^1 at and in a neighborhood of each critical point, and the matrix of the linearization associated with each critical point never has an eigenvalue equal to zero.

First we show that the dynamics of (3.1) restricted to $\mathcal{M}$ are trivial. Note that (3.1) restricted to $\mathcal{M}$ is equivalent to the two-dimensional system (2.16)–(2.17). The hypothesis (3.16) implies that the only candidates for interior critical points are of the form

$$E_{\lambda_{Si}, \lambda_{Rj}} \text{ and } E_{\mu_{Sk}, \mu_{Rl}}, \tag{3.17}$$

where $i, j, k, l = 1$ or 2 and $i \neq j$, $k \neq l$. In this case Lemma 2.1 can be used to show that Lemma 2.2 holds provided we replace Q and K by $\mathcal{Q}$ and $\mathcal{K}$ respectively. That the dynamics of (3.1) restricted to $\mathcal{M}$ are trivial now follows by a proof similar to the proof of Theorem 2.3.

To show that the dynamics of (3.1) are trivial, since $\mathcal{M}$ is globally attracting and all solutions are bounded, it suffices to show that the phase portrait of the system (2.16) [in (x_1, x_2) space] contains no saddle connections. If $\mathcal{G} = \varnothing$, i.e. there are no interior critical points of (2.16), then clearly there can be no saddle connections, since a saddle connection must contain a critical point in its interior. If $\mathcal{G} \neq \varnothing$, then the only interior critical points of (3.1) are of the form in (3.17), and hence the system (2.16) can have at most two interior critical points. By index theory, if both interior critical points of (2.16) are saddle points (or if there is a unique interior critical point, and it is a saddle point), then there are no saddle connections. To prove that the dynamics on $\mathcal{M}$ are trivial we showed that the competitor concentrations converge monotonely. The same method can be used to show that if we reverse time, competitor concentrations either converge monotonely or leave $\mathbf{R}_+^2$. Therefore, under the assumption (3.16), no interior critical point of (2.16) is a spiral. Since solutions in (x_1, x_2) space are eventually monotone both in positive and in negative time, by the Poincaré-Bendixson theorem and the generic nature of the critical points, there cannot be a unique unstable or a stable node inside a saddle connection, and by index theory there cannot be precisely two nodes inside a saddle connection. Thus there can be no interior critical point inside a saddle connection of (2.16), and so there can be no saddle connections. Therefore the dynamics of (3.1) are trivial. ■

As an immediate consequence of the previous two theorems we obtain the following result concerning the extinction of both competitors. The corollary is illustrated in Figure 6.

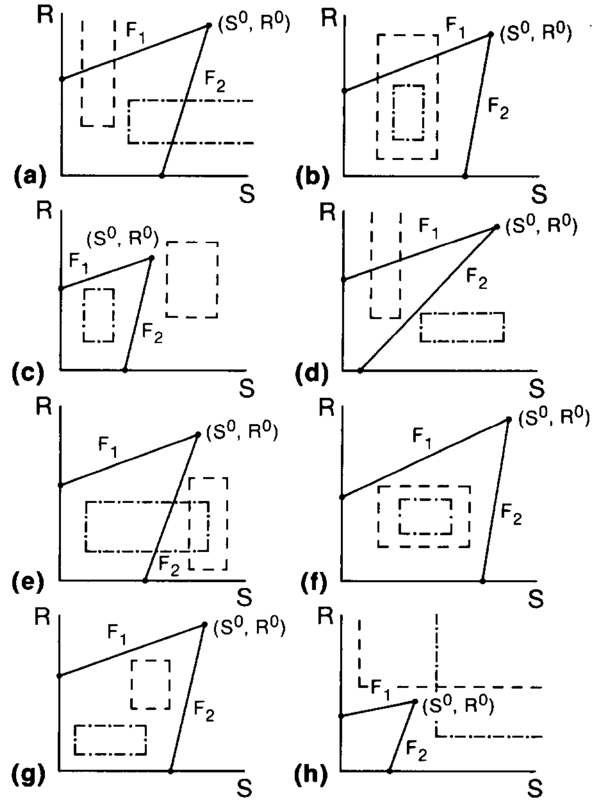

FIG. 6. Examples of competition-independent extinction. Dashed lines: $\partial\mathscr{B}_1$; dot-dash lines: $\partial\mathscr{B}_2$.

COROLLARY 3.6

If

(i) $\mathcal{G} = \varnothing$,
(ii) $\partial\mathcal{B}_1 \cap F_2 = \varnothing$, *and*
(iii) $\partial\mathcal{B}_2 \cap F_1 = \varnothing$,

then the critical point E_{S^0, R^0} *is globally asymptotically stable for* (3.1).

Proof. By Lemma 3.4, E_{S^0, R^0} is the only critical point of (3.1). The result is immediate from Theorem 3.5 and the fact that all solutions are bounded. ■

Other immediate consequences of Lemma 3.4 and Theorem 3.5 are the following results concerning competition-independent extinction.

COROLLARY 3.7

Let $(S(t), R(t), x_1(t)(x_2(t)))$ *be a solution of* (3.1). *If* $\mathcal{B}_i \cap \mathcal{F} = \varnothing$, *then* $\lim_{t\to\infty} x_i(t) = 0$, $i = 1,2$.

COROLLARY 3.8

Let $(S(t), R(t), x_1(t), x_2(t))$ *be a solution of* (3.1). *Assume* $i, j = 1,2$, $i \neq j$ *and* $x_{j0} = 0$. *(Therefore,* $x_j(t) = 0$ *for all* t.*) If* $\mathcal{B}_i \cap F_j = \varnothing$, *then* $\lim_{t\to\infty} x_i(t) = 0$.

This leads to a surprising result that seems to indicate that at times, the competitors are actually cooperating. There are situations in which in the absence of a rival each population would die out, but when a rival is present there is a possibility of coexistence. This is demonstrated in the following example and illustrated in Figure 7.

Example 3.9. Let

$$\begin{array}{llll} \lambda_{S1} = 2, & \lambda_{S2} = 3, & \mu_{S1} = 5, & \mu_{S2} = \infty, \\ \lambda_{R1} = 4, & \lambda_{R2} = 2, & \mu_{R1} = \infty, & \mu_{R2} = 9, \\ & S^0 = 20, & R^0 = 30, & D = 1, \\ y_{S1} = 2, & y_{S2} = 1, & y_{R1} = 1, & y_{R2} = 1. \end{array}$$

If x_i is absent (i.e. $x_{i0} = 0$), then $\lim_{t\to\infty} x_j = 0$, where $i, j = 1,2$ and $i \neq j$. This follows from Corollary 3.8 (see Figure 8), since there are no critical points on the boundary except E_{S^0, R^0}. However, the interior critical point $E_{\lambda_{S2}, \lambda_{R1}}$ is asymptotically stable (see Table 6), since

$$1 = C_2 < T_* = \tfrac{26}{17} < C_1 = 2,$$

and so there are initial conditions for which there is coexistence. This coexistence must in some sense be due to cooperation.

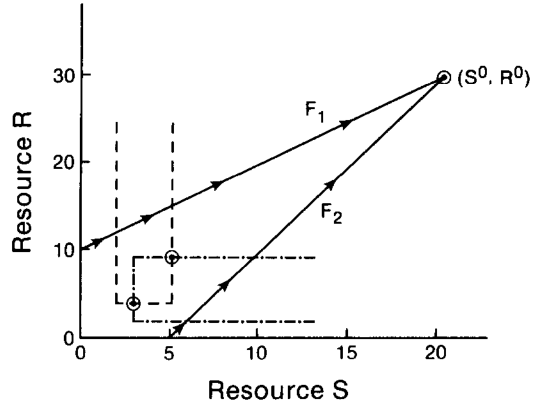

FIG. 7. Cooperative coexistence. Dashed lines: $\partial\mathcal{B}_1$; dot-dash lines: $\partial\mathcal{B}_2$; ⊙: critical points.

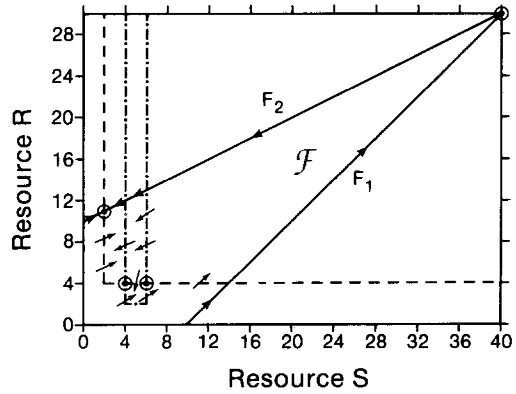

FIG. 8. $\mathcal{F}$, $\mathcal{B}_1$, and $\mathcal{B}_2$ for Example 3.10. Solid lines: $\partial\mathcal{F}$; dashed lines: $\partial\mathcal{B}_1$; dot-dash lines: $\partial\mathcal{B}_2$; →: direction of vector field; ⊙: critical points.

By Theorem 3.5 it follows that a necessary condition for (3.1) to have nontrivial dynamics is that there exists a critical point of the form given in (3.17), i.e. a critical point at which one competitor is S-limited and the other is R-limited, and one competitor is limited because a resource is in short supply whereas the other is limited because a resource is overabundant and thus inhibitory.

We consider two examples that illustrate that (3.1) can have nontrivial dynamics. The functions in both examples are chosen purely for their mathematical convenience rather than for any biological significance.

In the first example, only one resource is inhibitory to only one population at high concentrations; namely, resource S is inhibitory to population 2 at high concentrations. All the other kinetics are monotone with microbial responses modeled by Michaelis-Menten kinetics.

Example 3.10. Let

$$p_1(S) = \frac{5S}{8+S},$$

$$p_2(S) = 1 + \frac{(S-4)(6-S)}{24\left(A_1S^2 + \frac{7}{12}S + 1\right)} = \frac{(24A_1 - 1)S^2 + 4S}{24A_1S^2 + 14S + 24},$$

$$q_1(R) = \frac{10R}{4+9R},$$

$$q_2(R) = \frac{5.1R}{8.2+R}.$$

$$D = 1, \qquad S^0 = 40, \qquad R^0 = 30,$$

$$y_{S1} = 1, \qquad y_{S2} = 1, \qquad y_{R1} = 2, \qquad y_{R2} = 1.$$

Here,

$$\lambda_{S1} = 2, \qquad \lambda_{S2} = 4, \qquad \lambda_{R1} = 4, \qquad \lambda_{R2} = 2,$$

$$\mu_{S1} = \infty, \qquad \mu_{S2} = 6, \qquad \mu_{R1} = \infty, \qquad \mu_{R2} = \infty.$$

Thus we have the critical points shown in Table 8.

In this example, as A_1 decreases through $\frac{1}{12}$ the critical point $E_{\mu_{S2},\lambda_{R1}}$ changes its stability. For $A_1 > \frac{1}{12}$, $E_{\mu_{S2},\lambda_{R1}}$ is asymptotically stable, whereas

TABLE 8

Results of Example 3.10

Critical points	Local stability
$E_{S^0,R^0} = (40,30,0,0)$	Unstable
$E_{\lambda_{S1},*} = (2,11,38,0)$	Asymptotically stable
$E_{\lambda_{S2},\lambda_{R1}} = (4,4,20,16)$	Unstable
$E_{\mu_{S2},\lambda_{R1}} = (6,4,16,18)$	Asymptotically stable if $A_1 > \frac{1}{12}$, unstable if $A_1 < \frac{1}{12}$, Hopf bifurcation at $A_1 = \frac{1}{12}$.

for $A_1 < \frac{1}{12}$ it is unstable. This change in stability occurs via a Hopf bifurcation. The resulting periodic orbits appear for values of $A_1 < \frac{1}{12}$ and are orbitally asymptotically stable.

The calculations to show that there is a Hopf bifurcation at $A_1 = \frac{1}{12}$ and that the resulting periodic orbits exist for $A_1 < \frac{1}{12}$ and are asymptotically stable are usually very tedious if done by hand. Instead they were done by means of the symbol manipulation language REDUCE2 according to the method described in Marsden and McCracken [22, Section 4]. The computations for Example 3.10 are summarized in Appendix 1.A.

The feasible set in (S, R) space, $\mathscr{B}_1$, and $\mathscr{B}_2$ are shown in Figure 8. The next series of graphs are also in (S, R) space. In Figure 9 we show sample solutions for $A_1 = 0.08 < \frac{1}{12}$. The solutions in Figure 9 that are depicted by dotted lines were found by integrating backward in time, whereas all other solutions were integrated forward in time. However, all arrows indicate the evolution of solutions for positive time. In Figure 10 we focus on the critical point $E_{\mu_{S2},\lambda_{R1}}$ and the asymptotically stable periodic orbit surrounding $E_{\mu_{S2},\lambda_{R1}}$, and we show two solutions, one winding in towards the periodic orbit from the outside and one winding out towards the periodic orbit from the inside. Figure 11 is in (x_1, x_2) space. Here again we focus on the critical

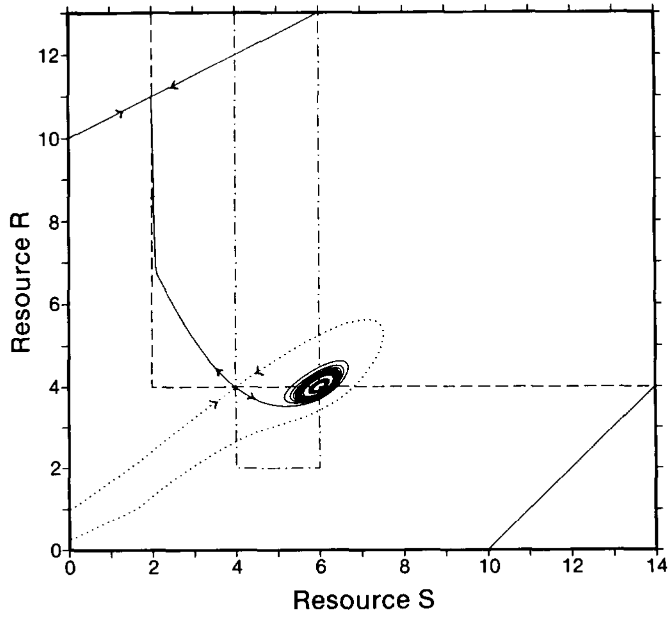

FIG. 9. Sample trajectories of Example 3.10; $A_1 = 0.08 < \frac{1}{12}$. Dashed lines: $\partial\mathscr{B}_1$; dot-dash lines: $\partial\mathscr{B}_2$.

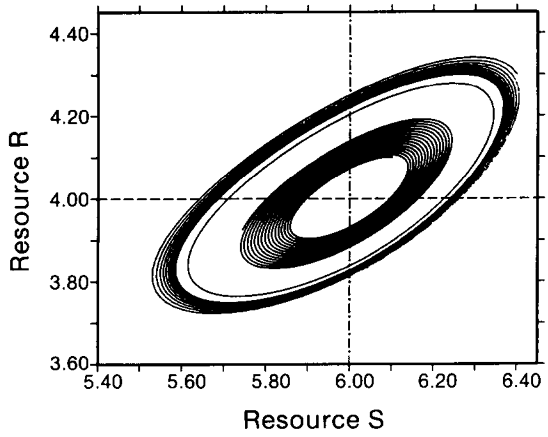

FIG. 10. The stable periodic orbit of Example 3.10 in (S, R) space.

point $E_{\mu_{S2},\lambda_{R1}}$ and show the periodic orbit with trajectories winding toward it.

It is interesting to note that in this example there is a range of choices of A_1 for which the critical point $E_{\lambda_{S1},*}$ is asymptotically stable, and for these same parameters there is a stable periodic orbit. Therefore there are at least two distinct biological outcomes possible.

That there is a Hopf bifurcation and that the bifurcating periodic orbit is asymptotically stable is actually independent of the choice of the functions $p_1(S)$ and $q_2(R)$ provided that for $p_1(S)$, $\lambda_{S1} < 6 < \mu_{S1}$ and for $q_2(R)$,

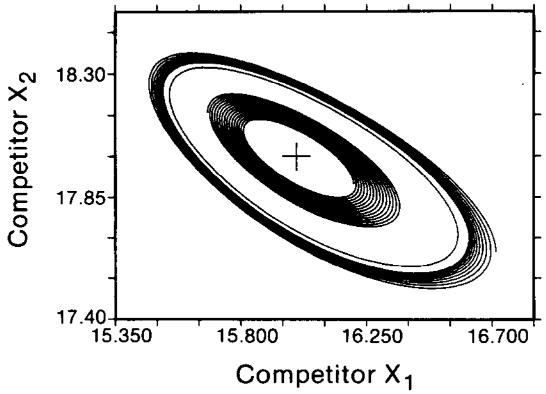

FIG. 11. The stable periodic orbit of Example 3.10 (x_1, x_2) space.

$\lambda_{R2} < 4 < \mu_{R2}$, thus ensuring that $E_{\mu_{S2},\lambda_{R1}}$ is an equilibrium point and that the vector field in a neighborhood of $E_{\mu_{S2},\lambda_{R1}}$ is analytic. This is because the Hopf bifurcation is a local phenomenon. However, it is interesting to note that in this example there are points at which the vector field is not differentiable. The choice of the functions $p_1(S)$ and $q_2(R)$ can affect how close a point at which the vector field is not differentiable is to an equilibrium point. This can influence the size of the parameter range $A_1 < \frac{1}{12}$ for which a periodic orbit exists. In our example, as A_1 decreases, the amplitude of the bifurcating periodic orbit increases. As A_1 continues to decrease, the amplitude of the periodic orbit continues to increase, and it may approach a point where the vector field is not differentiable. If A_1 is decreased even more, the orbit could disappear. That this can actually happen is demonstrated in Figure 12. We keep everything the same as before (including $A_1 = 0.08$), except that we replace $p_1(S)$ by

$$p_1(S) = \frac{1.004S}{0.008 + S}.$$

For this choice of $p_1(S)$, $E_{\mu_{S2},\lambda_{R1}}$ is still a critical point. With the previous choice for $p_1(S)$ there is a periodic orbit (see Figures 9–11). However, for this choice of the function $p_1(S)$ there is a discontinuity in the vector field at (approximately) the point (6.0, 4.10914), and this is apparently close

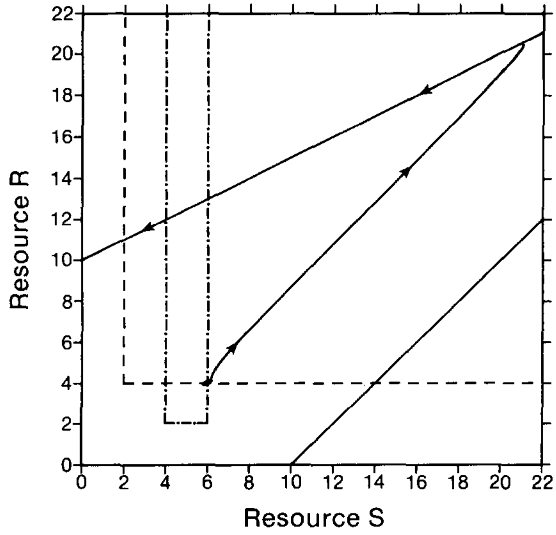

FIG. 12. Discontinuity in the vector field—periodic orbit disappears.

enough to $E_{\mu_{S2},\lambda_{R1}}$ so that there is no longer a periodic orbit for $A_1 = 0.08$. [Figure 12 is in (S, R) space. The initial conditions for the substrate are (6.05,4.05). Instead of cycling out to a periodic orbit, the solution escapes and converges to (2,11).]

In the second example both resources are inhibitory to both populations at high concentrations. In this example we can adjust the parameters to obtain simultaneous Hopf bifurcations about two distinct interior equilibria, one supercritical and the other subcritical. Therefore there can be both stable and unstable periodic orbits. In this way we again show that there can be two independent regimes of coexistence for the same value of the bifurcation parameter. Also, as in Example 3.9 this example depicts a case where both competitors wash out when their rival is absent but can otherwise coexist given certain initial conditions.

Example 3.11. Let

$$p_1(S) = 1 + \frac{(S-2)(8-S)}{16(0.0625S^2 + 0.125S + 1)},$$

$$p_2(S) = 1 + \frac{(S-4)(6-S)}{24(A_1S^2 + 10S + 1)},$$

$$q_1(R) = 1 + \frac{(R-4)(6-R)}{24(0.75R^2 + 7.625R + 1)},$$

$$q_2(R) = 1 + \frac{(R-2)(8-R)}{16(0.125R^2 + 0.1R + 1)},$$

$$D = 1, \qquad S^0 = 32, \qquad R^0 = 24,$$

$$y_{S1} = 1, \qquad y_{S2} = 1, \qquad y_{R1} = 2, \qquad y_{R2} = 1.$$

Here,

$$\lambda_{S1} = 2, \qquad \lambda_{S2} = 4, \qquad \lambda_{R1} = 4, \qquad \lambda_{R2} = 2,$$

$$\mu_{S1} = 8, \qquad \mu_{S2} = 6, \qquad \mu_{R1} = 6, \qquad \mu_{R2} = 8,$$

and we have the critical points shown in Table 9.

As in the previous example, the computations to show the existence of a Hopf bifurcation and the stability of bifurcating orbits were done using the REDUCE2 program in Appendix 3.1 of [38]. Computations for this example are outlined in Appendix 1.B and 1.C.

There is a simultaneous Hopf bifurcation of the critical points $E_{\mu_{S2},\lambda_{R1}}$ and $E_{\lambda_{S2},\mu_{R1}}$ as A_1 passes through $\frac{9}{8}$. For $E_{\mu_{S2},\lambda_{R1}}$, as in the previous example, the critical point loses stability as A_1 decreases through the critical value, and the bifurcating periodic orbit appears for values of $A_1 < \frac{9}{8}$ and is

TABLE 9

Results of Example 3.11

Critical points	Local stability
$E_{S^0,R^0} = (32,24,0,0)$	Asymptotically stable
$E_{\lambda_{S2},\lambda_{R1}} = (4,4,16,12)$	Unstable
$E_{\mu_{S2},\mu_{R1}} = (6,6,16,10)$	Unstable
$E_{\lambda_{S2},\mu_{R1}} = (4,6,20,8)$	Asymptotically stable if $A_1 < \frac{9}{8}$, unstable if $A_1 > \frac{9}{8}$, Hopf bifurcation at $A_1 = \frac{9}{8}$.
$E_{\mu_{S2},\lambda_{R1}} = (6,4,12,14)$	Asymptotically stable if $A_1 > \frac{9}{8}$, unstable if $A_1 < \frac{9}{8}$, Hopf bifurcation at $A_1 = \frac{9}{8}$.

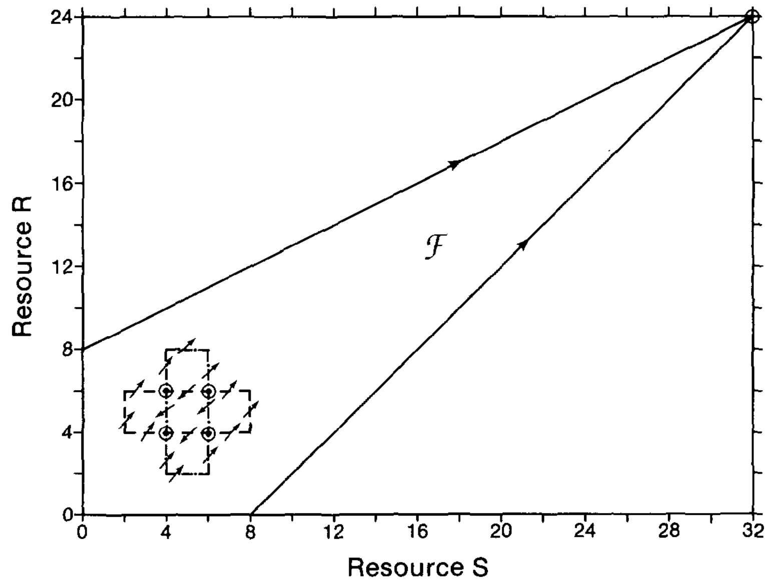

FIG. 13. $\mathcal{F}$, $\mathcal{B}_1$, and $\mathcal{B}_2$ for Example 3.11. Solid lines: $\partial\mathcal{F}$; dashed lines: $\partial\mathcal{B}_1$; dot-dash lines; $\partial\mathcal{B}_2$; arrow: direction of vector field; circles: critical points.

asymptotically stable. On the other hand $E_{\lambda_{S2},\mu_{R1}}$ goes from unstable to asymptotically stable as A_1 decreases below $\frac{9}{8}$, and the associated periodic orbit is unstable and exists for $A_1 < \frac{9}{8}$. From this we see that there is a range of parameters ($A_1 < \frac{9}{8}$) for which there is an asymptotically stable interior critical point surrounded by an unstable periodic orbit and for the same value of A_1 an orbitally asymptotically stable periodic orbit. Thus there are at least two different possibilities for coexistence, and the outcome depends on the initial condition. This was not possible in the monotone-kinetics case.

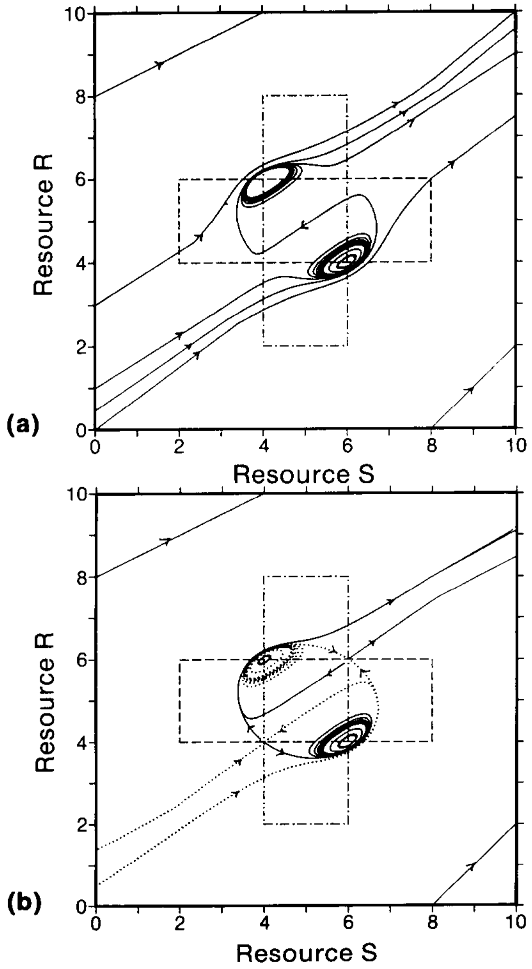

FIG. 14. Sample trajectories of Example 3.11; $A_1 = 1.1 < \frac{9}{8}$. Dashed lines: $\partial\mathscr{B}_1$; dot-dash lines: $\partial\mathscr{B}_2$.

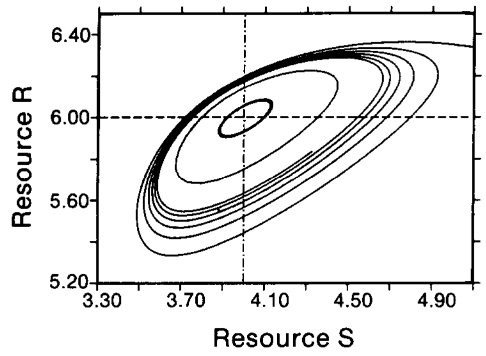

FIG. 15. The unstable periodic orbit of Example 3.11 in (S, R) space.

Recall that in that case the dynamics are always trivial and there is at most one interior critical point, which is either globally asymptotically stable or unstable.

The dynamics for this example are illustrated in Figures 13–18. The first series of graphs are in (S, R)-space. Figure 13 shows $\mathscr{F}$, $\mathscr{B}_1$ and $\mathscr{B}_2$. Figure 14 [(a) and (b)] depicts sample trajectories for $A_1 = 1.1 < \frac{9}{8}$. (As for Figure 9, the dotted line was found by integrating backward in time. However, all arrows indicate evolution of solutions for positive time.) In Figure 15 (Figure 17) we focus on the critical point $E_{\lambda_{S2},\mu_{R1}}$ $(E_{\mu_{S2},\lambda_{R1}})$ and the associated

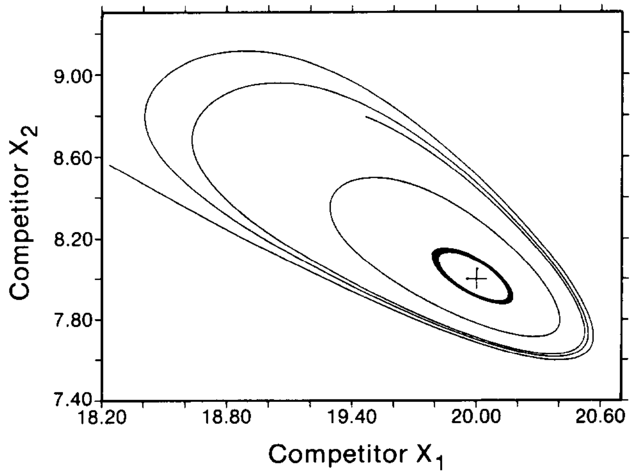

FIG. 16. The unstable periodic orbit of Example 3.11 in (x_1, x_2) space.

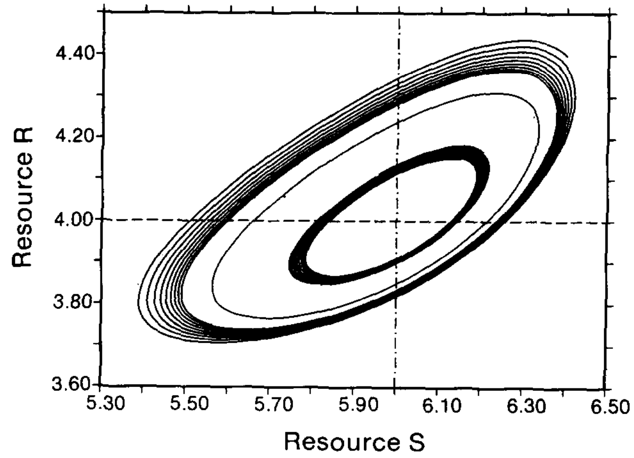

FIG. 17. The stable periodic orbit of Example 3.11 in (S, R) space.

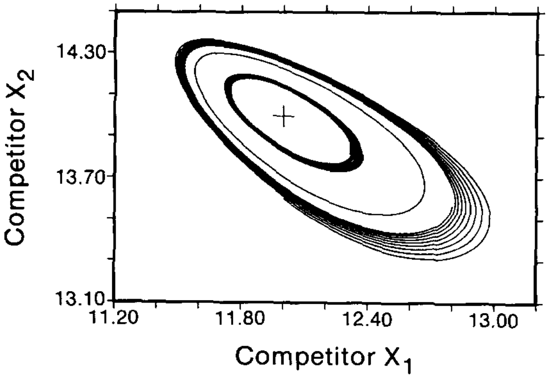

FIG. 18. The stable periodic orbit of example 3.11 in (x_1, x_2) space.

unstable (stable) periodic orbit in (S, R) space. Finally, in Figures 16 and 18 we again focus on these same critical points, but this time in (x_1, x_2) space.

4. DISCUSSION

In this paper we showed that if one models exploitative competition for two complementary resources in a chemostat with microbial responses modeled by general monotone kinetics, one obtains the same qualitative results as Hsu, Cheng, and Hubbell [16] did for microbial responses modeled by Holling Type II dynamics. However, we use a different technique which can be applied with some success in the nonmonotone case.

In the monotone case, we show that the dynamics are always trivial and that there are only five possible distinct biological outcomes. We summarize these results in Table 3 and in each case give criteria that guarantee each outcome.

In the nonmonotone case, which can arise if a resource is inhibitory at high concentrations, we give graphical criteria for the existence of critical points. We give sufficient conditions, also graphical, which ensure that the dynamics of the model are trivial. However, we show that the model permits nontrivial periodic solutions which may be either unstable or orbitally asymptotically stable (see Examples 3.10 and 3.11). This is only possible, however, if there is an interior critical point at which each resource is limiting to a different competitor population and one resource is limiting because it is in short supply whereas the other is limiting because it is overabundant. We have therefore shown that sustained oscillations are possible in a chemostat with nonreproducing nutrients and constant nutrient input rate. It has already been shown in [7, 8, 18, 23, 29] for a reproducing resource (prey) and by Hale and Somolinos [12] for a periodically fluctuating nutrient, that oscillatory behavior in a chemostat is possible.

It should be pointed out that the model with nonmonotone kinetics cannot be reduced to a competitive model in the sense of Hirsch [14], as it can be with monotone kinetics. In the nonmonotone case, under generic assumptions, up to nine distinct critical points are possible, whereas in the monotone case at most four distinct critical points are possible. This leads to a wealth of different possible biological outcomes even when the dynamics are trivial. There is actually the possibility that in the absence of its rival, a population dies out, whereas in the presence of its rival there is (depending on the initial conditions) a possibility of coexistence. Thus in some sense the competitors are cooperating (see Example 3.9). There is also another situation in which the competitors clearly do not compete. This is in the case that the resources are both overabundant and hence inhibitory to both competitors. The fact that the other population is consuming resource can only be of help.

An advantage of explicitly modeling the resources is that the model is predictive and the predictions are based on parameters that can be measured independently of competition, with each competitor limited by only one resource at a time. A disadvantage is that to simplify the mathematics certain assumptions were made that need not hold. For example, it was assumed that the individual death rates of each competitor population are insignificant compare to the washout rate. It might be appropriate in many cases to consider differential death rates. Also, most nutrients are probably imperfectly substitutable rather than perfectly complementary. It might also be the case that the per capita growth rate is not proportional to the consumption rate, as in the models of Tilman [31–34] or that the mechanism for inhibition of complementary resources does not lead to a model in which $f_i(S(t)), R(t) = \min(p_i(S(t)), q_i(R(t)))$.

In the context of simple enzyme-catalyzed reactions, a reaction can be considered to have two time-consuming parts. The first is the binding of the substrate with the enzyme, and the second is the actual reaction formation of the product. There is evidence, according to Dixon and Webb [10] and Palmer [25], that inhibition by high substrate concentrations (in the context of enzyme-catalyzed reactions) in some cases may be due to the specificity of certain enzymes. Many enzymes have two or more groups, and in an effective enzyme-substrate molecule complex a single substrate molecule must be combined with all these groups. However, it might be the case that a substrate molecule combines with only one of these groups if the other groups are combined with other substrate molecules, thus forming an ineffective complex. In this case a reaction cannot take place until some of the substrate molecules dissociate away. When the substrate concentration is high, the chance of forming ineffective complexes increases. Thus the inhibition can come into the enzyme-substrate complex formation only.

The analogous concepts for microbial growth might be the search time and processing time for nutrient, and the analogous mechanism for inhibition might be that at high resource concentrations the resource forms clumps too large for the microorganisms to handle. The microorganisms might have to wait until a clump dissociates in order to absorb it. If these mechanisms which affect only substrate-enzyme complex formation, or analogously search time, are responsible for the inhibition, then there is reason to assume that $f_i(S(t), R(t)) = \min(p_i(S(t)), q_i(R(t)))$. However, if the reaction time, or analogously the processing time, is slowed by high concentration of substrate, a different model might have to be considered. There is also experimental evidence to indicate that some microorganisms employ such strategies as luxury consumption and that there is probably a time delay between absorption of nutrient and conversion to biomass. Neither of these possibilities is taken into account in our model.

Finally we would like to point out that just as in the single-resource case studied in [9], in the two-resource case the qualitative outcomes depend on the relative values of the breakeven concentrations and on the concentration of nutrient in the feed bottle. In the single-resource case, the qualitative outcome is independent of the growth yield factors. However, in the two-resource case the growth yield factors play a significant role in determining the qualitative outcome, since their ratios C_1 and C_2 play an important part in determining both the position of the feasible set and the local stability of critical points.

APPENDIX 1. BIFURCATION AND STABILITY ANALYSIS

Since $\mathscr{M}$ is a global attractor for (3.1), it suffices to consider (3.1) restricted to $\mathscr{M}$. That is, we solve for x_1 and x_2 in terms of S and R and consider the resulting system of two differential equations in two unknowns R and S:

$$\begin{aligned} S'(t) &= \left(S^0 - S(t)\right)D - \sum_{i=1}^{2} \frac{x_i(t) f_i(S(t), R(t))}{y_{Si}}, \\ R'(t) &= \left(R^0 - R(t)\right)D - \sum_{i=1}^{2} \frac{x_i(t) f_i(S(t), R(t))}{y_{Ri}}, \end{aligned} \tag{A.1}$$

where

$$\begin{aligned} x_1(t) &= \frac{1}{\Delta}\left(\frac{R^0 - R(t)}{y_{S2}} - \frac{S^0 - S(t)}{y_{R2}}\right), \\ x_2(t) &= \frac{1}{\Delta}\left(\frac{S^0 - S(t)}{y_{R1}} - \frac{R^0 - R(t)}{y_{S1}}\right), \end{aligned}$$

and

$$\Delta = \frac{1}{y_{S2} y_{R1}} - \frac{1}{y_{S1} y_{R2}}.$$

It is then convenient to translate the critical point $(\bar{S}, \bar{R})$ of (A.1) to the origin by setting

$$\begin{aligned} \xi_1 &= S(t) - \bar{S} \\ \xi_2 &= R(t) - \bar{R}. \end{aligned} \tag{A.2}$$

A. BIFURCATION ANALYSIS FOR THE CRITICAL POINT $E_{\mu_{S2},\lambda_{R1}} = (6,4,16,18)$ *OF EXAMPLE* 3.10

After the change of variables (A.2) the system [near (0,0)] is

$$\begin{aligned} \xi_1' &= (34 - \xi_1) - \tilde{x}_1 \tilde{f}_1(\xi_1, \xi_2) - \tilde{x}_2 \tilde{f}_2(\xi_1, \xi_2), \\ \xi_2' &= (26 - \xi_2) - \tfrac{1}{2}\tilde{x}_1 \tilde{f}_1(\xi_1, \xi_2) - \tilde{x}_2 \tilde{f}_2(\xi_1, \xi_2), \end{aligned}$$

where

$$\tilde{x}_1 = \frac{(26 - \xi_2) - (34 - \xi_1)}{-\frac{1}{2},},$$

$$\tilde{x}_2 = \frac{\dfrac{(34 - \xi_1)}{2} - (26 - \xi_2)}{\left(-\frac{1}{2}\right)},$$

and

$$\tilde{f}_1(\xi_1,\xi_2)=10\frac{\xi_2+4}{4+9(\xi_2+4)},$$

$$\tilde{f}_2(\xi_1,\xi_2)=1+\frac{(\xi_1+2)(-\xi_1)}{24A_1(\xi_1+6)^2+14(\xi_1+6)+24}.$$

The variational matrix at the critical point (0,0) is

$$M=\begin{bmatrix} \dfrac{1}{24A_1+3} & -\dfrac{2}{5} \\ \dfrac{1}{24A_1+3} & -\dfrac{1}{5} \end{bmatrix}.$$

The characteristic equation is

$$(120A_1+15)\gamma^2+\gamma(24A_1-2)+1=0,$$

and so

$$\operatorname{Re}\gamma=\frac{-12A_1+1}{120A_1+15}.$$

Therefore, at the critical value $A_1=A_1^*\triangleq\frac{1}{12}$ there is a pair of pure imaginary roots: $\pm i/5$. Since

$$\left.\frac{d\operatorname{Re}\gamma}{dA_1}\right|_{\gamma=A_1^*}=-\frac{12}{25}<0,$$

$E_{\mu_{S2},\lambda_{R1}}$ is asymptotically stable for $A_1>A_1^*$ and is unstable for $A_1<A_1^*$.

To transform the variational matrix to canonical form

$$C=\begin{bmatrix} 0 & \frac{1}{5} \\ -\frac{1}{5} & 0 \end{bmatrix}$$

(for $A_1=A_1^*$) the matrix of the transformation is

$$V=\begin{bmatrix} 1 & 1 \\ 1 & 0 \end{bmatrix} \quad\text{and}\quad V^{-1}=\begin{bmatrix} 0 & 1 \\ 1 & -1 \end{bmatrix}.$$

Then $C=V^{-1}MV$.

Applying the change of variables

$$\begin{pmatrix} \eta_1 \\ \eta_2 \end{pmatrix}=V^{-1}\begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix},$$

the transformed system becomes

$$\begin{aligned}\eta_1' &= \tfrac{1}{7200}\big(88\eta_1^3 + 290\eta_1^2\eta_2 + 660\eta_1^2 + 242\eta_1\eta_2^2 \\ &\qquad + 1640\eta_1\eta_2 + 40\eta_2^3 + 800\eta_2^2 + 1440\eta_2\big) + \text{H.O.T.'s} \\ \eta_2' &= \tfrac{1}{3600}\big(-8\eta_1^3 + 3\eta_1^2\eta_2 - 152\eta_1^2 + 11\eta_1\eta_2^2 - 62\eta_1\eta_2 - 720\eta_1\big) + \text{H.O.T.'s}\end{aligned}$$

where H.O.T.'s is an abbreviation for "higher-order terms." Then the vague attractor condition given by the formula (4.2) on p. 126 of [22] becomes

$$V'''(0) = -\frac{21049}{14400}\pi < 0.$$

This implies that the bifurcating periodic orbits appear for values of $A_1 < A_1^*$ and are orbitally asymptotically stable.

B. *BIFURCATION ANALYSIS OF THE CRITICAL POINT* $E_{\mu_{S2},\lambda_{R1}} = (6,4,12,14)$ *OF EXAMPLE* 3.11

After applying the change of coordinates (A.2) to (A.1) near the origin, the system becomes

$$\begin{aligned}\xi_1' &= (26-\xi_1) - \tilde{x}_1\tilde{f}_1(\xi_1,\xi_2) - \tilde{x}_2\tilde{f}_1(\xi_1,\xi_2), \\ \xi_2' &= (20-\xi_2) - \tfrac{1}{2}\tilde{x}_1\tilde{f}_1(\xi_1,\xi_2) - \tilde{x}_2\tilde{f}_1(\xi_1,\xi_2),\end{aligned}$$

where

$$\tilde{x}_1 = \frac{(20-\xi_2)-(26-\xi_1)}{\left(-\frac{1}{2}\right)},$$

$$\tilde{x}_2 = \frac{\dfrac{(26-\xi_1)}{2} - (20-\xi_2)}{-\frac{1}{2}},$$

and

$$\tilde{f}_1(\xi_1,\xi_2) = 1 + \frac{\xi_2(2-\xi_2)}{18(\xi_2+4)^2 + 183(\xi_2+4) + 24},$$

$$\tilde{f}_2(\xi_1,\xi_2) = 1 + \frac{(\xi_1+2)(-\xi_1)}{24\left[A_1(\xi_1+6)^2 + 10(\xi_1+6) + 1\right]}.$$

The variational matrix at the critical point (0,0) is

$$M = \begin{bmatrix} \dfrac{7}{216A_1+366} & -\dfrac{2}{87} \\ \dfrac{7}{216A_1+366} & -\dfrac{1}{87} \end{bmatrix}.$$

The characteristic equation is

$$\gamma^2 + \gamma\frac{24A_1 - 27}{2088A_1 + 3538} + \frac{7}{18792A_1 + 31842} = 0,$$

and so

$$\operatorname{Re}\gamma = \frac{-24A_1 + 27}{4176A_1 + 7076}\cdot$$

Therefore, at the critical value $A_1 = A_1^* = \frac{9}{8}$ there is a pair of pure imaginary roots: $\pm i/87$. Since

$$\left.\frac{d\operatorname{Re}\gamma}{dA_1}\right|_{A_1 = A_1^*} = \frac{-12}{5887} < 0,$$

$E_{\mu_{S2},\lambda_{R1}}$ is asymptotically stable for $A_1 > A_1^*$ and is unstable for $A_1 < A_1^*$.

To transform the variational matrix to canonical form

$$C = \begin{bmatrix} 0 & \frac{1}{87} \\ -\frac{1}{87} & 0 \end{bmatrix}$$

the matrix of the transformation is

$$V = \begin{bmatrix} 1 & 1 \\ 1 & 0 \end{bmatrix} \quad \text{and} \quad V^{-1} = \begin{bmatrix} 0 & 1 \\ 1 & -1 \end{bmatrix}.$$

Then $C = V^{-1}MV$.

Applying the change of variables.

$$\begin{pmatrix} \eta_1 \\ \eta_2 \end{pmatrix} = V^{-1}\begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix},$$

the transformed system becomes

$$\begin{aligned} \eta_1' &= \tfrac{1}{847728}\big(2148\eta_1^3 + 3348\eta_1^2\eta_2 + 9844\eta_1^2 + 2360\eta_1\eta_2^2 \\ &\qquad + 12164\eta_1\eta_2 + 348\eta_2^3 + 5568\eta_2^2 + 9744\eta_2\big) + \text{H.O.T.'s} \\ \eta_2' &= \tfrac{1}{847728}\big(1020\eta_1^2 + 476\eta_1^2\eta_2 + 2616\eta_1^2 + 268\eta_1\eta_2^2 - 632\eta_1\eta_2 - 9744\eta_1\big) \\ &\quad + \text{H.O.T.'s} \end{aligned}$$

Then $V'''(0) = -\frac{2949797}{3956064}\pi < 0$. Therefore, the bifurcating periodic orbits appear for values of $A_1 < A_1^*$ and are orbitally asymptotically stable.

C. *BIFURCATION ANALYSIS FOR THE CRITICAL POINT* $E_{\lambda_{S2},\mu_{R1}} = (4,6,20,8)$ *FOR EXAMPLE* 3.11

After applying the change of variables (A.2) to (A.1) near the origin, the system becomes

$$\xi_1' = (28-\xi_1) - \tilde{x}_1 \tilde{f}_1(\xi_1,\xi_2) - \tilde{x}_2 \tilde{f}_2(\xi_1,\xi_2),$$
$$\xi_2' = (18-\xi_2) - \tfrac{1}{2}\tilde{x}_2 \tilde{f}_1(\xi_1,\xi_2) - \tilde{x}_2 \tilde{f}_2(\xi_1,\xi_2),$$

where

$$\tilde{x}_1 = \frac{(18-\xi_2)-(28-\xi_1)}{-\frac{1}{2}},$$
$$\tilde{x}_2 = \frac{(28-\xi_1)-(18-\xi_2)}{-\frac{1}{2}},$$

and

$$\tilde{f}_1(\xi_1,\xi_2) = 1 + \frac{(\xi_2+2)(-\xi_2)}{18A_1(\xi_2+4)^2 + 183(\xi_2+4) + 24},$$
$$\tilde{f}_2(\xi_1,\xi_2) = 1 + \frac{\xi_1(2-\xi_1)}{24\left(A_1(\xi_1+4)^2 + 10(\xi_1+4) + 1\right)}.$$

The variational matrix at the critical point (0,0) is

$$M = \begin{bmatrix} -\dfrac{2}{48A_1+123} & \dfrac{4}{177} \\ -\dfrac{2}{48A_1+123} & \dfrac{2}{177} \end{bmatrix}.$$

The characteristic equation is

$$\gamma^2 + \gamma\frac{-32A_1+36}{2832A_1+7257} + \frac{4}{8496A_1+21771} = 0,$$

and so

$$\operatorname{Re}\gamma = \frac{16A_1-18}{2832A_1+7257}.$$

Therefore, at the critical value $A_1 = A_1^* = \frac{9}{8}$ there is a pair of pure imaginary roots: $\pm 2i/177$. Since

$$\left.\frac{d\operatorname{Re}\gamma}{dA_1}\right|_{A_1=A_1^*} = \frac{16}{10443} > 0,$$

the critical point $E_{\mu_{S2},\lambda_{R1}}$ is unstable for $A_1 > A_1^*$ and is asymptotically stable for $A_1 < A_1^*$.

To transform the variational matrix to canonical form

$$C = \begin{bmatrix} 0 & \frac{2}{177} \\ -\frac{2}{177} & 0 \end{bmatrix}$$

the matrix of the transformation is

$$V = \begin{bmatrix} 1 & -1 \\ 1 & 0 \end{bmatrix} \quad \text{and} \quad V^{-1} = \begin{bmatrix} 0 & 1 \\ -1 & 1 \end{bmatrix}.$$

Then $C = V^{-1}MV$.

Applying the change of variables

$$\begin{pmatrix} \eta_1 \\ \eta_2 \end{pmatrix} = V^{-1} \begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix},$$

the transformed system becomes

$$\begin{aligned} \eta_1' = \tfrac{1}{835440}\big(&2344\eta_1^3 - 2546\eta_1^2\eta_2 + 11532\eta_1^2 \\ &+ 1264\eta_1\eta_2^2 - 9408\eta_1\eta_2 - 590\eta_2^3 + 3540\eta_2^2 + 9440\eta_2\big) + \text{H.O.T.'s}, \\ \eta_2' = \tfrac{1}{835440}\big(&-1700\eta_1^3 + 1104\eta_1^2\eta_2 - 7760\eta_1^2 \\ &+ 124\eta_1\eta_2^2 + 2096\eta_1\eta_2 - 9440\eta_1\big) + \text{H.O.T.'s}. \end{aligned}$$

Then $V'''(0) = \frac{827151}{1392400}\pi > 0$. Therefore the bifurcating periodic orbits appear for $A_1 < A_1^*$ and are unstable.

APPENDIX 2. BASIC FEASIBLE SOLUTIONS OF $\mathscr{M}$

We consider the following system of two linear equations in four unknowns (S, R, x_1 and x_2):

$$\begin{aligned} S + \frac{x_1}{y_{S1}} + \frac{x_2}{y_{S2}} &= S^0, \\ R + \frac{x_1}{y_{R1}} + \frac{x_2}{y_{R2}} &= R^0, \\ S, R, x_i \geqslant 0, &\qquad i = 1,2. \end{aligned}$$

Since the rank of this system is 2, there are $C_2^4 = 6$ possible basic feasible solutions of $\mathscr{M}$ and hence of $\mathscr{F}$. We generate these solutions by the method of pivoting used in linear programming (see Luenberger [21, Chapter 3]). (Recall that we are assuming $C_1 \neq C_2$.)

We start with S and R in the basis:

$$(\mathrm{I})\quad \begin{array}{c|cccc|c} & S & R & x_1 & x_2 & \\ \hline S & 1 & 0 & 1/y_{S1} & 1/y_{S2} & S^0 \\ R & 0 & 1 & 1/y_{R1} & 1/y_{R2} & R^0 \end{array}$$

Corresponding basic feasible solution: $(S^0, R^0, 0, 0)$.

If $R^0/S^0 \geqslant C_1$, then we replace S in the basis of tableau (I) by x_1 [i.e. pivot on the S-x_1 element, $1/y_{S1}$, of tableau (I)]:

$$(\mathrm{II})\quad \begin{array}{c|cccc|c} & S & R & x_1 & x_2 & \\ \hline x_1 & y_{S1} & 0 & 1 & y_{S1}/y_{S2} & y_{S1}S^0 \\ R & -y_{S1}/y_{R1} & 1 & 0 & * & R^0 - C_1S^0 \end{array}$$

Corresponding basic feasible solution $(0, R^0 - C_1S^0, y_{S1}S^0, 0)$.

$$* = \frac{y_{R1}y_{S2} - y_{S1}y_{R2}}{y_{R1}y_{R2}y_{S2}}.$$

If $R^0/S^0 \leqslant C_1$, then pivot on the $R - x_1$ element of tableau (I).

$$(\mathrm{III})\quad \begin{array}{c|cccc|c} & S & R & x_1 & x_2 & \\ \hline S & 1 & -y_{R1}/y_{S1} & 0 & * & S^0 - R^0/C_1 \\ x_1 & 0 & y_{R1} & 1 & y_{R1}/y_{R2} & y_{R1}R^0 \end{array}$$

Corresponding basic feasible solution: $(S^0 - R^0/C_1, 0, y_{R1}R^0, 0)$

$$* = \frac{y_{S1}y_{R2} - y_{R1}y_{S2}}{y_{S1}y_{S2}y_{R2}}.$$

If $R^0/S^0 \geqslant C_2$, then pivot on the $S - x_2$ element of tableau (I):

$$(\mathrm{IV})\quad \begin{array}{c|cccc|c} & S & R & x_1 & x_2 & \\ \hline x_2 & y_{S2} & 0 & y_{S2}/y_{S1} & 1 & y_{S2}S^0 \\ R & -y_{S2}/y_{R2} & 1 & * & 0 & R^0 - C_2S^0 \end{array}$$

Corresponding basic feasible solution: $(0, R^0 - C_2S^0, 0, y_{S2}S^0)$

$$* = \frac{y_{S1}y_{R2} - y_{S2}y_{R1}}{y_{S1}y_{R1}y_{R2}}.$$

If $R^0/S^0 \leqslant C_2$, then pivot on the $R - x_2$ element of tableau (I).

$$(\mathrm{V})\quad \begin{array}{c|cccc|c} & S & R & x_1 & x_2 & \\ \hline S & 1 & -y_{R2}/y_{S2} & * & 0 & S^0 - R^0/C_2 \\ x_2 & 0 & y_{R2} & y_{R2}/y_{R1} & 1 & y_{R2}R^0 \end{array}$$

Corresponding basic feasible solution: $(S^0 - R^0/C_2, 0, y_{R2}R^0, 0)$

$$* = \frac{y_{S2}y_{R1} - y_{S1}y_{R2}}{y_{S1}y_{S2}y_{R1}}.$$

If $C_1 \leqslant R^0/S^0 \leqslant C_2$ or $C_1 \geqslant R^0/S^0 \geqslant C_2$, then pivot on the $R - x_2$ element of tableau (II) to obtain the basic feasible solution

$$\left(0, 0, y_{S1} y_{R1} \frac{y_{S2} S^0 - y_{R2} R^0}{y_{S2} y_{R1} - y_{S1} y_{R2}}, y_{S2} y_{R2} \frac{y_{R1} R^0 - y_{S1} S^0}{y_{S2} y_{R1} - y_{S1} y_{R2}}\right).$$

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