Exploitative Competition in the Chemostat for Two Perfectly Substitutable Resources

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ABSTRACT

After formulating a general model involving two populations of microorganisms competing for two nonreproducing, growth-limiting resources in a chemostat, we focus on perfectly substitutable resources. León and Tumpson considered a model of perfectly substitutable resources in which the amount of each resource consumed is assumed to be independent of the concentration of the other resource. We extend their analysis and then consider a new model involving a class of response functions that takes into consideration the effects that the concentration of each resource has on the amount of the other resource consumed. This new model includes, as a special case, the model studied by Waltman, Hubbell, and Hsu in which Michaelis-Menten functional response for a single resource is generalized to two perfectly substitutable resources. Analytical methods are used to obtain information about the qualitative behavior of the models. The range of possible dynamics of model I of León and Tumpson and our new model is then compared. One surprising difference is that our model predicts that for certain parameter ranges it is possible that one of the species is unable to survive in the absence of a competitor even though there is a locally asymptotically stable coexistence equilibrium when a competitor is present. The dynamics of these models for perfectly substitutable resources are also compared with the dynamics of the classical growth and two-species competition models as well as models involving two perfectly complementary resources.

1. INTRODUCTION

The classical theory of ecological competition is attributed to Lotka [18] and Volterra [30] and is an extension of the basic logistic model for

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©Elsevier Science Publishing Co., Inc., 1993 655 Avenue of the Americas, New York, NY 10010 single-species growth due to Verhulst [29]. The appeal of this theory lies in its generality and simplicity. It seeks to describe how the numbers of competitors change without indicating the resources upon which competition is based or how these resources are used by the consumer. As it is difficult to estimate the parameters of the classical model governing the extent of interaction without actually growing the species together in competition, these models are often more phenomenological than predictive.

In response to these deficiencies, a more mechanistic, resource-based theory has developed (see, e.g., [12], [17], [21], and [22]). The resources are incorporated into the models to capture consumer-resource interactions as well as competitive interactions. The resulting mathematical models may be less general and more difficult to analyze (see, e.g., [1]–[6], [13]–[15], and [31], [32]). However, these models are often predictive because the parameters can be measured on species grown alone, in advance of competition (see, e.g., Hansen and Hubbell [10]). The models we consider here involve this resource-based approach.

We examine a model of competition for multiple resources under chemostat-like conditions. There are many articles devoted to such studies; as a very incomplete sample of these, we mention [1]–[3], [5], [8], [11], [14], [15], [17], [19], [23], and [25]–[28]. Here we restrict our attention to exploitative competition for two nonreproducing resources. With two resources available, it is important to consider how, once consumed, they are used by the individual competitors. This leads to the classification of resources as perfectly complementary, perfectly substitutable, and imperfectly substitutable (see León and Tumpson [17] and Rapport [24]).

This paper is organized as follows. First we describe a resource-based model of exploitative, two-species competition in the chemostat for two growth-limiting, nonreproducing resources. We have found that many of the characteristics of such a model can be described without restricting one's attention to specific resource types. We then describe the classification of resources provided by León and Tumpson [17] and Rapport [24] and specify the model in the extreme cases.

For the remainder, we consider the perfectly substitutable case. First, as in León and Tumpson [17], we focus on functional responses that are strictly monotone increasing functions of resource concentrations. Implicit in their model is the further assumption that one of the amount of cach resource consumed is independent of the concentration of the other resources. Under the assumption that an interior equilibrium exists, León and Tumpson [17] derive necessary and sufficient conditions for its local asymptotic stability and hence conditions for coexistence of the competitors. In this setting, restricting our attention to nonreproducing resources (in [17] both reproducing and nonreproducing resources are considered), we extend their work by giving a complete global analysis of the three-dimensional subsystems describing the growth of one species on the two resources. We then provide conditions that are necessary and sufficient to guarantee uniform persistence in the full four-dimensional competition model (i.e., coexistence of both species independent of their initial concentrations). Thus, these conditions are sufficient to guarantee the existence of a coexistence equilibrium. We then extend their model to a more general and more realistic setting, incorporating the possible inhibitory effects that the concentration of one resource may have on the consumption of the other, since the time spent handling one resource may reduce the amount of time available for handling the other resource. The model studied by Waltman et al. [31] is a special case. They specifically generalize the Monod model involving Michaelis-Menten functional response for a single resource to two perfectly substitutable resources. In the general setting, under the assumption that the intrinsic death rate is insignificant compared to the dilution rate, we give a complete global analysis of the three-dimensional subsystems describing the growth of one species on the two resources. Assuming differential death rates, in the full fourdimensional competition model we provide a characterization of those nutrient concentrations that yield coexistence equilibria. We use this characterization to obtain sufficient conditions for the existence of such equilibria and then consider local asymptotic stability. We provide an interesting example in which one species cannot survive in the absence of a competitor but for which there is a locally asymptotically stable coexistence equilibrium in the presence of a competitor. Finally, we provide conditions under which the competition model and the related three-dimensional one-species growth models are uniformly persistent.

We conclude the paper with a discussion in which we summarize our results and then examine the similarities and differences in the range of possible dynamics of our model and the classical model, the perfectly substitutable model studied in [17], and the perfectly complementary model studied in [17] and [5], restricting our attention to noninhibitory resources.

2. TWO-RESOURCE COMPETITION: A GENERAL FRAMEWORK

We discuss exploitative competition in the chemostat for two nonreproducing resources. In the two-competitor case, the dynamical system may be written

$$S'(t) = [S^{\circ} - S(t)] \frac{D}{V} - \sum_{i=1}^{2} x_i(t) \mathcal{U}_{Si}(S(t), R(t)), \quad (2.1a)$$

$$R'(t) = \left[R^o - R(t)\right] \frac{D}{V} - \sum_{i=1}^{2} x_i(t) \mathscr{U}_{Ri}(S(t), R(t)), \quad (2.1b)$$

$$x'_{i}(t) = x_{i}(t) \left(-\frac{D_{i}}{V} + \mathscr{G}_{i}(S(t), R(t)) \right), \quad i = 1, 2, \quad (2.1c)$$

$$S(0) \ge 0, \qquad R(0) \ge 0, \qquad x_i(0) \ge 0, \qquad i = 1, 2.$$

Assuming, for convenience, that the volume V of suspension in the culture vessel is one cubic unit, the quantities in (2.1) are described as follows. In these equations, $x_i(t)$ is the biomass of the *i*th population of microorganisms in the culture vessel at time t, i = 1, 2, while S(t) and R(t) represent the concentrations of the two nonreproducing resources in the culture vessel at time t. If only one feed bottle is used, S^o and R^o are the concentrations of resource S and resource R, respectively, in the feed bottle. The constant D is the input rate from the feed bottle to the culture vessel as well as the washout rate from the culture vessel to the receptacle. Thus constant volume is maintained. We assume that there is perfect mixing in the culture vessel so that nutrients, microorganisms, and by-products are removed in proportion to their concentrations. The constant D_i denotes the rate at which population x_i is eliminated from competition, either by death or by removal to the receptacle. Therefore, $D_i = D + \varepsilon_i$, $\varepsilon_i \ge 0$, where ε_i is the intrinsic death rate of population x_i , assumed to be a constant.

The functions $\mathscr{U}_{Si}(S(t), R(t))$ and $\mathscr{U}_{Ri}(S(t), R(t))$ represent the rate of consumption of resources S and R, respectively, per unit of biomass of population x_i as a function of the concentrations of S(t) and R(t) in the culture vessel. It is generally assumed that

$$\mathscr{U}_{Si}, \mathscr{U}_{Ri}: \mathbf{R}^2_+ \to \mathbf{R}_+ \tag{2.2}$$

and that

$$\mathscr{U}_{Si}, \mathscr{U}_{Ri}$$
 are continuously differentiable almost everywhere. (2.3)

It is natural to expect that if the concentration of resource S in the culture vessel is zero, there will be no consumption of resource S. A

similar statement holds for resource R. Therefore,

$$\begin{aligned} \mathscr{U}_{Si}(0,R) &= 0 & \text{ for all } R \ge 0, \\ \mathscr{U}_{Ri}(S,0) &= 0 & \text{ for all } S \ge 0. \end{aligned}$$
(2.4)

In focusing on the consumer-resource interactions, we wish to describe each population's functional response, that is, how the consumption rate of each population changes in response to fluctuations in resource concentrations. We assume that the rate of consumption of each resource is a monotone increasing function of the concentration of that resource. Let \mathring{R}^2_+ denote the interior of R^2_+ . Thus,

$$\frac{\partial}{\partial S} \mathscr{U}_{Si}(S,R) \ge 0 \qquad \text{for almost all } (S,R) \in \mathring{\mathbf{R}}_{+}^{2},$$

$$\frac{\partial}{\partial R} \mathscr{U}_{Ri}(S,R) \ge 0 \qquad \text{for almost all } (S,R) \in \mathring{\mathbf{R}}_{+}^{2}.$$
(2.5)

Why we require (2.5) to hold for almost all $(S, R) \in \mathring{\mathbf{R}}_+^2$ rather than for all $(S, R) \in \mathring{\mathbf{R}}_+^2$ will be explained later when we specify the model in the complementary resource case.

The function $\mathscr{G}_i(S(t), R(t))$ represents the rate of conversion of nutrient to biomass of population x_i as a function of the concentrations of resources S and R in the culture vessel. We discuss the properties of $\mathscr{G}_i(S(t), R(t))$ later when we discuss the perfectly complementary case and the perfectly substitutable case.

Let $\mathcal{G}_i(S, R)$ denote the rate of conversion of nutrient S to biomass of population x_i . Assuming that the conversion of nutrient to biomass is proportional to the amount of nutrient consumed, the consumption rate of resource S per unit of competitor x_i is of the form

$$\mathscr{U}_{Si}(S,R) = \frac{\mathscr{S}_i(S,R)}{\xi_i}, \qquad (2.6)$$

where ξ_i is the corresponding growth yield constant. Similarly, the rate of consumption of resource R per unit of competitor x_i is of the form

$$\mathscr{U}_{Ri}(S,R) = \frac{\mathscr{R}_i(S,R)}{\eta_i}, \qquad (2.7)$$

where $\mathscr{R}_i(S, R)$ is the rate of conversion of nutrient R to biomass of population x_i and η_i is the corresponding growth yield constant.

An important consideration that arises in the two-resource case is how the resources, once consumed, are used by the individual competitors for growth. Rapport [24] and León and Tumpson [17] classify resources in terms of consumer needs. This classification yields a spectrum of resource types and hence a continuum of competitive situations. At opposite extremes are the perfectly complementary and perfectly substitutable resources.

Between these extremes, we have the imperfectly substitutable resources. Although more realistic, this situation is more difficult to study as the nature of the corresponding conversion functions $\mathscr{S}_i(S, R)$, $\mathscr{R}_i(S, R)$, and $\mathscr{G}_i(S, R)$ is less clear. Hence, competitive situations involving the extreme resource types are examined initially. By understanding the similarities and differences we may be able to increase our understanding of the dynamics in the intermediate cases.

Perfectly complementary resources are substances that fulfill different essential needs in terms of growth and so must be taken together by the consumer. These resources must be used in fixed proportions to maintain a given rate of growth. If a higher growth rate is to be attained, it is necessary to increase the consumption rate of both resources. For example, a nitrogen source and a carbon source might be perfectly complementary for a bacterium. Following Butler and Wolkowicz [5], but restricting our attention to noninhibitory resources, we now describe the functions $\mathcal{S}_i(S, R)$, $\mathcal{R}_i(S, R)$, and $\mathcal{S}_i(S, R)$ in the perfectly complementary case.

Let $h_i(S)$ denote the rate of conversion of resource S to biomass of population x_i when resource S alone is limiting. Similarly, let $k_i(R)$ denote the rate of conversion of resource R to biomass of population x_i when resource R alone is limiting. It is assumed that

$$h_i, k_i: \mathbf{R}_+ \to \mathbf{R}_+, \tag{2.8}$$

$$h_i, k_i$$
 are continuously differentiable, (2.9)

and that

$$h'_i(S) > 0$$
 for all $S > 0$ and $k'_i(R) > 0$ for all $R > 0$.
(2.10)

For given concentrations of resources S and R, say $(\overline{S}, \overline{R})$, only one resource is, in fact, limiting—the one that is in relatively short supply—unless $h_i(\overline{S}) = k_i(\overline{R})$. The other resource, in comparison, can be thought of as being in abundant supply because increasing its concentration would not affect the growth rate. Thus, if resource S is limiting at $(\overline{S}, \overline{R})$, then the conversion rate is given by $\mathcal{G}_i(\overline{S}, \overline{R}) = h_i(\overline{S})$. The consumption rate of the limiting resource S is given by $\mathcal{U}_{Si}(\overline{S}, \overline{R}) =$ $h_i(\overline{S})/\xi_i$, and the rate of consumption of the nonlimiting resource Ris $\mathscr{U}_{Ri}(\overline{S},\overline{R}) = h_i(\overline{S})/\eta_i$. Note that $\mathscr{U}_{Ri}(\overline{S},\overline{R}) = (\xi_i/\eta_i)\mathscr{U}_{Si}(\overline{S},\overline{R})$. That is, the rate of consumption of the nonlimiting resource is proportional to the rate of consumption of the limiting resource, the constant of proportionality being the ratio of the growth yield constants ξ_i and η_i .

Thus, if the resources are perfectly complementary, the rate of conversion of nutrient to biomass of population x_i is given by $\mathscr{G}_i(S, R) = \min\{h_i(S), k_i(R)\}$, the rate of consumption of S is $\mathscr{U}_{Si}(S, R) = \mathscr{G}_i(S, R)/\xi_i$, and the rate of consumption of R is $\mathscr{U}_{Ri}(S, R) = \mathscr{G}_i(S, R)/\eta_i$. In this case, system (2.1) becomes

$$S'(t) = [S^o - S(t)] \frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i} \min\{h_i(S), k_i(R)\}, \quad (2.11a)$$

$$R'(t) = \left[R^o - R(t)\right] \frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} \min\{h_i(S), k_i(R)\}, \quad (2.11b)$$

$$x'_{i}(t) = x_{i}(t) \left(-\frac{D_{i}}{V} + \min\{h_{i}(S), k_{i}(R)\} \right), \quad i = 1, 2, \quad (2.11c)$$

$$S(0) \ge 0,$$
 $R(0) \ge 0,$ $x_i(0) \ge 0,$ $i = 1, 2.$

Note that at points where $h_i(S) = k_i(R)$, it is unlikely that $\mathscr{U}_{Si}(S, R)$, $\mathscr{U}_{Ri}(S, R)$, and $\mathscr{G}_i(S, R)$ are differentiable. It is for this reason that we require (2.5) to hold only for almost all $(S, R) \in \mathring{\mathbf{R}}^2_+$.

This is precisely model III of León and Tumpson [17] adapted to the chemostat. If $D_i = D$, i = 1, 2, that is, the death rate of each population is assumed to be negligible compared to the dilution rate, then (2.11) is precisely the model studied by Butler and Wolkowicz [5] in the noninhibitory kinetics case. If we further assume that the h_i 's and k_i 's satisfy Michaelis-Menten dynamics, this is the model studied by Hsu et al. [15].

Perfectly substitutable resources are alternative sources of the same essential nutrient. In this case, the rates of consumption of the different resources can be substituted in a fixed ratio to maintain a given growth rate. An example for a bacterium would be two carbon sources or two nitrogen sources.

For the remainder of our discussion we assume that resources S and R of system (2.1) are perfectly substitutable for both populations x_1 and x_2 .

3. THE MODEL IN THE SUBSTITUTABLE CASE

The model that we consider is

$$S'(t) = [S^{o} - S(t)] \frac{D}{V} - \sum_{i=1}^{2} \frac{x_{i}(t)}{\xi_{i}} \mathscr{S}_{i}(S(t), R(t)), \quad (3.1a)$$

$$R'(t) = [R^o - R(t)] \frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} \mathscr{R}_i(S(t), R(t)), \quad (3.1b)$$

$$x'_{i}(t) = x_{i}(t) \left(-\frac{D_{i}}{V} + \mathscr{G}_{i}(S(t), R(t)) \right), \quad i = 1, 2, \quad (3.1c)$$

$$S(0) \ge 0,$$
 $R(0) \ge 0,$ $x_i(0) \ge 0,$ $i = 1, 2.$

Since perfectly substitutable resources are alternative sources of the same essential nutrient, the rate of conversion of nutrient to biomass of population x_i is made up of a contribution from the consumption of resource S as well as a contribution from the consumption of resource R. Therefore,

$$\mathscr{G}_i(S(t), R(t)) = \mathscr{S}_i(S(t), R(t)) + \mathscr{R}_i(S(t), R(t)).$$
(3.2)

We strengthen hypothesis (2.3) by assuming that

$$\mathscr{S}_i, \mathscr{R}_i$$
 are continuously differentiable. (3.3)

The rate of consumption of each resource is assumed to be a strictly monotone increasing function of the concentration of that resource. Thus, hypothesis (2.5) becomes

$$\frac{\partial}{\partial S}\mathscr{S}_{i}(S,R) > 0 \quad \text{and} \quad \frac{\partial}{\partial R}\mathscr{R}_{i}(S,R) > 0 \quad \text{for all } (S,R) \in \mathring{\mathbf{R}}_{+}^{2}.$$
(3.4)

It should be noted that with two resources available, both serving the same need, it becomes necessary to determine how changes in the concentration of one resource affect the consumption rate of the other. It seems natural to assume that increasing the amount of one resource consumed might result in a reduction in the amount of the other resource consumed. In Holling terminology [12], the handling time devoted to the processing of a unit of one resource is time no longer available for the processing of the other resource. This is reflected in

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the assumption that

$$\frac{\partial}{\partial R}\mathscr{S}_{i}(S,R) \leq 0 \quad \text{and} \quad \frac{\partial}{\partial S}\mathscr{R}_{i}(S,R) \leq 0 \quad \text{for all } (S,R) \in \mathbf{R}^{2}_{+}.$$
(3.5)

By (2.4), (2.6), and (2.7),

 $\mathcal{S}_i(0,R) = 0$ for all $R \ge 0$ and $\mathcal{R}_i(S,0) = 0$ for all $S \ge 0$. (3.6)

Define

$$p_i(S) = \mathcal{S}_i(S,0) \quad \text{for all } S \ge 0 \quad (3.7a)$$

$$q_i(R) = \mathscr{R}_i(0, R) \quad \text{for all } R \ge 0.$$
(3.7b)

That is, $p_i(S)/\xi_i$ is the function describing the uptake of nutrient S in the absence of nutrient R. Similarly, $q_i(R)/\eta_i$ is the function describing the uptake of nutrient R in the absence of nutrient S. We assume that both $p_i(S)$ and $q_i(R)$ are strictly monotone increasing functions.

Further, define λ_i and μ_i so that

$$\mathscr{G}_i(\lambda_i, 0) \left[= p_i(\lambda_i) \right] = D_i \quad \text{and} \quad \mathscr{G}_i(0, \mu_i) \left[= q_i(\mu_i) \right] = D_i.$$
(3.8)

Thus λ_i and μ_i represent the breakeven concentrations for resources S and R, respectively, when none of the other resource is available. By the monotonicity of $p_i(S)$, λ_i is a uniquely defined extended positive real number provided we assume that $\lambda_i = \infty$ if $\mathscr{G}_i(S,0) < D_i$ for all $S \ge 0$. A similar statement can be made for μ_i and $q_i(R)$ provided we assume that $\mu_i = \infty$ if $\mathscr{G}_i(0, R) < D_i$ for all $R \ge 0$.

If the amount of each resource consumed is independent of the concentration of the other resource, that is, if $\mathscr{S}_i(S, R) = p_i(S)$ and $\mathscr{R}_i(S, R) = q_i(R)$ for all $S \ge 0$ and $R \ge 0$, then model (3.1) reduces to model I of León and Tumpson [17], adapted to the chemostat. However, model (3.1) allows for a more realistic selection of functions describing resource consumption, functions that take into consideration the possible effects that the consumption of one resource has on how much of the other resource is consumed.

With this in mind, we make the following assumptions regarding the functions that describe the rate of conversion of nutrient to biomass,

 $\mathcal{G}_i(S, R)$. Let

$$m_{S_i} = \lim_{S \to \infty} p_i(S)$$
 and $m_{R_i} = \lim_{R \to \infty} q_i(R)$ (3.9)

denote the maximal growth rates of population x_i on resources S and R, respectively, when none of the other resource is available. Assume that one of the resources, say S, is superior in the sense that

$$m_{S_i} \ge m_{R_i}.\tag{3.10}$$

Then it seems reasonable to assume that the more of resource S that is consumed, the better, that is,

$$\frac{\partial \mathscr{G}_i}{\partial S} > 0 \qquad \text{for all } (S, R) \in \mathring{\mathbf{R}}^2_+. \tag{3.11}$$

However, if the inequality in (3.10) is strict, a critical concentration of S, say S_i^c , will exist such that

$$\frac{\partial \mathscr{S}_i}{\partial R} > 0 \qquad \text{for all } R > 0; \ 0 < S < S_i^c,$$

$$\frac{\partial \mathscr{S}_i}{\partial R} < 0 \qquad \text{for all } R > 0; \ S > S_i^c,$$
(3.12)

where S_i^c is related to m_{R_i} in the following manner:

$$\mathscr{G}_i(S_i^c; R) = m_{R_i} \quad \text{for all } R \ge 0.$$
(3.13)

Thus when both resources are in *relatively* short supply, increasing the concentration of either resource is beneficial. However, once resource S is plentiful enough that m_{R_i} , the maximal growth rate of population x_i on resource R when there is no resource S available, would be exceeded by consuming only resource S, the presence of resource R would actually become detrimental. In any case, the presence of resource R would never be detrimental enough to decrease $\mathscr{G}_i(S, R)$ below m_{R_i} .

$$\lim_{R \to \infty} \mathscr{G}_i(S, R) = \lim_{R \to \infty} q_i(R) = m_{R_i} \quad \text{for each fixed } S \ge 0. \quad (3.14)$$

It is also assumed that $\mathscr{G}_i(S, R)$ can never increase above m_{S_i} , the maximal growth rate of population x_i on resource S when there is no

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resource R available, since an abundance of S and no R would be optimal for the growth of population x_i .

$$\lim_{S \to \infty} \mathscr{G}_i(S, R) = \lim_{S \to \infty} p_i(S) = m_{S_i} \quad \text{for each fixed } R \ge 0. \quad (3.15)$$

If, instead, $m_{R_i} > m_{S_i}$, a critical concentration of R, say R_i^c , can be defined in an analogous manner, making the appropriate changes in assumptions (3.11)–(3.15). If $m_{R_i} = m_{S_i}$, define $R_i^c = S_i^c = \infty$.

The following technical lemma summarizes some important consequences of assumptions (3.8)–(3.15). Also see Figure 1. An analogous result holds if $m_R > m_S$.

LEMMA 3.1

- (i) If $m_{S_i} \ge m_{R_i}$, then (a) $\mathscr{G}_i(S, R) < m_{R_i}$ if $R \ge 0$ and $0 \le S < S_i^c$, (b) $\mathscr{G}_i(S, R) > m_{R_i}$ if $R \ge 0$ and $S > S_i^c$, and (c) $\mathscr{G}_i(S, R) < m_{S_i}$ if $R \ge 0$ and $S \ge 0$. (ii) If $m_{S_i} \ge m_{R_i}$ and μ_i is finite, then (a) $m_{R_i} > D_i$ and
 - $(u) m_{R_i} > D_i u m u$
 - (b) λ_i is finite and $\lambda_i < S_i^c$.
- (iii) If $m_{S_i} \ge m_{R_i}$ and $\mu_i = \infty$, then either (a) $m_{R_i} < D_i$ and $\lambda_i > S_i^c$ or $\lambda_i = S_i^c = \infty$, or (b) $m_{R_i} = D_i$ and $\lambda_i = S_i^c \le \infty$.

Proof. Recall that $S_i^c = \infty$ if $m_{S_i} = m_{R_i}$.

(i)(a), (i)(b) These follow from (3.11) and (3.13).

(i)(c) If $m_{S_i} = m_{R_i}$, then the result follows immediately from (i)(a), since $S_i^c = \infty$. Suppose $m_{S_i} > m_{R_i}$. If $0 \le S \le S_i^c$, then by (i)(a) and (3.13), $\mathscr{G}_i(S, R) \le m_{R_i} < m_{S_i}$ for all $R \ge 0$. If $S > S_i^c$, then $\mathscr{G}_i(S, 0) \ge \mathscr{G}_i(S, R)$ for all $R \ge 0$ and, by (3.11), $\mathscr{G}_i(S, 0) \le \lim_{S \to \infty} \mathscr{G}_i(S, 0) = m_{S_i}$.

(ii)(a) $m_{R_i} = \mathscr{G}_i(S_i^c, \mu_i) > \mathscr{G}_i(0, \mu_i) = D_i$.

(ii)(b) See Figure 1a. Since, in (ii)(a), $m_{S_i} \ge m_{R_i} > D_i$, it follows that λ_i is finite. If $m_{S_i} = m_{R_i}$, then $S_i^c = \infty$. If $m_{S_i} > m_{R_i}$, then S_i^c is finite and $\mathcal{G}_i(S_i^c, 0) = m_{R_i} > D_i = \mathcal{G}_i(\lambda_i, 0)$.

(iii) See Figure 1b and c. $\mu_i = \infty$ implies that $\mathscr{G}_i(0, R) < D_i$ for all $R \ge 0$. This implies that $m_{R_i} = \lim_{R \to \infty} \mathscr{G}_i(0, R) \le D_i$. If $S_i^c = \infty$, then $\mathscr{G}_i(S,0) < m_{R_i} \le D_i$ for all $S \ge 0$, and so $\lambda_i = \infty$. If S_i^c is finite, then $\mathscr{G}_i(S_i^c,0) = m_{R_i} \le D_i = \mathscr{G}_i(\lambda_i,0)$.

The functions $\mathscr{S}_i(S, R)$ and $\mathscr{R}_i(S, R)$ of Waltman et al. [31] generalize the familiar Michaelis-Menten prototype of functional response to a single resource and are given by

$$\mathscr{S}_{i}(S,R) = \frac{m_{S_{i}}S}{K_{S_{i}}(1 + S/K_{S_{i}} + R/K_{R_{i}})}$$
(3.16a)



FIG. 1. Schematic diagram for Lemma 3.1. (a) $m_{S_i} > m_{R_i} > D_i$; (b) $m_{S_i} > D_i > m_{R_i}$; (c) $D_i > m_{S_i} > m_{R_i}$.



FIG. 1. continued.

and

$$\mathscr{R}_{i}(S,R) = \frac{m_{R_{i}}R}{K_{R_{i}}(1 + S/K_{S_{i}} + R/K_{R_{i}})}$$
(3.16b)

where m_{S_i} , m_{R_i} , K_{S_i} , and K_{R_i} are positive constants, so that

$$\mathscr{G}_{i}(S,R) = \frac{\left(m_{S_{i}}/K_{S_{i}}\right)S + \left(m_{R_{i}}/K_{R_{i}}\right)R}{1 + S/K_{S_{i}} + R/K_{R_{i}}}.$$
(3.17)

The functions $\mathscr{S}_i(S, R)$ and $\mathscr{R}_i(S, R)$ in (3.16) satisfy all assumptions (3.3)–(3.7), and $\mathscr{S}_i(S, R)$ in (3.17) satisfies all assumptions (3.2) and (3.8)–(3.15). In fact,

$$\lambda_{i} = \begin{cases} D_{i}K_{S_{i}}/(m_{S_{i}}-D_{i}) & \text{if } m_{S_{i}} > D_{i}, \\ \infty & \text{otherwise} \end{cases}$$
(3.18a)

and

$$\mu_{i} = \begin{cases} D_{i}K_{R_{i}}/(m_{R_{i}} - D_{i}) & \text{if } m_{R_{i}} > D_{i}, \\ \infty & \text{otherwise} \end{cases}$$
(3.18b)

and

$$\frac{\partial \mathcal{G}_{i}}{\partial S} = \frac{R(m_{S_{i}} - m_{R_{i}}) + m_{S_{i}}K_{R_{i}}}{K_{S_{i}}K_{R_{i}}(1 + S/K_{S_{i}} + R/K_{R_{i}})^{2}}$$
(3.19a)

and

$$\frac{\partial \mathcal{G}_{i}}{\partial R} = \frac{S(m_{R_{i}} - m_{S_{i}}) + m_{R_{i}}K_{S_{i}}}{K_{S_{i}}K_{R_{i}}(1 + S/K_{S_{i}} + R/K_{R_{i}})^{2}}.$$
(3.19b)

If $m_{S_i} > m_{R_i}$, then $S_i^c = m_{R_i} K_{S_i} / (m_{S_i} - m_{R_i})$.

If $\mathscr{S}_i(S, R) = p_i(S)$ and $\mathscr{R}_i(S, R) = q_i(R)$ for all $S \ge 0$ and $R \ge 0$, as in model I of León and Tumpson [17], then (3.2)-(3.11) hold but (3.12)-(3.15) do not hold. Since $\mathscr{S}_i(S, R) = p_i(S) + q_i(R)$, instead, $\partial \mathscr{S}_i / \partial R > 0$ for all R > 0 and S > 0, and

$$\sup_{(S,R)\in \mathbf{R}^2_+} \mathscr{G}_i(S,R) = m_{S_i} + m_{R_i}.$$

3.1. THE SCALED VERSION: SOME PRELIMINARY RESULTS

It follows immediately from (3.1) that if S^o and R^o are both zero, then neither species survives. Also, if only one of S^o or R^o is zero, say $S^o = 0$ and $R^o \neq 0$, then

$$S'(t) = -S(t)\frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i} \mathscr{S}_i(S(t), R(t)) \leq -S(t)\frac{D}{V}.$$

Therefore, $S(t) \leq S(0)e^{-Dt/V}$, and so for sufficiently large t, (3.1) is approximated by

$$S'(t) = 0, \qquad R'(t) = \left[R^o - R(t)\right] \frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} q_i(R(t)),$$
$$x'_i(t) = x_i(t) \left(-\frac{D_i}{V} + q_i(R(t))\right), \qquad i = 1, 2,$$
$$S(0) = 0, \qquad R(0) \ge 0, \qquad x_i(0) \ge 0, \qquad i = 1, 2.$$

This is the model of exploitative competition in the chemostat for one limiting resource studied by Wolkowicz and Lu [32]. They considered n competitors and allowed both monotone kinetics and inhibitory kinetics. They extended some of the results of Butler and Wolkowicz [4], who restricted $D_i = D$ for i = 1, ..., n. Under the additional assumption that q_i assumes the form of Michaelis-Menten kinetics, the model is the

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Monod model examined by Hsu et al. [14] in the case $D_i = D$ for i = 1, ..., n and by Hsu [13] in the differential death rate case. For our purposes, we assume that neither S^o nor R^o is zero.

It will be more convenient to analyze the model after the following substitutions:

$$\overline{t} = t \frac{D}{V}, \qquad \overline{S} = \frac{S}{S^o}, \qquad \overline{R} = \frac{R}{R^o}, \qquad (3.20a)$$

$$\overline{\mathscr{S}}_{i}(\overline{S},\overline{R}) = \frac{V\mathscr{S}_{i}(S,R)}{D}, \qquad \overline{\mathscr{R}}_{i}(\overline{S},\overline{R}) = \frac{V\mathscr{R}_{i}(S,R)}{D}, \quad (3.20b)$$

$$\overline{\varepsilon}_i = \frac{\varepsilon_i}{D}, \qquad \overline{x}_i = \frac{x_i}{S^o}, \qquad \overline{\eta}_i = \frac{R^o}{S^o} \eta_i.$$
(3.20c)

Removing the bars to simplify notation, we obtain

$$S'(t) = 1 - S(t) - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i} \mathscr{S}_i(S(t), R(t)), \qquad (3.21a)$$

$$R'(t) = 1 - R(t) - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} \mathscr{R}_i(S(t), R(t)), \qquad (3.21b)$$

$$x'_{i}(t) = x_{i}(t) [-D_{i} + \mathscr{G}_{i}(S(t), R(t))], \quad i = 1, 2, \quad (3.21c)$$

$$S(0) \ge 0$$
, $R(0) \ge 0$, $x_i(0) \ge 0$, $i = 1, 2$.

All of the corresponding assumptions hold for this version of the model, so there will be no loss of generality if we study (3.21) instead of (3.1). Our results can be reinterpreted in terms of the unscaled variables using (3.20).

We first note that all solutions of (3.21) are positive and bounded. These are minimum requirements for a reasonable model of the chemostat.

THEOREM 3.2

(i) All solutions S(t), R(t), $x_i(t)$, i = 1, 2, of (3.21) for which $x_i(0) > 0$, i = 1, 2, are positive and bounded for t > 0.

(ii) Given any $\delta > 0$, for all solutions S(t), R(t) of (3.21), $S(t) < 1 + \delta$ and $R(t) < 1 + \delta$ for all sufficiently large t.

(iii) If there exists a $t_0 \ge 0$ such that $S(t_0) \le 1$, then S(t) < 1 for all $t > t_0$. A similar result holds for R(t).

Proof. The proof of (i) is similar to the proof given in [4]. By considering

$$z(t) = S(t) + R(t) + \frac{x_1(t)}{\max\{\xi_1, \eta_1\}} + \frac{x_2(t)}{\max\{\xi_2, \eta_2\}},$$

it can in fact be shown that

$$z(t) \leq \begin{cases} 2 & \text{if } z(0) < 2, \\ z(0) & \text{otherwise.} \end{cases}$$

The proofs of (ii) and (iii) are immediate from (3.21).

Remark Concerning Theorem 3.2. Suppose

$$\xi_1 / \eta_1 = \xi_2 / \eta_2 \tag{3.22}$$

$$D_i = 1, \qquad i = 1, 2,$$
 (3.23)

and define

$$z(t) = \xi_1 S(t) + \eta_1 R(t) + x_1(t) + \frac{\xi_1}{\xi_2} x_2(t).$$

Then from (3.21), $z'(t) = (\xi_1 + \eta_1) - z(t)$, so that $z(t) = [z(0) - (\xi_1 + \eta_1)]e^{-t} + (\xi_1 + \eta_1)$ and $z(t) \rightarrow (\xi_1 + \eta_1)$ as $t \rightarrow \infty$. Therefore, under assumptions (3.22) and (3.23), system (3.21) is conservative in the sense that the simplex

$$\left\{ (S, R, x_1, x_2) \colon S, R, x_1, x_2 \ge 0, \, \xi_1 S + \eta_1 R + x_1 + \frac{\xi_1}{\xi_2} x_2 = (\xi_1 + \eta_1) \right\}$$

is a global attractor for (3.21). Although there is some biological merit in assumption (3.22), our analysis does not require (3.22) or (3.23).

THEOREM 3.3

The equilibrium solution $E_0 = (1, 1, 0, 0)$ is locally asymptotically stable for (3.21) if $\mathcal{G}_i(1, 1)D_i$ for i = 1, 2, and E_0 is unstable if $\mathcal{G}_i(1, 1) > D_i$ for i = 1 or 2.

Proof. See Section 3.3 for the local stability analysis.

The next result concerns competition-independent extinction of a population. It gives conditions under which there is total washout of both competing species.

THEOREM 3.4

Define $\Gamma_{\varepsilon} \equiv \{(S, R): 0 \leq S \leq 1 + \varepsilon, 0 \leq R \leq 1 + \varepsilon\}$. Assume that $m_{S_i} \geq m_{R_i}$.

(i) If either $(\mu_i \text{ is finite and } \mathcal{G}_i(1,1) < D_i)$ or $(\mu_i = \infty \text{ and } \lambda_i > 1)$, then there exists a $\delta_i > 0$ such that $\max_{(S,R) \in \Gamma_{\delta_i}} \mathcal{G}_i(S,R) < D_i$.

(ii) If either $(\mu_i \text{ is finite and } \mathcal{G}_i(1,1) < D_i)$ or $(\mu_i = \infty \text{ and } \lambda_i \ge 1)$, then $x_i(t) \to 0$ as $t \to \infty$, in (3.21).

(iii) If $x_i(t) \to 0$ as $t \to \infty$ for i = 1, 2, then $E_0 = (1, 1, 0, 0)$ is globally asymptotically stable for (3.21) with respect to all solutions satisfying $x_i(0) \ge 0$ for i = 1, 2.

Proof. (i) Since $m_{S_i} \ge m_{R_i}$, it follows from part (ii)(b) of Lemma 3.1 that if μ_i is finite, then λ_i is finite. Therefore, it suffices to consider the following three cases:

- (1) μ_i and λ_i are both finite,
- (2) $\mu_i = \infty$, but λ_i is finite,
- (3) $\mu_i = \infty$ and $\lambda_i = \infty$.

Case 1. By hypothesis, $\mathscr{G}_i(1,1) < D_i$. By Lemma 3.1(ii)(b), $\lambda_i < S_i^c$, and so $D_i = \mathscr{G}_i(\lambda_i, 0) < \mathscr{G}_i(\lambda_i, 1)$. If $\lambda_i \le 1$, then $D_i < \mathscr{G}_i(\lambda_i, 1) \le \mathscr{G}_i(1,1) < D_i$, a contradiction. It follows that $\lambda_i > 1$. Therefore, $\delta_i > 0$ can be chosen sufficiently small that $S_i^c > 1 + \delta_i$ and, by the continuity of \mathscr{G}_i , so that $\mathscr{G}_i(1 + \delta_i, 1 + \delta_i) < D_i$. Therefore, $\max_{(S,R) \in \Gamma_{\delta_i}} \mathscr{G}_i(S,R) = \mathscr{G}_i(1 + \delta_i, 1 + \delta_i) < D_i$.

Case 2. By hypothesis, $\lambda_i > 1$. By Lemma 3.1(iii) $\lambda_i \ge S_i^c$, and so either $\lambda_i > 1 \ge S_i^c$ or $\lambda_i \ge S_i^c > 1$. If $\lambda_i > 1 \ge S_i^c$, then $\mathcal{G}_i(1,1) \le \mathcal{G}_i(1,0) \le \mathcal{G}_i(\lambda_i,0) = D_i$, and if $\lambda_i \ge S_i^c > 1$, then $\mathcal{G}_i(1,1) \le \mathcal{G}_i(S_i^c,1) = m_{R_i} \le D_i$. In either case, it follows that $\mathcal{G}_i(1,1) < D_i$, and hence, by the continuity of \mathcal{G}_i , there exists $\delta_i > 0$ such that $\mathcal{G}_i(1+\delta_i, 1+\delta_i) < D_i$ and $\lambda_i > 1+\delta_i$. If $\lambda_i > 1 \ge S_i^c$, then $\max_{(S,R) \in \Gamma_{\delta_i}} \mathcal{G}_i(S,R) = \mathcal{G}_i(1+\delta_i,0) < \mathcal{G}_i(\lambda_i,0) = D_i$, and if $\lambda_i \ge S_i^c > 1$, δ_i can be chosen so that $S_i^c > 1+\delta_i$, and so $\max_{(S,R) \in \Gamma_{\delta_i}} \mathcal{G}_i(S,R) = \mathcal{G}_i(1+\delta_i,1+\delta_i) < D_i$.

Case 3. In this case, since $\mu_i = \infty$ and $\lambda_i = \infty$, $m_{R_i} \le m_{S_i} \le D_i$. Therefore, for any fixed $\delta_i > 0$, if $(\overline{S}, \overline{R}) \in \Gamma_{\delta_i}$, then $\mathscr{G}_i(\overline{S}, \overline{R}) < \lim_{S \to \infty} \mathscr{G}_i(S, \overline{R}) = m_{S_i} \le D_i$.

(ii) Suppose that either μ_i is finite and $\mathscr{G}_i(1,1) < D_i$, or $\mu_i = \infty$ and $\lambda_i > 1$. Choose $\delta_i > 0$ as in part (i). By Theorem 3.2(ii), $S(t) < 1 + \delta_i$ and $R(t) < 1 + \delta_i$ for all sufficiently large t, and so, by (3.21), $x'_i(t) < 0$ for all sufficiently large t. Also, $x''_i(t)$ is bounded below. It follows, by a result of Miller [20], that $x'_i(t) \to 0$ as $t \to \infty$. However, $\limsup_{t \to \infty} \mathscr{G}_i(S(t), R(t)) \leq \max_{(S,R) \in \Gamma_{\delta_i}} \mathscr{G}_i(S,R) < D_i$, and so the only possibility is that $x_i(t) \to 0$ as $t \to \infty$.

Suppose that $\mu_i = \infty$ and $\lambda_i = 1$. Without loss of generality, assume that i = 1. First, consider $m_{R_1} = D_1$. Then $S_1^c = \lambda_1$. By Theorem 3.2(iii), either S(t) > 1 for all $t \ge 0$ or S(t) < 1 for all sufficiently large t.

Suppose S(t) > 1 for all $t \ge 0$. Then S'(t) < 0 for all $t \ge 0$, so that $S(t) \searrow S^* \ge 1$. If $S^* > 1$, then $S'(t) \le 1 - S(t) \le 1 - S^* < 0$, so that $S(t) \to -\infty$ as $t \to \infty$, a contradiction. Therefore, $S(t) \searrow 1$ as $t \to \infty$. Since S(t) > 1 for all $t \ge 0$, $\mathcal{G}_1(S(t), R(t)) > D_1$ for all $t \ge 0$ by part (i)(b) of Lemma 3.1. Then $x'_1(t) > 0$ for all $t \ge 0$, so that $x_1(t) \nearrow x_1^* > 0$. Define $R_{\max} = \sup\{R(t): t \ge 0\}$. Then $R_{\max} \le \max\{R(0), 1\}$, so

$$S'(t) \leq 1 - S(t) - \frac{x_1(t)}{\eta_1} \mathscr{S}_1(S(t), R(t)) \leq -\frac{x_1(0)}{\eta_1} \mathscr{S}_1(1, R_{\max}) < 0,$$

so that $S(t) \rightarrow -\infty$ as $t \rightarrow \infty$, a contradiction.

Therefore, S(t) < 1 for all sufficiently large t. By part (i)(a) of Lemma 3.1, $\mathscr{G}_1(S(t), R(t)) < D_1$ for all sufficiently large t, so that $x'_1(t) < 0$ for all sufficiently large t. Therefore, $x_1(t) \searrow x_1^* \ge 0$. Since $x''_1(t)$ is bounded, $x'_1(t) \to 0$ as $t \to \infty$. If $x_1^* > 0$, then $\mathscr{G}_1(S(t), R(t)) \to D_1$ as $t \to \infty$, implying that $S(t) \to 1$ as $t \to \infty$. But then S'(t) < 0 for all sufficiently large t. Since S(t) < 1 for all sufficiently large t, S(t) cannot decrease to 1. This contradiction implies that $x_1^* = 0$.

Now consider $m_{R_1} < D_1$. Then $S_1^c < \lambda_1 = 1$. Again, either S(t) > 1 for all $t \ge 0$ or S(t) < 1 for all sufficiently large t.

Suppose S(t) > 1 for all $t \ge 0$. As above, $S(t) \ge 1$ as $t \to \infty$. If $\liminf_{t \to \infty} x_1(t) > 0$, then there exists $\varepsilon > 0$ such that $x_1(t) > \varepsilon$ for all sufficiently large t. Then

$$S'(t) \leq 1 - S(t) - \frac{x_1(t)}{\eta_1} \mathscr{S}_1(S(t), R(t)) \leq -\frac{\varepsilon}{\eta_1} \mathscr{S}_1(1, R_{\max}) < 0$$

for all sufficiently large t, so $S(t) \to -\infty$ as $t \to \infty$, a contradiction. Therefore, $\liminf_{t \to \infty} x_1(t) = 0$.

Suppose $\limsup_{t \to \infty} x_1(t) = x_1^* > 0$. Then there exist sequences of consecutive local minima $\{\tau_n\}_{n=1}^{\infty}$ and consecutive local maxima $\{\sigma_n\}_{n=1}^{\infty}$ of $x_1(t)$ satisfying $\tau_n \to \infty$, $\sigma_n \to \infty$ as $n \to \infty$, $\tau_n < \sigma_n < \tau_{n+1} < \sigma_{n+1}$,

$$\begin{aligned} x_1'(\tau_n) &= 0 = x_1'(\sigma_n), \\ x_1'(t) &\ge 0 \qquad \text{if } \tau_n < t < \sigma_n, \\ x_1'(t) &\le 0 \qquad \text{if } \sigma_n < t < \tau_{n+1}. \end{aligned}$$

Therefore, since $x_1(t) > 0$ for all $t \ge 0$,

$$\mathscr{G}_1(S(\tau_n), R(\tau_n)) = D_1 = \mathscr{G}_1(S(\sigma_n), R(\sigma_n)), \qquad (3.24a)$$

$$\mathscr{G}_1(S(t), R(t)) \ge D_1 \qquad \text{if } \tau_n < t < \sigma_n, \qquad (3.24b)$$

$$\mathscr{G}_1(S(t), R(t)) \leq D_1 \qquad \text{if } \sigma_n < t < \tau_{n+1}. \tag{3.24c}$$

But then $R(\tau_n) = \varphi_1(S(\tau_n))$ for all *n*. Since $\varphi_1(1) = 0, \varphi_1(S)$ is continuous, and $S(\tau_n) \to 1$ as $n \to \infty$, $R(\tau_n) \to 0$ as $n \to \infty$. Now,

$$R'(\tau_n) = 1 - R(\tau_n) - \frac{x_1(\tau_n)}{\xi_1} \mathscr{R}_1(S(\tau_n), R(\tau_n))$$
$$- \frac{x_2(\tau_n)}{\xi_2} \mathscr{R}_2(S(\tau_n), R(\tau_n)).$$

Since $R(\tau_n) \to 0$ as $n \to \infty$, $\mathscr{R}_i(S(\tau_n), R(\tau_n)) \to 0$, i = 1, 2, as $n \to \infty$ by (3.6), and since $x_i(t)$ is bounded for all $t \ge 0$, $R'(\tau_n) \to 1$ as $n \to \infty$. Therefore, $S'(\tau_n) < 0$ and $R'(\tau_n) > 0$ for all sufficiently large *n*, and so there

exists an N > 0 and an $\varepsilon(N) > 0$ such that $\mathscr{G}_1(S(t), R(t)) < \mathscr{G}_1(S(\tau_N), R(\tau_N)) = D_1$ for all $\tau_N < t < \tau_N + \varepsilon(N)$, contradicting (3.24b). Therefore, $\limsup_{t \to \infty} x_1(t) = 0$, and hence $\lim_{t \to \infty} x_1(t) = 0$.

If S(t) < 1 for all sufficiently large t, then the proof of $x_1(t) \to 0$ as $t \to \infty$ is similar to the proof given for $m_{R_1} = D_1$.

(iii) Take $Q \in \{(S, R, x_1, x_2) \in \mathbf{R}^4_+: x_1 > 0, x_2 > 0\}$. Let $\Omega(Q)$ denote the omega limit set of the orbit through Q. By the hypothesis, any $P = (\underline{S}, \underline{R}, \underline{x}_1, \underline{x}_2) \in \Omega(Q)$ satisfies $\underline{x}_1 = 0$ and $\underline{x}_2 = 0$. On $\{(S, R, 0, 0) \in \mathbf{R}^4_+\}$ the system reduces to

$$S'(t) = 1 - S(t), \qquad R'(t) = 1 - R(t),$$

and hence $S(t) \to 1$ and $R(t) \to 1$. Therefore, $\{E_0\} \in \Omega(Q)$. By Theorem 3.2, $\Omega(Q)$ is a nonempty, compact subset of \mathbb{R}^4_+ . If $P \in \Omega(Q)$, then the entire trajectory through P is in $\Omega(Q)$. Hence, E_0 is the only candidate.

Remarks Concerning Theorem 3.4

(1) An analogous result holds if $m_{R_i} \ge m_{S_i}$. Just interchange the roles of λ_i and μ_i in the previous theorem.

(2) It can be shown that if $\mathscr{S}_i(S, R) = p_i(S)$ and $\mathscr{R}_i(S, R) = q_i(R)$ for all $S \ge 0$ and $R \ge 0$, as in the model of León and Tumpson [17], then $\mathscr{S}_i(1,1) < D_i$ implies $x_i(t) \to 0$ as $t \to \infty$ regardless of the relative values of m_{S_i}, m_{R_i} , and D_i .

Next we discuss subsistence curves, $\varphi_i(S)$ and $\sigma_i(R)$, in the (S, R)-plane. These are curves that give the concentrations of S and R at which the biomass of population x_i in the culture vessel is neither increasing nor decreasing.

LEMMA 3.5

(i) If λ_i and μ_i are both finite, then there exist C^1 functions $\varphi_i(S)$ and $\sigma_i(R)$ satisfying

$$\begin{split} \varphi_i \colon [0, \lambda_i] \to [0, \mu_i], & \sigma_i \colon [0, \mu_i] \to [0, \lambda_i], \\ \mathscr{G}_i(S, \varphi_i(S)) = D_i, & \mathscr{G}_i(\sigma_i(R), R) = D_i, \\ \varphi_i'(S) < 0, & \sigma_i'(R) < 0. \end{split}$$

(ii) If $m_{S_i} > D_i > m_{R_i}$, and $0 < \lambda_i \leq 1$, then there exist C^1 functions $\varphi_i(S)$ and $\sigma_i(R)$ satisfying

$$\begin{split} \varphi_i &: \left[\lambda_i, M_i^S \right] \to [0, 1], \qquad \sigma_i &: \left[0, \varphi_i \left(M_i^S \right) \right] \to \left[\lambda_i, M_i^S \right], \\ \mathcal{G}_i (S, \varphi_i (S)) &= D_i, \qquad \qquad \mathcal{G}_i (\sigma_i (R), R) = D_i, \\ \varphi_i' (S) &> 0, \qquad \qquad \sigma_i' (R) > 0, \end{split}$$

where

$$M_i^S \equiv \max_{\substack{\lambda_i \leqslant S \leqslant 1, \\ \mathscr{G}_i(S,1) \leqslant D_i}} S.$$
(3.25)

(iii) If $m_{R_i} > D_i > m_{S_i}$, and $0 < \mu_i \le 1$, then there exist C^1 functions $\varphi_i(S)$ and $\sigma_i(R)$ satisfying

$$\begin{split} \sigma_i &: \left[\begin{array}{c} \mu_i, M_i^R \end{array} \right] \to \left[0, 1 \right], \qquad \varphi_i &: \left[0, \sigma_i \left(M_i^R \right) \right] \to \left[\begin{array}{c} \mu_i, M_i^R \right], \\ & \mathcal{G}_i (S, \varphi_i(S)) = D_i, \qquad \qquad \mathcal{G}_i (\sigma_i(R), R) = D_i, \\ & \varphi_i'(S) > 0, \qquad \qquad \sigma_i'(R) > 0, \end{split}$$

where

$$M_i^R \equiv \max_{\substack{\mu_i \leqslant R \leqslant 1, \\ \mathscr{G}_i(1,R) \leqslant D_i}} R.$$
(3.26)

Proof.

(i) By Lemma 3.1 and (3.8), $\mathscr{G}_i(S,0) < D_i$ and $\mathscr{G}_i(S,\mu_i) > D_i$ for each $S \in (0, \lambda_i)$. Therefore, by (3.3), (3.11), and (3.12), to each fixed

 $S \in (0, \lambda_i)$, there corresponds a unique $R_S \in (0, \mu_i)$ such that $\mathcal{G}_i(S, R_S) = D_i$. Define $\varphi_i: [0, \lambda_i] \rightarrow [0, \mu_i]$ by setting $\varphi_i(S) = R_S$. Then $\mathcal{G}_i(S, \varphi_i(S)) = D_i$ for all $0 \le S \le \lambda_i$. In view of (3.11) and (3.12), by a straightforward application of the implicit function theorem, it follows that $\varphi_i \in C^1$ and $\varphi'_i(S) < 0$ for all $0 < S < \lambda_i$.

In a similar manner, one can define a function $\sigma_i: [0, \mu_i] \rightarrow [0, \lambda_i]$ such that $\mathscr{G}_i(\sigma_i(R), R) = D_i$ for all $0 \le R \le \mu_i$, with $\sigma_i \in C^1$ and $\sigma'_i(R) < 0$ for all $0 < R < \mu_i$.

(ii) In this case, by Lemma 3.1(iii), $\lambda_i > S_i^c$ and so $\mathscr{G}_i(\lambda_i, 1) < D_i$. Thus, $\mathscr{G}_i(S,0) > D_i$ and $\mathscr{G}_i(S,1) < D_i$ for each $S \in (\lambda_i, M_i^S)$. Therefore, by (3.3), (3.11), and (3.12), for each fixed $S \in [\lambda_i, M_i^S]$, there corresponds a unique $R_s \in [0,1]$ such that $\mathscr{G}_i(S, R_s) = D_i$. Define $\varphi_i : [\lambda_i, M_i^S] \to [0,1]$ by setting $\varphi_i(S) = R_s$. Continue now as in the proof of (i).

(iii) The proof is similar to the proof of (ii).

Remarks Concerning Lemma 3.5

(1) Note that $M_i^S = 1$ if and only if $\mathcal{G}_i(M_i^S, 1) = \mathcal{G}_i(1, 1) \leq D_i$. This implies that $\varphi_i(M_i^S) \leq 1$. Also, $M_i^S < 1$ if and only if $\mathcal{G}_i(1, 1) > \mathcal{G}_i(M_i^S, 1) = D_i$. This implies that $\varphi_i(M_i^S) = 1$.

(2) For the functions (3.16) and (3.17), the subsistence curves

$$\varphi_i(S) = \left[1 + S\left(\frac{D_i - m_{S_i}}{D_i K_{S_i}}\right)\right] \left(\frac{D_i K_{R_i}}{m_{R_i} - D_i}\right)$$

and

$$\sigma_i(R) = \left[1 + R\left(\frac{D_i - m_{R_i}}{D_i K_{R_i}}\right)\right] \left(\frac{D_i K_{S_i}}{m_{S_i} - D_i}\right)$$

are both linear functions.

Before proceeding, we discuss the function $\mathscr{G}_i(S, R)$ described above in the context of the classifications given by Rapport [24], León and Tumpson [17], and Tilman [28] and relate the subsistence curves to what they call indifference curves. Assume $m_{S_i} \ge m_{R_i}$. Consider

$$\Phi_i(S,R) \equiv \frac{x'_i}{x_i} = \mathscr{G}_i(S,R) - D_i = C,$$

where C is any constant such that $-D_i < C < m_{S_i} - D_i$. The curve $\Phi_i(S, R) = C$ projected onto the $(\mathscr{S}_i(S, R), \mathscr{R}_i(S, R))$ -plane gives an indifference curve, that is, a curve along which any combination of values of $\mathscr{S}_i(S, R)$ and $\mathscr{R}_i(S, R)$ gives the same rate of growth C. By (3.2), these curves are linear and decreasing, precisely as in Figure 1D

of [24] and Figure 1(a) of [17]. Since $\Phi_i(S, R) = 0 = \Phi_i(S, \varphi_i(S)) = \Phi_i(\sigma_i(R), R)$, these curves can be projected into the (S, R)-plane. Under our assumptions, Figure 2 depicts the indifference curves in the (S, R)plane in the case that $m_{S_i} > m_{R_i}$. For $C = m_{R_i} - D_i$, the indifference curve in (S, R)-space is the vertical line $S = S_i^c$. For $C < m_{R_i} - D_i$, the indifference curves are decreasing, and for $C > m_{R_i} - D_i$, they are increasing. If $m_{S_i} = m_{R_i}$, so that $S_i^c = R_i^c = \infty$, then the indifference curves in the (S, R)-plane are decreasing. In the special case that the indifference curves in the (S, R)-plane are linear, as is the case when $\mathscr{G}_i(S, R)$ is defined by (3.17) (see Remark 2 following Lemma 3.5), then resources S and R are perfectly substitutable in the sense of Tilman [28]. In the classification in [28], the resources S and R are considered perfectly substitutable if S and R, rather than the rates of consumption of S and R, can be substituted in a fixed ratio in order to maintain a given growth rate.

3.2. SINGLE-SPECIES GROWTH—THE THREE-DIMENSIONAL SUBSYSTEMS

There are only two three-dimensional subsystems of (3.21) of interest. Each involves one population of microorganisms consuming the two nonreproducing, perfectly substitutable resources. Due to symmetry, both subsystems exhibit the same dynamics. Throughout this section, the same notation as in the previous sections is used, but the subscripts



FIG. 2. "Indifference" curves in the (S, R)-plane and the "subsistence" curve, for $m_{S_i} > m_{R_i}$. Since $\Phi_i(S, R) = 0 = \Phi_i(S, \varphi_i(S)) = \Phi_i(\sigma_i(R), R)$, the indifference curve with C = 0 gives the subsistence curve.

are omitted. We examine the system

$$S'(t) = 1 - S(t) - \frac{x(t)}{\xi} \mathscr{S}(S(t), R(t)), \qquad (3.27a)$$

$$R'(t) = 1 - R(t) - \frac{x(t)}{\eta} \mathscr{R}(S(t), R(t)), \qquad (3.27b)$$

$$x'(t) = x(t) [-d + \mathscr{G}(S(t), R(t))], \qquad (3.27c)$$

$$S(0) \ge 0, \qquad R(0) \ge 0, \qquad x(0) \ge 0.$$

Here, *d* represents the rate of removal of the microbial population from competition; that is, $d = 1 + \varepsilon$, $\varepsilon \ge 0$, where ε is the intrinsic death rate. The functions $\mathscr{S}(S(t), R(t))$, $\mathscr{R}(S(t), R(t))$, and $\mathscr{G}(S(t), R(t))$ are assumed to satisfy all of the assumptions (2.2)–(2.10) and (3.2)–(3.15).

By Theorem 3.2(i), all solutions S(t), R(t), x(t) of (3.27) for which x(0) > 0 are positive and bounded for all t > 0. By Theorems 3.3 and 3.4(ii), if μ is finite and $\mathscr{G}(1,1) < d$, or if $\mu = \infty$ and $\lambda \ge 1$, then $E_0 = (1,1,0)$ is globally asymptotically stable for (3.27) [with respect to solutions for which $x(0) \ge 0$].

Besides $E_0 = (1, 1, 0)$, any other critical points must be one-species survival equilibria. A one-species survival equilibrium of (3.27) is a solution $(\overline{S}, \overline{R}, \overline{x})$ of the system

$$x\mathscr{S}(S,R) = \xi(1-S) \tag{3.28a}$$

$$x\mathscr{R}(S,R) = \eta(1-R) \tag{3.28b}$$

$$\mathscr{G}(S,R) = d \tag{3.28c}$$

with $(\overline{S}, \overline{R}, \overline{x}) \in \mathring{\mathbf{R}}^3_+$.

LEMMA 3.6

Assume that $m_{s} \ge m_{R}$. Suppose that a one-species survival equilibrium $(\overline{S}, \overline{R}, \overline{x})$ of (3.27) exists.

(i) If μ is finite, then $0 < \overline{S} < \min\{1, \lambda\}$ and $0 < \overline{R} < \min\{1, \mu\}$. (ii) If $\mu = \infty$ and $\lambda \leq 1$, then either

 $m_R < d$, and so $S^c < \lambda$ and $\lambda < \overline{S} < M^S \leq 1$, $0 < \overline{R} < \varphi(M^S) \leq 1$,

or

$$m_R = d$$
, and so $S^c = \lambda$ and $\lambda = S < 1$, $0 < R < 1$,

where M^{S} is defined by (3.25).

Proof. First, note that, from (3.28), $\bar{x} > 0$ implies that $0 < \bar{S} < 1$ and $0 < \bar{R} < 1$.

(i) If μ is finite, then, by part (ii)(b) of Lemma 3.1, λ is finite and $\lambda < S^c$. Therefore, $\mathscr{G}(S, R) > \mathscr{G}(S, 0) > \mathscr{G}(\lambda, 0) = d$ for all $S > \lambda$, R > 0; and $\mathscr{G}(S, R) > \mathscr{G}(0, R) > \mathscr{G}(0, \mu) = d$ for all S > 0, $R > \mu$; and so $0 < \overline{S} < \min\{1, \lambda\}$ and $0 < \overline{R} < \min\{1, \mu\}$.

(ii) In this case, by part (iii) of Lemma 3.1, $S^c \leq \lambda$. First, consider $S^c < \lambda$. Then $\mathscr{G}(S, R) \leq \mathscr{G}(S^c, R) = m_R < d$ for all $0 < S \leq S^c$, R > 0; $\mathscr{G}(S, R) \leq \mathscr{G}(\lambda, R) < \mathscr{G}(\lambda, 0) = d$ for all $S^c < S \leq \lambda$, R > 0; and $\mathscr{G}(S, R) \geq \mathscr{G}(M^S, R) > \mathscr{G}(M^S, \varphi(M^S)) = d$ for all $S \geq M^S, \varphi(M^S) > R > 0$; and so $\lambda < \overline{S} < M^S \leq 1$ and $0 < \overline{R} < \varphi(M^S)$. If, on the other hand, $S^c = \lambda$, then $\mathscr{G}(S^c, R) = d = m_R$ for all $R \geq 0$, and, by part (i)(a, b) of Lemma 3.1, $\mathscr{G}(S, R) \neq d$ for any $R \geq 0$, $S \neq S^c$; and so $\lambda = \overline{S} < 1$ and $0 < \overline{R} < 1$.

THEOREM 3.7

Assume that $m_s \ge m_R$.

(i) If μ is finite, then a one-species survival equilibrium of (3.27) exists if and only if $\mathcal{G}(1,1) > d$. When a one-species survival equilibrium exists, it is unique. In particular, if $\lambda < 1$ or $\mu < 1$, then $\mathcal{G}(1,1) > d$.

(ii) Suppose $\mu = \infty$.

(a) If $\lambda \ge 1$ or $\lambda = \infty$, then (3.27) has no one-species survival equilibrium.

(b) If $m_R = d$, then $\mathcal{G}(1,1) > d$ if and only if $\lambda < 1$, and a one-species survival equilibrium of (3.27) exists if and only if $\mathcal{G}(1,1) > d$. When a one-species survival equilibrium exists, it is unique.

(c) If $m_R < d$, then $\mathcal{G}(1,1) > d$ if and only if $M^S < 1$, and if $\mathcal{G}(1,1) > d$, then (3.27) has at least one one-species survival equilibrium.

Proof. (i) First we show that if μ is finite and a one-species survival equilibrium $(\overline{S}, \overline{R}, \overline{x})$ exists, then $\mathscr{G}(1,1) > d$. By Lemma 3.6, $0 < \overline{S} < \min\{\lambda, 1\}$ and $0 < \overline{R} < \min\{\mu, 1\}$. By Lemma 3.1(ii)(a, b), $m_R > d$ and $S^c > \lambda > \overline{S}$. If $S^c > 1$, then $d = \mathscr{G}(\overline{S}, \overline{R}) < \mathscr{G}(1, \overline{R}) < \mathscr{G}(1, 1)$. If $S^c \leq 1$, then $d < m_R = \mathscr{G}(S^c, 1) \leq \mathscr{G}(1, 1)$.

Next we show that if $\mathscr{G}(1,1) > d$, then a one-species survival equilibrium exists. For $S \in (0, \lambda)$, define

$$x_{S}(S) = \frac{\xi(1-S)}{\mathscr{S}(S,\varphi(S))} \quad \text{and} \quad x_{R}(S) = \frac{\eta(1-\varphi(S))}{\mathscr{R}(S,\varphi(S))}, \quad (3.29)$$

where, by Lemma 3.5, $\mathscr{G}(S, \varphi(S)) = d$ for all $0 \le S \le \lambda$. If $\mu > 1$, then $\mathscr{G}(0,1) < d$, and since $\mathscr{G}(\lambda,1) > d$ and $\mathscr{G}(1,1) > d$, there exists a unique

 $\tilde{S} \in (0, \min\{1, \lambda\})$ such that $\mathscr{G}(\tilde{S}, 1) = d$ and $\varphi(\tilde{S}) = 1$. By Lemma 3.5, $0 < \varphi(S) < \mu$ for $S \in (0, \min\{1, \lambda\})$ if $\mu \leq 1$, and $0 < \varphi(S) < 1$ for $S \in (\tilde{S}, \min\{1, \lambda\})$ if $\mu > 1$. In both cases, by (3.4), (3.5), and Lemma 3.5, $x_S(S)$ is a decreasing function, $x_R(S)$ is an increasing function, and both functions are continuous. There are four cases to consider.

Case 1. $\lambda \leq 1$ and $\mu \leq 1$ (see Figure 3a).

$$x_s(0) = \infty$$
 and $x_R(0) = \frac{\eta(1-\mu)}{d}$,
 $x_s(\lambda) = \frac{\xi(1-\lambda)}{d}$ and $x_R(\lambda) = \infty$.

Case 2. $\lambda > 1$ and $\mu > 1$ (see Figure 3b).

$$x_{S}(\tilde{S}) = \frac{\xi(1-\tilde{S})}{\mathscr{S}(\tilde{S},1)} > 0 \quad \text{and} \quad x_{R}(\tilde{S}) = 0,$$
$$x_{S}(1) = 0 \quad \text{and} \quad x_{R}(1) = \frac{\eta(1-\varphi(1))}{\mathscr{R}(1,\varphi(1))} > 0.$$

Case 3. $\lambda \leq 1$ and $\mu \geq 1$ (see Figure 3c).

$$x_{S}(\tilde{S}) = \frac{\xi(1-\tilde{S})}{\mathscr{S}(\tilde{S},1)} > 0 \quad \text{and} \quad x_{R}(\tilde{S}) = 0,$$
$$x_{S}(\lambda) = \frac{\xi(1-\lambda)}{d} \quad \text{and} \quad x_{R}(\lambda) = \infty.$$

Case 4. $\lambda \ge 1$ and $\mu \le 1$ (see Figure 3d).

$$x_S(0) = \infty$$
 and $x_R(0) = \frac{\eta(1-\mu)}{d}$,
 $x_S(1) = 0$ and $x_R(1) = \frac{\eta(1-\varphi(1))}{\mathscr{R}(1,\varphi(1))}$.

Therefore, in each case there exists a unique $\hat{S} \in (0, \lambda)$ such that $x_S(\hat{S}) = x_R(\hat{S})$, and hence a unique one-species survival equilibrium, with $\overline{S} = \hat{S}$, $\overline{R} = \varphi(\hat{S})$, and $\overline{x} = x_S(\hat{S}) = x_R(\hat{S})$.

In particular, since $S^c > \lambda$, if $\lambda < 1$, then $\mathscr{G}(1,1) > \mathscr{G}(\lambda,1) > d$, and if $\mu < 1$, then $\mathscr{G}(1,1) > \mathscr{G}(0,1) > \mathscr{G}(0,\mu) = d$.

(ii)(a) By Theorem 3.4(ii), if $\mu = \infty$ and $\lambda \ge 1$, then $x(t) \to 0$ as $t \to \infty$, and so there can be no one-species survival equilibrium.



FIG. 3. Schematic diagram for Theorem 3.7. For $m_S \ge m_R > d$: (a) $\lambda \le 1$ and $\mu \le 1$; (b) $\lambda > 1$ and $\mu > 1$; (c) $\lambda \le 1$ and $\mu \ge 1$; (d) $\lambda \ge 1$ and $\mu \le 1$. For $m_S > d \ge m_R$: (e) $m_R = d$; (f) $m_R < d$ and $M^S < 1$.

(ii)(b) If $m_R = d$, then $S^c = \lambda$.

Suppose that $\mathscr{G}(1,1) > d = m_R$. If $\lambda \ge 1$, then $m_R = \mathscr{G}(S^c, 1) = \mathscr{G}(\lambda, 1) \ge \mathscr{G}(1, 1) > d = m_R$, a contradiction. It follows that $\lambda < 1$.

Suppose $\lambda < 1$. Then $d = m_R = \mathcal{G}(S^c, 1) = \mathcal{G}(\lambda, 1) < \mathcal{G}(1, 1)$, and so $\mathcal{G}(1, 1) > d$.

Next we show that if $\mathscr{G}(1,1) > d = m_R$, then there exists a unique one-species survival equilibrium. Since $S^c = \lambda$, by Lemma 3.6(ii), $\overline{S} = \lambda$, and so $\mathscr{G}(\lambda, R) = d$ for all $R \ge 0$. Therefore, by (3.28), a one-species survival equilibrium exists if and only if R satisfies

$$f(R) \equiv \xi(1-\lambda)\mathscr{R}(\lambda,R) = \eta(1-R)\mathscr{S}(\lambda,R) \equiv g(R).$$

By (3.4) and (3.5), f(R) is an increasing function and g(R) is a decreasing function on [0,1], with f(0) = 0, $f(1) = \xi(1-\lambda)\mathscr{R}(\lambda,1) > 0$, $g(0) = \eta d > 0$, and g(1) = 0. (See Figure 3e.) Hence, there exists a unique \overline{R} satisfying $f(\overline{R}) = g(\overline{R})$, and hence a unique one-species survival equilibrium, $(\lambda, \overline{R}, \overline{x})$, where $\overline{x} = \xi(1-\lambda)/\mathscr{R}(\lambda, \overline{R}) = \eta(1-\overline{R})/\mathscr{R}(\lambda, \overline{R})$. Finally, if a one-species survival equilibrium exists in this case, then by (ii)(a), $\lambda < 1$, and hence $\mathscr{G}(1,1) > d$.

(ii)(c) If $m_R < d$, then $S^c < \lambda$. Suppose $m_R < d$ and $\mathscr{G}(1,1) > d$. Since $M^S \leq 1$, and $M^S = 1$ implies that $\mathscr{G}(1,1) \leq d$, it follows that $M^S < 1$. Suppose $m_R < d$ and $M^S < 1$. Then $\mathscr{G}(1,1) > \mathscr{G}(M^S,1) = d$.

Next we show that if $m_R < d$ and $\mathscr{G}(1,1) > d$ (and hence $\lambda < M^S < 1$), then at least one one-species survival equilibrium exists. Define $x_S(S)$ and $x_R(S)$ as in (3.29) for $S \in (\lambda, M^S)$, where by Lemma 3.5, $\mathscr{G}(S, \varphi(S)) = d$ for all $S \in [\lambda, M^S]$. Then $\varphi(\lambda) = 0$, $\varphi(M^S) = 1$, and $0 < \varphi(S) < 1$ for all $S \in (\lambda, M^S)$, and so x_S and x_R are continuous for all $S \in (\lambda, M^S)$. Since (see Figure 3f)

$$x_{S}(\lambda) = \frac{\xi(1-\lambda)}{d} > 0$$
 and $x_{R}(\lambda) = \infty$,
 $x_{S}(M^{S}) = \frac{\xi(1-M^{S})}{\mathscr{P}(M^{S},1)} > 0$ and $x_{R}(M^{S}) = 0$,

there exists at least one point $\hat{S} \in (\lambda, M^S)$ such that $x_S(\hat{S}) = x_R(\hat{S})$. Hence, there exists at least one one-species survival equilibrium, $(\hat{S}, \varphi(\hat{S}), x_S(\hat{S}))$.

Remarks Concerning Theorem 3.7

(1) If $m_s < m_R$, an analogous result holds. Just interchange the roles of λ and μ , and those of m_s and m_R .

(2) If μ is finite, it is possible for $\lambda > 1$, $\mu > 1$, and $\mathscr{G}(1,1) > d$. For example, consider

$$\mathscr{G}(S,R) = \frac{4S+3R}{1+S+R}, \qquad d = \frac{13}{6}.$$

 $\mathscr{G}(1,0) = 2 < d$, and so $\lambda > 1$, $\mathscr{G}(0,1) = 3/2 < d$, and so $\mu > 1$, and $\mathscr{G}(1,1) = 7/3 > d$.

(3) If $\mu = \infty$ with $m_R < d$, then $\lambda < 1$ need not imply that $\mathscr{G}(1,1) > d$. Rather, it is possible that $M^S = 1$, and so $\mathscr{G}(1,1) \le d$. There may or may not be one-species survival equilibria in this case, and multiple one-species survival equilibria are possible. For example, consider

$$\mathscr{G}(S,R) = \frac{4S+R}{1+S+R}, \qquad d = \frac{11}{6}.$$

Then $m_R = 1 < d$, $\mathscr{G}(11/13,0) = d$, and so $\lambda = 11/13 < 1$, but $\mathscr{G}(1,1) = 5/3 < d$. For a one-species survival equilibrium $(\overline{S}, \overline{R}, \overline{x})$ to exist, by Lemma 3.6(ii), $\lambda < \overline{S} < 1$ and $0 < \varphi(\overline{S}) < 1$. Thus $\overline{S} \in (11/13, 1)$, and since $\varphi(S) = (13S - 11)/5$, $\varphi(\overline{S}) \in (0, 2/5)$. Also, since \overline{S} must satisfy $x_S(\overline{S}) = x_R(\overline{S})$, where $x_S(S)$ and $x_R(R)$ are given in (3.29),

$$\frac{\xi}{\eta} = \frac{4\overline{S}(16-13\overline{S})}{(1-\overline{S})(13\overline{S}-11)}.$$

Since $\overline{S} \in (11/13, 1)$, it follows that $\xi/\eta > 190.628$ must hold. Therefore, if $\xi/\eta < 190$, then there is no one-species survival equilibrium. However, if $\xi/\eta > 191$, then there is at least one one-species survival equilibrium. In particular, if $\xi = 1/2$ and $\eta = 1/384$, so that $\xi/\eta = 192$, then there are exactly two one-species survival equilibria:

$$\left(\frac{12}{13}, \frac{1}{5}, \frac{23}{1040}\right)$$
 and $\left(\frac{44}{47}, \frac{11}{47}, \frac{153}{8272}\right)$.

(4) Note that if $\mathscr{S}(S,R) = p(S)$ and $\mathscr{R}(S,R) = q(R)$ for all $S \ge 0$ and $R \ge 0$, then, regardless of the relative values of m_S , m_R , and d, a one-species survival equilibrium exists if and only if $\mathscr{S}(1,1) > d$, and if one exists then it is unique.

Let us denote a one-species survival equilibrium, when it exists, by $E = (\overline{S}, \overline{R}, \overline{x})$. Next we investigate the local stability properties of the equilibria of (3.27) through an examination of the linearized system about each equilibrium.

COMPETITION FOR SUBSTITUTABLE RESOURCES

The eigenvalues of $V_3(1,1,0)$, the variational matrix of (3.27) evaluated at $E_0 = (1,1,0)$, are $\alpha_1 = \alpha_2 = -1$ and $\alpha_3 = \mathcal{G}(1,1) - d$. Thus, if $\mathcal{G}(1,1) > d$, then E_0 is unstable, and by Theorem 3.7 at least one one-species survival equilibrium exists. Also, if $\mathcal{G}(1,1) < d$, then E_0 is locally asymptotically stable, and, provided that $m_R \ge d$ and $m_S \ge d$, no one-species survival equilibrium exists. In fact, by Theorem 3.4, E_0 is globally asymptotically stable in this case. However, if $m_R < d$ or $m_S < d$, it is possible for a one-species survival equilibrium to exist even though E_0 is locally asymptotically stable. For an example, see Remark 3 following Theorem 3.7.

Let us assume that the one-species survival equilibrium $E = (S, \overline{R}, \overline{x})$ exists, and examine the local stability properties of E. The characteristic equation of $V_3(\overline{S}, \overline{R}, \overline{x})$, the variational matrix evaluated at E, is given by $\alpha^3 + A_1 \alpha^2 + A_2 \alpha + A_3$, where

$$A_{1} = 2 + \bar{x} \left[\frac{1}{\xi} \frac{\partial}{\partial S} \mathscr{S}(\bar{S}, \bar{R}) + \frac{1}{\eta} \frac{\partial}{\partial R} \mathscr{R}(\bar{S}, \bar{R}) \right], \qquad (3.30a)$$

$$A_{2} = 1 + \bar{x} \left[\frac{1}{\xi} \frac{\partial}{\partial S} \mathscr{S}(\bar{S}, \bar{R}) + \frac{1}{\eta} \frac{\partial}{\partial R} \mathscr{R}(\bar{S}, \bar{R}) \right]$$

$$+ \bar{x} \left[\frac{1}{\xi} \mathscr{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial S} \mathscr{S}(\bar{S}, \bar{R}) + \frac{1}{\eta} \mathscr{R}(\bar{S}, \bar{R}) \frac{\partial}{\partial R} \mathscr{S}(\bar{S}, \bar{R}) \right] \qquad (3.30b)$$

$$+ \frac{\bar{x}^{2}}{\xi \eta} \left[\frac{\partial}{\partial S} \mathscr{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial R} (\bar{S}, \bar{R}) - \frac{\partial}{\partial R} \mathscr{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial S} \mathscr{R}(\bar{S}, \bar{R}) \right], \qquad (3.30b)$$

and

$$A_{3} = \bar{x} \left[\frac{1}{\xi} \mathscr{S}(\bar{S},\bar{R}) \frac{\partial}{\partial S} \mathscr{S}(\bar{S},\bar{R}) + \frac{1}{\eta} \mathscr{R}(\bar{S},\bar{R}) \frac{\partial}{\partial R} \mathscr{S}(\bar{S},\bar{R}) \right] + \frac{\bar{x}^{2}}{\xi \eta} d \left[\frac{\partial}{\partial S} \mathscr{S}(\bar{S},\bar{R}) \frac{\partial}{\partial R} \mathscr{R}(\bar{S},\bar{R}) - \frac{\partial}{\partial R} \mathscr{S}(\bar{S},\bar{R}) \frac{\partial}{\partial S} \mathscr{R}(\bar{S},\bar{R}) \right].$$
(3.30c)

If $m_R < d$ or $m_S < d$, the stability of E is, in general, difficult to determine. However, if $m_R \ge d$ and $m_S \ge d$, then by hypotheses (3.2), (3.4), (3.5), (3.11), and (3.12), it follows that

$$\frac{\partial}{\partial S}\mathscr{S}(\bar{S},\bar{R})\frac{\partial}{\partial R}\mathscr{R}(\bar{S},\bar{R}) - \frac{\partial}{\partial R}\mathscr{S}(\bar{S},\bar{R})\frac{\partial}{\partial S}\mathscr{R}(\bar{S},\bar{R}) > 0. \quad (3.31)$$

Hence, A_1 , A_2 , and A_3 are all positive so that, by the Routh-Hurwicz criterion, to determine the stability of E it suffices to determine the sign of $A_1A_2 - A_3$, where $A_1A_2 - A_3$ is given by

$$2+3\bar{x}\left[\frac{1}{\xi}\frac{\partial}{\partial S}\mathscr{S}(\bar{S},\bar{R})+\frac{1}{\eta}\frac{\partial}{\partial R}\mathscr{R}(\bar{S},\bar{R})\right]$$

$$+\bar{x}\left[\frac{1}{\xi}\mathscr{S}(\bar{S},\bar{R})\frac{\partial}{\partial S}\mathscr{S}(\bar{S},\bar{R})+\frac{1}{\eta}\mathscr{R}(\bar{S},\bar{R})\frac{\partial}{\partial R}\mathscr{S}(\bar{S},\bar{R})\right]$$

$$+\bar{x}^{2}\left[\frac{1}{\xi}\frac{\partial}{\partial S}\mathscr{S}(\bar{S},\bar{R})+\frac{1}{\eta}\frac{\partial}{\partial R}\mathscr{R}(\bar{S},\bar{R})\right]$$

$$\times\left[\frac{1}{\xi}\mathscr{S}(\bar{S},\bar{R})\frac{\partial}{\partial S}\mathscr{S}(\bar{S},\bar{R})+\frac{1}{\eta}\mathscr{R}(\bar{S},\bar{R})\frac{\partial}{\partial R}\mathscr{S}(\bar{S},\bar{R})\right]$$

$$+\bar{x}^{2}\left[\frac{1}{\xi}\frac{\partial}{\partial S}\mathscr{S}(\bar{S},\bar{R})+\frac{1}{\eta}\frac{\partial}{\partial R}\mathscr{R}(\bar{S},\bar{R})\right]^{2} \qquad (3.32)$$

$$+\left(\frac{\bar{x}^{3}}{\xi\eta}\right)\left[\left(\frac{1}{\xi}\right)\frac{\partial}{\partial S}\mathscr{S}(\bar{S},\bar{R})+\left(\frac{1}{\eta}\right)\frac{\partial}{\partial R}\mathscr{R}(\bar{S},\bar{R})\right]$$

$$\times\left[\frac{\partial}{\partial S}\mathscr{S}(\bar{S},\bar{R})\frac{\partial}{\partial R}\mathscr{R}(\bar{S},\bar{R})-\frac{\partial}{\partial R}\mathscr{S}(\bar{S},\bar{R})\frac{\partial}{\partial S}\mathscr{R}(\bar{S},\bar{R})\right]$$

$$+\frac{\bar{x}^{2}}{\xi\eta}(2-d)\left[\frac{\partial}{\partial S}\mathscr{S}(\bar{S},\bar{R})\frac{\partial}{\partial R}\mathscr{R}(\bar{S},\bar{R})-\frac{\partial}{\partial R}\mathscr{S}(\bar{S},\bar{R})\frac{\partial}{\partial S}\mathscr{R}(\bar{S},\bar{R})\right].$$

Assuming that $m_R \ge d$ and $m_S \ge d$, a superficial examination of this expression yields a range of values of the intrinsic death rate ε for which $A_1A_2 - A_3$ is positive and hence E is locally asymptotically stable. In particular, a sufficient condition for the local asymptotic stability of E is $d \le 2$ (so that $\varepsilon \le 1$). For example, if it is assumed that the intrinsic death rate is insignificant compared to the dilution rate, then d = 1, and so E is locally asymptotically stable. Moreover, if, by increasing d, E can lose its stability, it can do so only by means of a Hopf bifurcation, since $A_3 > 0$ implies that no root can equal zero. However, given $p(\alpha) = \alpha^3 + A_1\alpha^2 + A_2\alpha + A_3$ with A_1 , A_2 , and A_3 positive, if $A_1A_2 - A_3 < 0$, then p has one negative real root and a pair of complex conjugate roots with positive real part. Since, by Theorem 3.7, parts (i) and (ii)(b), E exists only if $\mathcal{G}(1,1) > d$, a Hopf bifurcation can occur only for $2 < d < \mathcal{G}(1,1)$. Therefore, if $m_s \ge d$, $m_R \ge d$, and $\mathscr{G}(1,1) \leq 2$, then no change in stability can occur. Although we have not ruled out the possibility of a Hopf bifurcation, this was not observed in any of the specific examples we studied.

If we assume that $\mathscr{S}(S, R) = p(S)$ and $\mathscr{R}(S, R) = q(R)$ for all $S \ge 0$ and $R \ge 0$, as in model I of León and Tumpson [17], as long as E exists, A_1 , A_2 , and A_3 are always positive, and $A_1A_2 - A_3$ is given by

$$2 + \bar{x} \left\{ 3 \left[\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right] + \frac{p(\bar{S})p'(\bar{S})}{\xi} + \frac{q(\bar{R})q'(\bar{R})}{\eta} \right\} + \bar{x}^2 \frac{2}{\xi \eta} p'(\bar{S})q'(\bar{R}) + \bar{x}^2 \left\{ \left[\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right]^2 + p(\bar{S}) \left[\frac{p'(\bar{S})}{\xi} \right]^2 + q(\bar{R}) \left[\frac{q'(\bar{R})}{\eta} \right]^2 \right\} + \bar{x}^3 \left[\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right] p'(\bar{S})q'(\bar{R}).$$
(3.33)

Clearly, $A_1A_2 - A_3$ is also always positive, regardless of the relative values of m_s , m_R , and d. Therefore, by the Routh-Hurwicz criterion, whenever E exists, it is locally asymptotically stable.

Before examining the global properties of system (3.27), we define the terms persistent and uniformly persistent, as in [9]. Let $f = (f_1, ..., f_n)$ be a continuously differentiable function from \mathbf{R}^n to \mathbf{R}^n such that

$$f_i(w) \ge 0$$
 whenever $w = (w_1, \dots, w_n)$ satisfies $w_i = 0$ and
 $w_j \ge 0, \quad i \ne j.$

Consider the system

$$w'(t) = f(w(t)), \quad w_i(0) \ge 0, \quad i = 1, ..., n.$$
 (3.34)

The conditions on f guarantee that (3.34) defines a dynamical system that leaves the positive cone in \mathbf{R}^n positively invariant.

DEFINITION 3.1

If every solution $w(t) = (w_1(t), \dots, w_n(t))$ of (3.34) with $w_i(0) > 0$, $i = 1, \dots, n$, satisfies $\liminf_{t \to \infty} w_i(t) > 0$, $i = 1, \dots, n$, then system (3.34) is persistent.

DEFINITION 3.2

If there exists a $\delta > 0$ such that every solution $w(t) = (w_1(t), \dots, w_n(t))$ of (3.34) with $w_i(0) > 0$, $i = 1, \dots, n$ satisfies $\liminf_{t \to \infty} w_i(t) \ge \delta$, $i = 1, \dots, n$, then system (3.34) is uniformly persistent.

THEOREM 3.8

Suppose $\mathscr{G}(1,1) > d$. Then system (3.27) is uniformly persistent with respect to all solutions for which x(0) > 0.

Proof. Identify (S, R, x)-space with \mathbf{R}^3_+ . Choose $\underline{X} = (S(0), R(0), x(0)) \in \mathbf{R}^3_+$. By Theorem 3.2(i), $\Omega(\underline{X})$ is a nonempty, compact invariant set with respect to (3.27), and x(t) > 0 and bounded. Thus, by (3.3) and (3.6), S'(t) > 0 if S(t) is sufficiently close to zero and R'(t) > 0 if R(t) is sufficiently close to zero and R(t) are also bounded by Theorem 3.2(i), it follows that any point in $\Omega(\underline{X})$ must satisfy lim $\inf_{t \to \infty} S(t) > 0$ and $\liminf_{t \to \infty} R(t) > 0$. If we can show that $\liminf_{t \to \infty} x(t) > 0$, then (3.27) is persistent.

Suppose $\{E_0\} \in \Omega(\underline{X})$. Since $\mathscr{G}(1,1) > d$, E_0 is an unstable, hyperbolic critical point. From (3.27) it is clear that E_0 is globally attracting with respect to solutions initiating in its stable manifold M^+ $(E_0) = \{(S, R, 0) \in \mathbb{R}^3_+\}$. Since $\underline{X} \notin M^+(E_0), \{E_0\} \neq \Omega(\underline{X})$. Therefore, by the Butler-McGehee lemma (see Lemma A1 of [9]), there exists $P \in (M^+(E_0) \setminus \{E_0\}) \cap \Omega(\underline{X})$ and hence $\operatorname{cl} \mathscr{O}(P) \subset \Omega(\underline{X})$, where $\mathscr{O}(P)$ denotes the entire orbit through P and $\operatorname{cl} \mathscr{O}(P)$ denotes the closure of $\mathscr{O}(P)$. But then, as $t \to -\infty$, either $\mathscr{O}(P)$ becomes unbounded or one of the S or R components becomes negative. In either case we have a contradiction, and therefore $\{E_0\} \notin \Omega(\underline{X})$.

Suppose $\liminf_{t \to \infty} x(t) = 0$. Then there exists a point $\tilde{P} = (\underline{S}, \underline{R}, 0) \in \Omega(\underline{X})$, which implies that $\operatorname{cl} \mathscr{O}(\tilde{P}) \subset \Omega(\underline{X})$. But then $\{E_0\} \in \Omega(\underline{X})$, a contradiction. Thus $\liminf_{t \to \infty} x(t) > 0$, and so (3.27) is persistent. It now follows from the main result of [7] that system (3.27) is uniformly persistent.

If in (3.27) the intrinsic death rate is assumed to be insignificant compared to the dilution rate, so that d = 1, and $m_s \ge 1$ and $m_R \ge 1$, then the results of Theorem 3.8 can be significantly strengthened.

THEOREM 3.9

Assume d = 1 *in* (3.27).

(i) Suppose that $m_s \ge 1$ and $m_R \ge 1$. If $\mathscr{G}(1,1) > 1$, then there exists a unique one-species survival equilibrium E, and E is globally asymptotically stable with respect to all solutions for which $S(0) \ge 0$, $R(0) \ge 0$, and x(0) > 0.

(ii) If no one-species survival equilibrium E exists, then E_0 is globally asymptotically stable with respect to all solutions for which $S(0) \ge 0$, $R(0) \ge 0$, and $x(0) \ge 0$.

Proof. (i) The existence and uniqueness of the one-species survival equilibrium E is given by Theorem 3.7, parts (i) and (ii)(b).

Define $z(t) = \xi S(t) + \eta R(t) + x(t)$. Then, since d = 1, $z'(t) = (\xi + \eta) - z(t)$, so that $z(t) = [z(0) - (\xi + \eta)]e^{-t} + (\xi + \eta)$. Therefore, the simplex $\mathscr{L} = \{(S, R, x): S, R, x \ge 0; \xi S + \eta R + x = \xi + \eta\}$ is a global attractor, and so we restrict our attention to \mathscr{L} . Since \mathscr{L} is positively invariant, let $x(t) = \xi(1 - S(t)) + \eta(1 - R(t))$, and consider the system

$$S'(t) = 1 - S(t) - \frac{1}{\xi} \left[\xi(1 - S(t)) + \eta(1 - R(t)) \right] \mathscr{S}(S(t), R(t)),$$
(3.35a)

$$R'(t) = 1 - R(t) - \frac{1}{\eta} \left[\xi(1 - S(t)) + \eta(1 - R(t)) \right] \mathscr{R}(S(t), R(t)),$$
(3.35b)

 $S(0) \ge 0,$ $R(0) \ge 0,$ $\xi + \eta \ge \xi S(0) + \eta R(0).$

From the local stability analysis it follows that the equilibrium $\overline{E} = (\overline{S}, \overline{R})$ of (3.35) is locally asymptotically stable and that $\overline{E}_0 = (1, 1)$ is unstable.

Fix S(t) = 1 in (3.35) and define

$$F_1(R(t)) \equiv S'(t) = -\frac{\eta}{\xi} [1 - R(t)] \mathscr{S}(1, R(t)).$$

Then $F_1(1) = 0$, and by (2.2) and (3.5),

$$\frac{d}{dR}F_1(R) = -\frac{\eta}{\xi}(1-R)\frac{\partial}{\partial R}\mathscr{S}(1,R) + \frac{\eta}{\xi}\mathscr{S}(1,R) > 0$$

for all $0 \le R \le 1$. Therefore, S'(t) < 0 at all points (1, R) where $0 \le R < 1$. Fix $S(t) = \overline{S}$ in (3.35), and define

$$F_2(R(t)) \equiv S'(t) = 1 - \overline{S} - \frac{1}{\xi} \left[\xi(1 - \overline{S}) + \eta(1 - R(t)) \right] \mathscr{S}(\overline{S}, R(t)).$$

Then $F_2(\vec{R}) = 0$, and by (2.2) and (3.5),

$$\frac{d}{dR}F_2(R) = -\frac{1}{\xi} \left[\xi(1-\overline{S}) + \eta(1-R) \right] \frac{\partial}{\partial R} \mathscr{S}(\overline{S},R) + \frac{\eta}{\xi} \mathscr{S}(\overline{S},R) > 0$$

for all $0 \le R \le 1$. Therefore, S'(t) < 0 at all points (\overline{S}, R) where $0 \le R < \overline{R}$, and S'(t) > 0 at all points (\overline{S}, R) where $\overline{R} < R \le 1$.

Similarly, fixing R(t) = 1 and $R(t) = \overline{R}$, we obtain the partial vector field shown in Figure 4. It is clear that no periodic orbits exist in \mathcal{L} , and so $\overline{E} = (\overline{S}, \overline{R})$ is globally asymptotically stable for (3.35) with respect to all solutions for which $S(0) \ge 0$, $R(0) \ge 0$, and $\xi + \eta > \xi S(0) + \eta R(0) > 0$ [i.e., $x(0) \equiv \xi + \eta - \xi S(0) - \eta R(0) > 0$].

First recall that the omega limit set of any solution of system (3.27) is contained in \mathscr{L} , and note that by Theorem 3.8, system (3.27) is uniformly persistent and so there is no point of the form $(S, R, 0) \in \mathbb{R}^3_+$ in the omega limit set of any solution of system (3.27) with $S(0) \ge 0$, $R(0) \ge 0$, x(0) > 0. Since $\overline{E} = (\overline{S}, \overline{R})$ corresponds to $E = (\overline{S}, \overline{R}, \overline{x})$, the global stability of \overline{E} implies that E is in omega limit set of any solution of system (3.27) with $S(0) \ge 0$, $R(0) \ge 0$, x(0) > 0. Since E is locally asymptotically stable for (3.27) with d = 1, it follows that it is the only point in the omega limit set, and so it must be globally asymptotically stable for (3.27) with d = 1 with respect to all solutions satisfying $S(0) \ge 0$, $R(0) \ge 0$, and x(0) > 0.

(ii) The proof is similar to the proof of (i).



FIG. 4. Partial vector field for Theorem 3.9. Vectors parallel to the S axis indicate the sign of S'(t) along the indicated line. Vectors parallel to the R axis indicate the sign of R'(t) along the indicated line.

If in (3.27) $\mathscr{S}(S,R) = p(S)$ and $\mathscr{R}(S,R) = q(R)$ as in model I of León and Tumpson [17] (with d not necessarily equal to 1), then the results of Theorem 3.8 can again be significantly strengthened, regardless of the relative values of m_S , m_R , and d.

THEOREM 3.10

Assume that $\mathcal{S}(S,R) = p(S)$ and $\mathcal{R}(S,R) = q(R)$ for all $S \ge 0$ and $R \ge 0$.

(i) If $\mathscr{G}(1,1) \leq d$, then E_0 is globally asymptotically stable for (3.27) with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$, and $x(0) \geq 0$.

(ii) If $\mathscr{G}(1,1) > d$, then there exists a unique one-species survival equilibrium *E*, and *E* is globally asymptotically stable for (3.27) with respect to all solutions for which $S(0) \ge 0$, $R(0) \ge 0$, and x(0) > 0.

Proof. (ii) The proof of existence and uniqueness of the one-species survival equilibrium E is similar to the proof of part (i) of Theorem 3.7. To prove the global stability of this equilibrium, define $L: \mathring{\mathbf{R}}^3_+ \to \mathbf{R}$ by

$$L(S,R,x) = \xi \int_{\overline{S}}^{S} \frac{-p(\overline{S}) + p(\tau)}{p(\tau)} d\tau + \eta \int_{\overline{R}}^{R} \frac{-q(\overline{R}) + q(\tau)}{q(\tau)} d\tau + x - \overline{x} - \overline{x} \ln\left(\frac{x}{\overline{x}}\right).$$

Since p(S) and q(R) are continuous on $\mathring{\mathbf{R}}_{+}^{3}$, we have $L \in C^{1}(\mathring{\mathbf{R}}_{+}^{3})$. Also, $E = (\overline{S}, \overline{R}, \overline{x})$ is the global minimum of L on \mathbf{R}_{+}^{3} , and $L(\overline{S}, \overline{R}, \overline{x}) = 0$. The time derivative of L computed along solutions of (3.27) is

$$\dot{L}(S,R,x) = \xi \left(\frac{p(S) - p(\bar{S})}{p(S)} \right) (1 - S) + \eta \left(\frac{q(R) - q(\bar{R})}{q(R)} \right) (1 - R)$$
$$- \bar{x} [-d + \mathcal{G}(S,R)]$$
$$+ x \left\{ -d + \mathcal{G}(S,R) - \left[p(S) - p(\bar{S}) \right] - \left[q(R) - q(\bar{R}) \right] \right\}$$

Noting that $\bar{x} = \xi(1-\bar{S})/p(\bar{S}) = \eta(1-\bar{R})/q(\bar{R})$ and $d = p(\bar{S}) + q(\bar{R})$, we have

$$\dot{L}(S,R,x) = \xi \left(p(S) - p(\overline{S}) \right) \left(\frac{1-S}{p(S)} - \frac{1-\overline{S}}{p(\overline{S})} \right) + \eta \left(q(R) - q(\overline{R}) \right) \left(\frac{1-R}{q(R)} - \frac{1-\overline{R}}{q(\overline{R})} \right).$$

For $0 < S < \overline{S}$, $p(S) - p(\overline{S}) < 0$ and $(1 - S)/p(S) - (1 - \overline{S})/p(\overline{S}) > 0$, whereas for $S > \overline{S}$, $p(S) - p(\overline{S}) > 0$ and $(1 - S)/p(S) - (1 - \overline{S})/p(\overline{S}) < 0$. A similar result holds for *R*.

Thus, $\dot{L}(S, R, x) \leq 0$, and so L is a Lyapunov function for (3.27) in $\mathring{\mathbf{R}}^3_+$. Note that $\dot{L}(S, R, x) = 0$ if and only if $S = \overline{S}$ and $R = \overline{R}$. Hence, by Theorem 3.2(i) and LaSalle's extension theorem [16], every solution of (3.27) for which x(0) > 0 approaches \mathscr{M} , where \mathscr{M} is the largest invariant subset of $\{(S, R, x) \in \mathbb{R}^3_+ : S = \overline{S}, R = \overline{R}, x \ge 0\}$. But then $\mathscr{M} = \{E\}$, a single point, since by Theorem 3.7 the one-species survival equilibrium is unique, and since $x \neq \overline{x}$ implies that either $S' \neq 0$ or $R' \neq 0$, $x \neq \overline{x}$ would violate the invariance of \mathscr{M} . This completes the proof.

(i) Take

$$L(S,R,x) = \xi \int_{1}^{S} \frac{-p(1)+p(\tau)}{p(\tau)} d\tau + \eta \int_{1}^{R} \frac{-q(1)+q(\tau)}{q(\tau)} d\tau + x,$$

and argue as in (ii).

In the next section we use the information from this section to determine existence and local stability properties of the equilibria of the four-dimensional system as well as to determine criteria for uniform persistence of the four-dimensional system.

3.3. TWO-SPECIES COMPETITION—THE FOUR-DIMENSIONAL SYSTEM

We now return to a study of the full four-dimensional system; that is,

$$S'(t) = 1 - S(t) - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i} \mathscr{S}_i(S(t), R(t)), \qquad (3.36a)$$

$$R'(t) = 1 - R(t) - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} \mathscr{R}_i(S(t), R(t)), \qquad (3.36b)$$

$$x'_{i}(t) = x_{i}(t) [-D_{i} + \mathscr{G}_{i}(S(t), R(t))], \quad i = 1, 2, \quad (3.36c)$$

$$S(0) \ge 0,$$
 $R(0) \ge 0,$ $x_i(0) \ge 0,$ $i = 1, 2.$

Three of the critical points of (3.36) are readily determined and will be denoted

$$E_0 = (1, 1, 0, 0), \qquad E_1 = (\overline{S}_1, \overline{R}_1, \overline{x}_1, 0), \qquad E_2 = (\overline{S}_2, \overline{R}_2, 0, \overline{x}_2).$$

Conditions for the existence, and in some cases the uniqueness, of

equilibria of the form E_i , i = 1, 2, are given in Theorem 3.7 (with the appropriate subscripts included and d replaced by D_i).

We first determine the local stability properties of these equilibria of (3.36) through an examination of the linearized system about each equilibrium point.

The eigenvalues of $V_4(1,1,0,0)$, the variational matrix of (3.36) evaluated at $E_0 = (1,1,0,0)$, are $\alpha_1 = \alpha_2 = -1$, $\alpha_3 = \mathscr{G}_1(1,1) - D_1$, and $\alpha_4 = \mathscr{G}_2(1,1) - D_2$. Thus, if either $\mathscr{G}_1(1,1) > D_1$ or $\mathscr{G}_2(1,1) > D_2$, then E_0 is unstable, and by Theorem 3.7 at least one one-species equilibrium exists. Also, if $\mathscr{G}_1(1,1) < D_1$ and $\mathscr{G}_2(1,1) < D_2$, then E_0 is locally asymptotically stable and, provided that $m_{S_i} > D_i$ and $m_{R_i} > D_i$ for i = 1 and 2, no one-species equilibrium exists. In fact, by Theorem 3.4, E_0 is globally asymptotically stable in this case.

Now assume that $\mathscr{G}_1(1,1) > D_1$, so that $E_1 = (\overline{S}_1, \overline{R}_1, \overline{x}_1, 0)$ exists. The characteristic polynomial of $V_4(\overline{S}_1, \overline{R}_1, \overline{x}_1, 0)$, the variational matrix of (3.36) evaluated at E_1 , is given by

$$\left\{\alpha - \left[\mathscr{G}_{2}\left(\overline{S}_{1}, \overline{R}_{1}\right) - D_{2}\right]\right\}\left(\alpha^{3} + A_{1}\alpha^{2} + A_{2}\alpha + A_{3}\right),\right\}$$

where $\alpha^3 + A_1 \alpha^2 + A_2 \alpha + A_3$ is the characteristic polynomial of $V_3(\overline{S}_1, \overline{R}_1, \overline{x}_1)$ given in (3.30) with $\mathscr{P}(S, R) = \mathscr{P}_1(S, R)$, $\mathscr{R}(S, R) = \mathscr{P}_1(S, R)$, $\mathscr{P}(S, R) = \mathscr{P}_1(S, R)$, $\mathscr{P}(S, R) = \mathscr{P}_1(S, R)$, and $d = D_1$. From this, together with a local stability analysis of the one-species equilibrium in (S, R, x_1) -space, we see that if $m_{S_1} \ge D_1$, $m_{R_1} \ge D_1$, $\mathscr{P}_1(1, 1) \le 2$, and $\mathscr{P}_2(\overline{S}_1, \overline{R}_1) < D_2$, then E_1 is locally asymptotically stable.

In the special case that $\mathscr{S}_1(S, R) = p_1(S)$ and $\mathscr{R}_1(S, R) = q_1(R)$ for all $S \ge 0$ and $R \ge 0$, E_1 exists if and only if $\mathscr{S}_1(1,1) > D_1$ and is locally asymptotically stable if $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) < D_2$. A similar result holds for E_2 .

If any other equilibria of (3.36) exist, they must be interior equilibria. An interior equilibrium of (3.36) is a solution $E^* = (S^*, R^*, x_1^*, x_2^*)$ of the system

$$\begin{cases} \mathscr{G}_1(S,R) = D_1, \\ \mathscr{G}_2(S,R) = D_2; \end{cases}$$
(3.37a)

$$\begin{cases} (x_1 / \xi_1) \mathscr{S}_1(S, R) + (x_2 / \xi_2) \mathscr{S}_2(S, R) = 1 - S, \\ (x_1 / \eta_1) \mathscr{R}_1(S, R) + (x_2 / \eta_2) \mathscr{R}_2(S, R) = 1 - R; \end{cases} (3.37b)$$

with $(S^*, R^*, x_1^*, x_2^*) \in \mathring{\mathbf{R}}_+^4$. As in Lemma 3.6, one can show that S^* and R^* must satisfy the inequalities of Table 1. The following theorem is an immediate consequence of Theorem 3.4(ii).

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Equilibrium
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TABLE 1

$m_{S_i \ge m_{R_i}}, m_{S_i \ge 1,2}$	$m_{R_1} > D_1$	$m_{R_1} = D_1$	$m_{R_1} < D_1$
$m_{R_2} > D_2$	$0 < S^* < \min\{1, \lambda_1, \lambda_2\}, \\ 0 < R^* < \min\{1, \mu_1, \mu_2\}$	$\lambda_1 = S^* < \min\{1, \lambda_2\},\ 0 < R^* < \min\{1, u_*\}$	$\lambda_1 < S^* < \min\{\lambda_2, M_1^S\}, \\ 0 < R^* < \min\{\omega, M_2^S\}, \dots\}$
$m_{R_2} = D_2$	$\lambda_2 = S^* < \min\{1, \lambda_1\}, 0 < R^* < \min\{1, u_r\}$	$\lambda_1 = \lambda_2 = S^* < 1,$ $0 < R^* < 1$	$\lambda_1 < \lambda_2 = S^* < M_1^S$ $0 < R^* < \omega_1(M_2^S)$
$m_{R_2} < D_2$	$\begin{split} \lambda_2 < S^* < \min\{\lambda_1, M_2^S\}, \\ 0 < R^* < \min\{\varphi_2(M_2^S), \mu_1\} \end{split}$	$\lambda_2 < \lambda_1 = S^* < M_2^S,$ $0 < R^* < \varphi_2(M_2^S)$	$\max\{\lambda_1, \lambda_2\} < S^* < \min\{M_1^S, M_2^S\}, \\ 0 < R^* < \min\{\varphi_1(M_1^S), \varphi_2(M_2^S)\}$
$m_{S_1} \ge m_{R_1}, m_{S_2} < m_{R_2}$	$m_{R_1} > D_1$	$m_{R_1} = D_1$	$m_{R_1} < D_1$
$m_{S_2} > D_2$	$0 < S^* < \min\{1, \lambda_1, \lambda_2\}, \\ 0 < R^* < \min\{1, u_1, u_2\}$	$\lambda_1 = S^* < \min\{1, \lambda_2\},\ 0 < R^* < \min\{1, \mu_2\}$	$\lambda_1 < S^* < \min\{\lambda_2, M_1^S\}, 0 < R^* < \min\{\alpha_2, M_2^S\}, \dots$
$m_{S_2} = D_2$	$0 < S^* < \min\{1, \lambda_1\}, \\ u_2 = R^* < \min\{1, u_1\}$	$\lambda_1 = S^* < 1,$ $\mu_2 = R^* < 1$	$\lambda_1 < S^* < M_1^S,$ $\mu_2 = R^* < \omega_1(M_2^S)$
$m_{S_2} < D_2$	$0 \le S^* < \min\{\sigma_2^*(M_2^R), \lambda_1\}, \\ \mu_2 < R^* < \min\{\mu_1, M_2^R\}$	$\lambda_1 = S^* < \sigma_2(M_2^R),$ $\mu_2 < R^* < M_2^R$	$\lambda_1 < S^* < \min\{M_1^S, \sigma_2(M_7^R)\}, \mu_2 < R^* < \min\{\phi_1(M_1^S), M_2^R\}$
^a If $m_{R_i} > m_{S_i}$ in the first poi table.	for $i = 1$ and 2, replace λ_i by <i>i</i> trion of the table. If $m_{S_1} < m_R$	μ_i, S^* by R^*, M_i^S by M_i^H , and $m_{S_2} \ge m_{R_2}$, replace	°, $\varphi_i(M_i^S)$ by $\varphi_i(M_i^R)$, and vice versa, e 1 by 2 in the second portion of the

THEOREM 3.11

If $\lambda_i = \infty$, $\mu_i \ge 1$ or $\mu_i = \infty$, $\lambda_i \ge 1$ for at least one $i \in \{1, 2\}$, then no interior equilibrium E^* exists.

THEOREM 3.12

(i) If E^* exists and, for i = 1 or 2, $m_{S_i} \ge D_i$ and $m_{R_i} \ge D_i$, then E_i exists and is unique.

(ii) If E^* exists and, for i = 1 or 2, $m_{R_i} < D_i$, $M_i^S < 1$ or $m_{S_i} < D_i$, $M_i^R < 1$, then at least one E_i exists.

Proof. (i) Suppose $m_{S_i} \ge m_{R_i}$. If $m_{R_i} > D_i$, then $0 < S^* < \min\{1, \lambda_i\} < S_i^c$ and $0 < R^* < \min\{1, \mu_i\}$. By (3.11) and (3.12), $D_i = \mathscr{G}_i(S^*, R^*) < \mathscr{G}_i(1, 1)$. Therefore, by Theorem 3.7, part (i), E_i exists and is unique. If $m_{R_i} = D_i$, then $S_i^c = \lambda_i = S^* < 1$ and $0 < R^* < 1$, so that $D_i = \mathscr{G}_i(S^*, R^*) = \mathscr{G}_i(S^*, 1) < \mathscr{G}_i(1, 1)$. Therefore, by Theorem 3.7, part (ii)(b) E_i exists and is unique. The argument is similar when $m_{R_i} \ge m_{S_i} \ge D_i$.

(ii) Suppose $m_{R_i} < D_i$. Since E^* exists, $\lambda_i < 1$ and so $D_i < m_{S_i}$. From Table 1, $\lambda_i < S^* < M_i^S$ and $0 < R^* < \varphi_i(M_i^S)$. If $M_i^S < 1$, then $\varphi_i(M_i^S) = 1$, and by (3.11) $D_i = \mathcal{G}_i(S^*, R^*) = \mathcal{G}_i(M_i^S, 1) < \mathcal{G}_i(1, 1)$. Therefore, by Theorem 3.7(ii)(c), at least one E_i exists. The argument is similar when $m_{S_i} < D_i$ and $M_i^R < 1$.

Remark Concerning Theorem 3.12. As Theorem 3.12(ii) would indicate, the cases $m_{R_i} < D_i$, $M_i^S = 1$ and $m_{S_i} < D_i$, $M_i^R = 1$ are special. In these cases, it is, in fact, possible to construct examples in which one species cannot survive in the absence of competition and yet a locally asymptotically stable coexistence equilibrium exists when a competitor population is present. We now describe one such example.

In this example, population x_1 cannot survive in the absence of competition, but population x_2 can. If we take

$$\mathscr{G}_1(S,R) = \frac{(9/4)S + (1/2)R}{1+S+R}$$
 and $D_1 = 1$,

then (as in the example described in Remark 3 concerning Theorem 3.7), provided that $\xi_1 / \eta_1 < 119$, no equilibrium of the form E_1 exists. By Theorem 3.9(ii), E_0 is globally asymptotically stable with respect to (S, R, x_1) -space, and so species x_1 cannot survive in the absence of competition. If we take

$$\mathscr{G}_2(S,R) = \frac{3S+3R}{1+S+R}$$
 and $D_2 = \frac{3}{2}$,

then $\mathscr{G}_2(1,1) = 2 > D_2$, and hence by Theorem 3.7(i), a unique equilibrium of the form E_2 exists. Moreover, E_2 is locally asymptotically stable with respect to (S, R, x_2) -space and is unstable with respect to (S, R, x_1, x_2) -space. In this case, a coexistence equilibrium, E^* , exists if and only if $S^* = 6/7$, $R^* = 1/7$, and

$$x_1^* = \frac{4\xi_1\eta_1(\xi_2 - 36\eta_2)}{3(9\xi_2\eta_1 - 2\xi_1\eta_2)} > 0, \qquad x_2^* = \frac{2\xi_2\eta_2(162\eta_1 - \xi_1)}{9(9\xi_2\eta_1 - 2\xi_1\eta_2)} > 0.$$

Assuming that $\xi_1/\eta_1 < 119$, then $x_1^* > 0$ and $x_2^* > 0$ if and only if $\xi_2/\eta_2 > 36$. If we wish to assume as well that $\xi_1/\eta_1 = \xi_2/\eta_2$, then this condition becomes $36 < \xi_1/\eta_1 = \xi_2/\eta_2 < 119$. In any case, it can also be shown (using a standard linear analysis involving the Routh-Hurwicz criterion) that whenever E^* lies in the positive cone, it is locally asymptotically stable.

To investigate under what conditions E^* exists in general, we begin with an examination of system (3.37b). Note that for fixed values of S and R, a solution of (3.37b) with both x_1 and x_2 positive is required. Define

$$\Delta(S,R) = \left(\frac{\mathscr{S}_1(S,R)}{\xi_1}\right) \left(\frac{\mathscr{R}_2(S,R)}{\eta_2}\right) - \left(\frac{\mathscr{S}_2(S,R)}{\xi_2}\right) \left(\frac{\mathscr{R}_1(S,R)}{\eta_1}\right)$$
(3.38)

for $(S, R) \in \mathbf{R}^2_+$. It follows from (3.37b) and Cramer's rule that

$$x_{1} = \frac{(1/\eta_{2})\mathscr{R}_{2}(S,R)(1-S) - (1/\xi_{2})\mathscr{S}_{2}(S,R)(1-R)}{\bigtriangleup(S,R)},$$

$$x_{2} = \frac{(1/\xi_{1})\mathscr{S}_{1}(S,R)(1-R) - (1/\eta_{1})\mathscr{R}_{1}(S,R)(1-S)}{\bigtriangleup(S,R)},$$
(3.39)

provided $\triangle(S, R) \neq 0$. The following lemma is a direct consequence of (3.38) and (3.39).

LEMMA 3.13

Let (x_1^*, x_2^*) be a solution of (3.37b) for fixed S, R satisfying 0 < S < 1and 0 < R < 1. Then $x_1^* > 0$ and $x_2^* > 0$ if and only if the numerators of x_1^* and x_2^* as given in (3.39) are nonzero and of the same sign.

For the remainder of this section we study the existence and stability of E^* . As in the one-species growth model, it is difficult to determine criteria in the case that $m_{R_i} < D_i$ or $m_{S_i} < D_i$, i = 1 or 2. In what follows we assume that $m_{R_i} \ge D_i$ and $m_{S_i} \ge D_i$ for i = 1 and 2.

Using Lemma 3.13 we are now able to provide a characterization of the solutions (S^*, R^*) of equations (3.37a) that yield an interior equilibrium.

THEOREM 3.14

(i) Suppose $(m_{R_i} \ge m_{S_i} \ge D_i, i = 1 \text{ and } 2)$, or $(m_{S_2} \ge m_{R_2} > D_2 \text{ and } m_{R_1} \ge m_{S_1} \ge D_1)$, or $(m_{R_2} > m_{S_2} = D_2 \text{ and } m_{S_1} \ge m_{R_1} \ge D_1)$. Suppose further that there exists a solution (S^*, R^*) of (3.37a) and that E_i exists, i = 1 and 2, with $\overline{S}_1 \ne \overline{S}_2$. If λ_i is finite and $\varphi_i(0) > 1$, then let \hat{S}_i be the unique solution of the equation $\varphi_i(S) = 1$; otherwise, take $\hat{S}_i = 0$. Take $i, j \in \{1, 2\}, i \ne j$. For $\overline{S}_i < \overline{S}_j$, define

$$I_{ij} = \left[\overline{S}_i, \min\{1, \lambda_i\}\right] \cap \left[\hat{S}_j, \overline{S}_j\right].$$

Then the corresponding solution (x_1^*, x_2^*) of (3.37b) satisfies $x_1^* > 0$ and $x_2^* > 0$ if and only if $S^* \in I_{ii}$.

(ii) Suppose $(m_{S_i} \ge m_{R_i} \ge D_i, i = 1 \text{ and } 2)$, or $(m_{R_2} \ge m_{S_2} > D_2 \text{ and } m_{S_1} \ge m_{R_1} \ge D_1)$, or $(m_{S_2} \ge m_{R_2} = D_2 \text{ and } m_{R_1} \ge m_{S_1} \ge D_1)$. Suppose further that there exists a solution (S^*, R^*) of (3.37a) and that E_i exists, i = 1 and 2, with $\overline{R}_1 \ne \overline{R}_2$. If μ_i is finite and $\sigma_i(0) > 1$, then let \hat{R}_i be the unique solution of the equation $\sigma_i(R) = 1$; otherwise, take $\hat{R}_i = 0$. Take $i, j \in \{1, 2\}, i \ne j$. For $\overline{R}_i < \overline{R}_j$ define

$$I_{ij} = \left[\overline{R}_i, \min\{1, \mu_i\}\right] \cap \left[\hat{R}_j, \overline{R}_j\right].$$

Then the corresponding solution (x_1^*, x_2^*) of (3.37b) satisfies $x_1^* > 0$ and $x_2^* > 0$ if and only if $R^* \in I_{ij}^{\circ}$.

(iii) Take $i, j \in \{1, 2\}, i \neq j$. Suppose $m_{S_i} > m_{R_i} = D_i$ and $m_{R_j} > m_{S_j} = D_j$. Suppose further that there exists a solution (S^*, R^*) of (3.37a). Then the corresponding solution (x_1^*, x_2^*) of (3.37b) satisfies $x_1^* > 0$ and $x_2^* > 0$ if and only if $(\lambda_i < \overline{S_i}$ and $\mu_i < \overline{R_i})$ or $(\overline{S_i} < \lambda_i$ and $\overline{R_i} < \mu_i)$.

Proof. (i) Note that by Theorem 3.12(i), there is no loss of generality in assuming the existence of E_1 and E_2 . Suppose first that λ_i and μ_i are all finite, i = 1 and 2. Define

$$\mathcal{N}x_{1}(S) = \frac{\mathscr{R}_{2}(S,\varphi_{2}(S))}{\eta_{2}}(1-S) - \frac{\mathscr{P}_{2}(S,\varphi_{2}(S))}{\xi_{2}} [1-\varphi_{2}(S)], \\ 0 \le S \le \lambda_{2}, \\ \mathcal{N}x_{2}(S) = \frac{\mathscr{P}_{1}(S,\varphi_{1}(S))}{\xi_{1}} [1-\varphi_{1}(S)] - \frac{\mathscr{R}_{1}(S,\varphi_{1}(S))}{\eta_{1}} (1-S), \\ 0 \le S \le \lambda_{1}. \end{cases}$$

Then $\mathscr{N}x_i(S)$ is the numerator of x_i as given in (3.39) with R replaced by $\varphi_j(S)$, where i, j = 1, 2 and $i \neq j$. By Lemma 3.5(i) and hypotheses (3.4) and (3.5), $\mathscr{N}x_1(S)$ is a decreasing function of S and $\mathscr{N}x_2(S)$ is an increasing function of S provided $S \leq 1$ and $\varphi_i(S) \leq 1$, i = 1, 2.

Recall that at $E_2 = (\overline{S}_2, \overline{R}_2, 0, \overline{x}_2), \quad 0 < \overline{S}_2 < \min\{1, \lambda_2\}, \quad 0 < \overline{R}_2 < \min\{1, \mu_2\}, \text{ and}$

$$\bar{x}_2 = \frac{\xi_2(1-\bar{S}_2)}{\mathscr{S}_2(\bar{S}_2,\varphi_2(\bar{S}_2))} = \frac{\eta_2(1-\varphi_2(\bar{S}_2))}{\mathscr{R}_2(\bar{S}_2,\varphi_2(\bar{S}_2))}$$

Therefore,

$$\mathscr{N}x_1(\overline{S}_2) = \frac{\mathscr{R}_2(\overline{S}_2, \varphi_2(\overline{S}_2))}{\eta_2} (1 - \overline{S}_2) - \frac{\mathscr{S}_2(\overline{S}_2, \varphi_2(\overline{S}_2))}{\xi_2} [1 - \varphi_2(\overline{S}_2)] = 0.$$

Similarly, $\mathcal{N}x_2(\overline{S}_1) = 0$.

Note that $\hat{S}_i \in [0, \overline{S}_i)$, since $0 < \varphi_i(\overline{S}_i) = \overline{R}_i < \min\{1, \mu_i\}$ and $0 \le \varphi_i(S) \le 1$ for all $S \in [\hat{S}_i, \lambda_i]$.

If $\overline{S}_1 < \overline{S}_2$, then $\varphi_1(S) < 1$ for all $S \in [\overline{S}_1, \min\{1, \lambda_1\}]$ and $\varphi_2(S) \le 1$ for all $S \in [\widehat{S}_2, \min\{1, \lambda_2\}]$. Therefore, $\mathscr{N}x_1(S)$ and $\mathscr{N}x_2(S)$ are both positive for all $S \in \mathring{I}_{12}$.

If $\overline{S}_2 < \overline{S}_1$, then $\varphi_2(S) < 1$ for all $S \in [\overline{S}_2, \min\{1, \lambda_2\}]$ and $\varphi_1(S) \leq 1$ for all $S \in [\hat{S}_1, \min\{1, \lambda_1\}]$. Therefore, $\mathscr{N}x_1(S)$ and $\mathscr{N}x_2(S)$ are both negative for all $S \in I_{21}$. Combining this with Lemma 3.13, the result follows.

For the other cases, define $\mathscr{N}x_1(S)$ as follows. In the numerator of x_1 as given in (3.39), if λ_2 is finite, then define $\mathscr{N}x_1$ as above; otherwise take

$$\mathscr{N}x_1(S) = \frac{\mathscr{R}_2(S,\mu_2)}{\eta_2}(1-S) - \frac{\mathscr{S}_2(S,\mu_2)}{\xi_2}(1-\mu_2), \qquad S \ge 0.$$

Define $\mathcal{N}x_2(S)$ similarly, and proceed as above.

(ii) Define $\mathcal{N}x_1(R)$ as follows. In the numerator of x_1 as given in (3.39), if μ_2 is finite, then let

$$\mathscr{N}x_{1}(R) = \frac{\mathscr{R}_{2}(\sigma_{2}(R), R)}{\eta_{2}} \left[1 - \sigma_{2}(R)\right] - \frac{\mathscr{S}_{2}(\sigma_{2}(R), R)}{\xi_{2}} (1 - R),$$
$$0 \le R \le \mu_{2};$$

otherwise take

$$\mathscr{N}x_1(R) = \frac{\mathscr{R}_2(\lambda_2, R)}{\eta_2}(1-\lambda_2) - \frac{\mathscr{S}_2(\lambda_2, R)}{\xi_2}(1-R), \qquad R \ge 0.$$

Define $\mathcal{N}x_2(R)$ similarly, and proceed as in (i).

(iii) Proceed as above.

Remarks Concerning Theorem 3.14

(1) Note that under the hypotheses of Theorem 3.14, $\overline{S}_1 < \overline{S}_2$ if and only if $\overline{R}_2 < \overline{R}_1$, and $\overline{S}_2 < \overline{S}_1$ if and only if $\overline{R}_1 < \overline{R}_2$.

(2) (a) If $\overline{S_1} < \overline{S_2}$, then $(\mathscr{N}x_1(S) > 0 \text{ and } \mathscr{N}x_2(S) > 0 \text{ for all } S \in \mathring{I}_{12})$ or $(\mathscr{N}x_1(R) > 0 \text{ and } \mathscr{N}x_2(R) > 0 \text{ for all } R \in \mathring{I}_{12})$. Therefore, by Lemma 3.13, $\triangle(S^*, R^*) > 0$ for any solution (S^*, R^*) of (3.37a) with $S^* \in \mathring{I}_{12}$ or $R^* \in \mathring{I}_{12}$.

(b) If $\overline{S}_2 < \overline{S}_1$, then $(\mathscr{N}x_1(S) < 0 \text{ and } \mathscr{N}x_2(S) < 0 \text{ for all } S \in \mathring{I}_{21})$ or $(\mathscr{N}x_1(R) < 0 \text{ and } \mathscr{N}x_2(R) < 0 \text{ for all } R \in \mathring{I}_{21})$. Therefore, by Lemma 3.13, $\triangle(S^*, R^*) < 0$ for any solution (S^*, R^*) of (3.37a) with $S^* \in \mathring{I}_{21}$ or $R^* \in \mathring{I}_{21}$.

The next result links the existence of an interior equilibrium E^* with the stability of the one-species equilibria E_1 and E_2 . We will require the following hypotheses:

$$\lambda_i$$
 and μ_i are finite, $i = 1$ and 2; and $\varphi_i(S)$ is linear, $i = 1$ and 2;
(3.40)

$$\lambda_i$$
 or μ_i is infinite, $i = 1$ or 2. (3.41)

THEOREM 3.15

Suppose $m_{S_i} \ge D_i$, $m_{R_i} \ge D_i$, and the E_i exist, i = 1 and 2. Suppose further that for $i \in \{1, 2\}$, at least one λ_i is finite and at least one μ_i is finite.

(i) If $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) < D_1$ and $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) < D_2$, then E^* exists. If (3.40) or (3.41) holds as well, then E^* is unique.

(ii) If $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) > D_1$ and $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) > D_2$, then E^* exists. If (3.40) or (3.41) holds as well, then E^* is unique.

(iii) If either $(\mathcal{G}_1(\overline{S}_2, \overline{R}_2) > D_1 \text{ and } \mathcal{G}_2(\overline{S}_1, \overline{R}_1) < D_2)$ or $(\mathcal{G}_1(\overline{S}_2, \overline{R}_2) < D_1 \text{ and } \mathcal{G}_2(\overline{S}_1, \overline{R}_1) > D_2)$ and either (3.40) or (3.41) holds, then E^* does not exist.

Proof. (i) Suppose λ_i and μ_i are finite, i = 1 and 2. Without loss of generality, assume that $\overline{S}_1 < \overline{S}_2$. Since $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) < D_2$, then $\varphi_2(\overline{S}_1) > 0$

 $\varphi_1(\overline{S}_1) = \overline{R}_1$. Since $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) < D_1$, then $\varphi_1(\overline{S}_2) > \varphi_2(\overline{S}_2) = \overline{R}_2 > 0$ and $\lambda_1 > \overline{S}_2$. This implies that a solution (S^*, R^*) of (3.37a) exists, with $\overline{S}_1 < S^* < \overline{S}_2$. If $\varphi_2(\overline{S}_1) \leq 1$, then $I_{12} = [\overline{S}_1, \overline{S}_2]$. If $\varphi_2(\overline{S}_1) > 1$, then $I_{12} = [\hat{S}_2, \overline{S}_2]$, where $\hat{S}_2 \in (\overline{S}_1, \overline{S}_2)$ because $\varphi_2(\overline{S}_2) = \overline{R}_2 < 1$. Also, $\varphi_1(S) \leq \overline{R}_1 < 1$ and $\varphi_2(S) \geq 1$ for all $\overline{S}_1 < S < \hat{S}_2$, so φ_1 and φ_2 do not intersect on $[\overline{S}_1, \hat{S}_2]$. Therefore, φ_1 and φ_2 must intersect at some $S^* \in I_{12}^\circ$, so, by Theorem 3.14, E^* exists. If, in addition, φ_1 and φ_2 are linear, then S^* is unique, so E^* is unique.

In the other cases, the existence of E^* is proved similarly, and its uniqueness is immediate.

(ii) Suppose λ_i and μ_i are finite, i = 1 and 2. Without loss of generality, assume that $\overline{S}_1 < \overline{S}_2$. Since $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) > D_2$, it follows that $\varphi_2(\overline{S}_1) < \varphi_1(\overline{S}_1) = \overline{R}_1 < 1$ and $\hat{S}_2 < \overline{S}_1$. Since $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) > D_1$, either φ_1 is defined at \overline{S}_2 (so $\lambda_1 \ge \overline{S}_2$) and $\varphi_1(\overline{S}_2) < \varphi_2(\overline{S}_2) = \overline{R}_2$, or φ_1 is not defined at \overline{S}_2 (so $\lambda_1 < \overline{S}_2$). Then $I_{12} = [\overline{S}_1, \overline{S}_2]$ if $\lambda_1 \ge \overline{S}_2$, and $I_{12} = [\overline{S}_1, \lambda_1]$ otherwise. In either case, φ_1 and φ_2 must intersect at some $S^* \in I_{12}$, so, by Theorem 3.14, E^* exists. If, in addition, φ_1 and φ_2 are linear, then S^* is unique.

In other cases, the existence of E^* is proved similarly, and its uniqueness is immediate.

(iii) Consider $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) > D_1$ and $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) < D_2$, and suppose that (3.40) holds. Without loss of generality, assume that $\overline{S}_1 < \overline{S}_2$. Since $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) > D_1$, $\varphi_1(\overline{S}_2) < \varphi_2(\overline{S}_2) = \overline{R}_2$, and since $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) < D_2$, $\overline{R}_1 = \varphi_1(\overline{S}_1) < \varphi_2(\overline{S}_1)$. Since φ_1 and φ_2 are linear, $\varphi_1(S) \neq \varphi_2(S)$ for every $S \in \mathring{I}_{12}$, so, by Theorem 3.14, E^* does not exist.

The other cases, where the linearity hypothesis is not required, are proved similarly.

Remarks Concerning Theorem 3.15. From the characteristic polynomial of $V_4(\overline{S}_1, \overline{R}_1, \overline{x}_1, 0)$, it follows that if $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) < D_2$, then E_1 is attracting from the interior, and if $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) > D_2$, then E_1 is repelling into the interior. A similar result holds for E_2 .

Now, assuming that a solution $E^* = (S^*, R^*, x_1^*, x_2^*) \in \mathring{\mathbf{R}}_+^4$ of (3.37) exists, we investigate its stability. Define

$$\nabla(S,R) = \frac{\partial}{\partial S} \mathscr{G}_1(S,R) \frac{\partial}{\partial R} \mathscr{G}_2(S,R) - \frac{\partial}{\partial R} \mathscr{G}_1(S,R) \frac{\partial}{\partial S} \mathscr{G}_2(S,R).$$

Evaluating the variational matrix $V_4(E^*)$, the associated characteristic polynomial is

$$\alpha^4 + B_1 \alpha^3 + B_2 \alpha^2 + B_3 \alpha + B_4. \tag{3.42}$$

If $m_{S_i} < D_i$ or $m_{R_i} < D_i$ for i = 1 or 2, it is difficult, in general, to provide even a partial analysis of the roots of (3.42). However, if $m_{S_i} \ge D_i$ and $m_{R_i} \ge D_i$ for i = 1 and 2, then some conclusions can be reached. By hypotheses (3.2), (3.4), (3.5), (3.11), and (3.12), it follows that $B_1 > 0$, $B_2 > 0$, and $B_3 > 0$. Also,

$$B_4 = x_1^* x_2^* \lor (S^*, R^*) \vartriangle (S^*, R^*),$$

where $\triangle(S, R)$ was given in (3.38), and so by the Routh-Hurwicz criterion, a necessary condition for the local asymptotic stability of E^* is that $\nabla(S^*, R^*)$ and $\triangle(S^*, R^*)$ have the same sign.

Suppose that $m_{S_i} \ge D_i$, $m_{R_i} \ge D_i$, i = 1 and 2, $\overline{S_1} < \overline{S_2}$, and (S^*, R^*) is an isolated solution of (3.37a). By Remark 2 following Theorem 3.14, $\triangle(S^*, R^*) > 0$. If $|\varphi'_1(S^*)| < |\varphi'_2(S^*)|$, then, since

$$\varphi_i'(S) = -\frac{(\partial/\partial S)\mathscr{G}_i(S,R)}{(\partial/\partial R)\mathscr{G}_i(S,R)},$$

it follows that

$$\frac{(\partial/\partial S)\mathscr{G}_1(S^*,R^*)}{(\partial/\partial R)\mathscr{G}_1(S^*,R^*)} < \frac{(\partial/\partial S)\mathscr{G}_2(S^*,R^*)}{(\partial/\partial R)\mathscr{G}_2(S^*,R^*)}.$$

After rearranging,

$$\nabla (S^*, R^*) = \frac{\partial}{\partial S} \mathscr{G}_1(S^*, R^*) \frac{\partial}{\partial R} \mathscr{G}_2(S^*, R^*)$$
$$- \frac{\partial}{\partial R} \mathscr{G}_1(S^*, R^*) \frac{\partial}{\partial S} \mathscr{G}_2(S^*, R^*) < 0$$

Therefore, $B_4 < 0$, and E^* is unstable. If $|\varphi'_1(S^*)| > |\varphi'_2(S^*)|$, then

$$\frac{(\partial/\partial S)\mathscr{G}_{1}(S^{*},R^{*})}{(\partial/\partial R)\mathscr{G}_{1}(S^{*},R^{*})} > \frac{(\partial/\partial S)\mathscr{G}_{2}(S^{*},R^{*})}{(\partial/\partial R)\mathscr{G}_{2}(S^{*},R^{*})},$$

so

$$\nabla (S^*, R^*) = \frac{\partial}{\partial S} \mathscr{G}_1(S^*, R^*) \frac{\partial}{\partial R} \mathscr{G}_2(S^*, R^*)$$
$$- \frac{\partial}{\partial R} \mathscr{G}_1(S^*, R^*) \frac{\partial}{\partial S} \mathscr{G}_2(S^*, R^*) > 0.$$

Since $\triangle(S^*, R^*) > 0$, then $B_4 > 0$. A similar result holds when $\overline{S}_2 < \overline{S}_1$.

For example, suppose the hypotheses of Theorem 3.15(i) and hypothesis (3.40) hold. Then E^* exists and is unique. If $\overline{S}_1 < \overline{S}_2$, then $|\varphi'_1(S^*)| < |\varphi'_2(S^*)|$, so $\nabla(S^*, R^*) < 0$ and E^* is unstable. Similarly, if $\overline{S}_2 < \overline{S}_1$, then $|\varphi'_2(S^*)| < |\varphi'_1(S^*)|$, so $\nabla(S^*, R^*) > 0$ and, since $\Delta(S^*, R^*) < 0$, E^* is unstable.

Suppose the hypotheses of Theorem 3.15(ii) and hypothesis (3.40) hold. Then E^* exists and is unique. If $\overline{S}_1 < \overline{S}_2$, then $|\varphi'_2(S^*)| < |\varphi'_1(S^*)|$, so $\nabla(S^*, R^*) > 0$ and $B_4 > 0$. Similarly, if $\overline{S}_2 < \overline{S}_1$, then $|\varphi'_1(S^*)| < |\varphi'_2(S^*)|$, so $\nabla(S^*, R^*) < 0$ and $B_4 > 0$.

If $\mathscr{S}_i(S, R) = p_i(S)$ and $\mathscr{R}_i(S, R) = q_i(R)$ for all $S \ge 0$, and $R \ge 0$, i = 1, 2, then as shown by León and Tumpson [17], $B_4 > 0$ is a necessary and sufficient condition for all roots of (3.42) to have negative real part, and hence sufficient for the local asymptotic stability of an interior equilibrium. This follows from the fact that, in this case, the characteristic equation of $V_4(E^*)$ satisfies all other conditions of the Routh-Hurwicz criterion. As in [17],

$$B_{4} = \left[\left(\frac{\partial x_{1}'}{\partial S} \right)_{E^{*}} \left(\frac{\partial x_{2}'}{\partial R} \right)_{E^{*}} - \left(\frac{\partial x_{1}'}{\partial R} \right)_{E^{*}} \left(\frac{\partial x_{2}'}{\partial S} \right)_{E^{*}} \right] \\ \times \left[\frac{p_{1}(S^{*})}{\xi_{1}} \left(\frac{q_{2}(R^{*})}{\eta_{2}} \right) - \frac{p_{2}(S^{*})}{\xi_{2}} \left(\frac{q_{1}(R^{*})}{\eta_{1}} \right) \right].$$

Therefore, two species competing for two perfectly substitutable resources will coexist stably at equilibrium if at that point each competitor removes at a higher rate that resource which contributes more to its own rate of growth.

Finally we study a global property of the model. In the following, let

$$\begin{aligned} \mathcal{T}_0 &= \left\{ (S, R, 0, 0) \in \mathbf{R}_+^4 \right\}, \\ \mathcal{T}_1 &= \left\{ (S, R, x_1, x_2) \in \mathbf{R}_+^4 \colon x_1 > 0, \, x_2 = 0 \right\}, \\ \mathcal{T}_2 &= \left\{ (S, R, x_1, x_2) \in \mathbf{R}_+^4 \colon x_1 = 0, \, x_2 > 0 \right\}. \end{aligned}$$

THEOREM 3.16

(i) Assume that $\mathscr{G}_i(1,1) > D_i$, i = 1 and 2. Assume also that E_i is globally asymptotically stable with respect to all solutions initiating in \mathscr{T}_i for i = 1 and 2 and that $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) > D_1$ and $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) > D_2$. Then system (3.36) is uniformly persistent with respect to all solutions for which $x_1(0) > 0$ and $x_2(0) > 0$.

(ii) Assume that $\mathscr{G}_2(1,1) > D_2$, that E_2 is as in (i), and that $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) > D_1$. Assume also that no equilibrium of the form E_1 exists. Then

system (3.36) is uniformly persistent with respect to all solutions for which $x_1(0) > 0$ and $x_2(0) > 0$.

Proof. (i) Since $\mathscr{G}_i(1,1) > D_i$, i = 1 and 2, by Theorem 3.6, at least one E_i exists for each i = 1 and 2. Identify (S, R, x_1, x_2) -space with \mathbf{R}^4_+ , and choose $\underline{X} = (S(0), R(0), x_1(0), x_2(0)) \in \mathbf{R}^4_+$. By Theorem 3.2(i), $\Omega(\underline{X})$ is a nonempty, compact, invariant set with respect to (3.36).

By an argument similar to that given in Theorem 3.8, it follows that any point in $\Omega(\underline{X})$ must satisfy $\liminf_{t \to \infty} S(t) > 0$ and $\liminf_{t \to \infty} R(t) > 0$. Therefore, to show that (3.36) is persistent, it remains to show that $\liminf_{t \to \infty} x_i(t) > 0$, i = 1, 2.

Note that E_0 is globally attracting with respect to all solutions initiating in \mathcal{T}_0 . By an argument similar to that used in Theorem 3.8, $E_0 \notin \Omega(\underline{X})$.

Suppose $\{E_1\} \in \Omega(\underline{X})$. Since $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) > D_2, E_1$ is an unstable hyperbolic critical point, and therefore dim $[M^+(E_1)] < 4$. Since $M^+(E_1) \supset \mathscr{F}_1$, dim $[M^+(E_1)] \ge 3$. Therefore, $M^+(E_1) = \mathscr{F}_1$ and hence does not intersect $\mathbf{\mathring{R}}_+^4$. This implies that $\{E_1\} \ne \Omega(\underline{X})$. Therefore, by the Butler-McGehee lemma (see Lemma A1 of [9]), there exists $P \in$ $(M^+(E_1) \setminus \{E_1\}) \cap \Omega(\underline{X})$ and hence $\operatorname{cl} \mathscr{O}(P) \subset \Omega(\underline{X})$. But then, as $t \to -\infty, \mathscr{O}(P)$ either becomes unbounded or leaves the positive cone or $\operatorname{cl} \mathscr{O}(P) \supset \{E_0\}$. In any case, we have a contradiction, and therefore $\{E_1\} \notin \Omega(\underline{X})$. Similarly, $\{E_2\} \notin \Omega(\underline{X})$.

Suppose (3.36) is not persistent. Then there exists a point $\tilde{P} \in \Omega(\underline{X})$ such that $\tilde{P} \in \mathcal{T}_i$ for some $i \in \{0, 1, 2\}$. Now $\tilde{P} \in \Omega(\underline{X})$ implies that $\operatorname{cl} \mathscr{O}(\tilde{P}) \subset \Omega(\underline{X})$. However, if $\tilde{P} \in \mathcal{T}_i$, then $\{E_i\} \in \operatorname{cl} \mathscr{O}(\tilde{P})$, because E_i is globally attracting with respect to all solutions initiating in the set \mathcal{T}_i , implying that $\{E_i\} \in \Omega(\underline{X})$, a contradiction. Thus $\liminf_{t \to \infty} x_i(t) > 0$, i = 1, 2, and so (3.36) is persistent. It now follows from the main result of [7] that (3.36) is uniformly persistent.

(ii) The proof follows from Theorem 3.9(ii) and is similar to the proof of (i).

Note that uniform persistence of (3.36) implies immediately that there is at least one coexistence equilibrium.

Note also that if $m_{S_i} \ge D_i$, $m_{R_i} \ge D_i$, $D_i = 1$ for i = 1 and 2 or if $\mathscr{S}_i(S, R) = p_i(S)$ and $\mathscr{R}_i(S, R) = q_i(R)$ for all $S \ge 0$ and $R \ge 0$, i = 1, 2 (regardless of the relative values of m_{S_i} , m_{R_i} , and D_i and with D_i not necessarily equal to 1), then by Theorem 3.9(i) and Theorem 3.10(ii), respectively, E_i is globally asymptotically stable with respect to all solutions initiating in $\{(S, R, x_1, x_2) \in \mathbb{R}^4_+: x_i > 0, x_j = 0\}$, where $i \ne j \in \{1, 2\}$. Therefore, Theorem 3.16(i) gives necessary and sufficient conditions for uniform persistence in these cases.

4. SUMMARY OF RESULTS AND DISCUSSION

In this section we summarize the results of our analysis in terms of the original unscaled variables, both for model I of León and Tumpson and for model (3.1). We then compare the dynamics with the dynamics of the classical growth and two-species competition models and the corresponding models for perfectly complementary resources. For convenience, we retain the notation of Section 3 for the equilibria E_1 , E_2 , and E^* . However, it is to be understood that by the scaling (3.20), the S and x_i components of the equilibria of (3.1) should be multiplied by S^o and the R components of the equilibria of (3.1) should be multiplied by R^o . To facilitate the description of the quantities governing the dynamics of (3.1), we assume that the volume V of suspension in the growth vessel is 1 cubic unit. In (3.1), D, D_1 , and D_2 are divided by the actual volume V.

4.1. MODEL I OF LEÓN AND TUMPSON ADAPTED TO THE CHEMOSTAT

We obtained our most complete results when the amount of each resource consumed was assumed to be independent of the concentration of the other resource, that is, $\mathcal{S}_i(S, R) = p_i(S)$ and $\mathcal{R}_i(S, R) = q_i(R)$, for i = 1 and 2. First we considered the one-species growth models [the (S, R, x_i) subsystems of (3.1), $i \in \{1, 2\}$. We showed that for each $i \in \{1, 2\}$ {1,2}, x_i avoids extinction if and only if $\mathscr{G}_i(S^o, R^o) > D_i$. In other words, if a species cannot consume enough resource to compensate for the rate D_i at which it is being removed, even if the growth vessel is maintained at the input concentrations S^o and R^o of resources S and R, then that species will become extinct. Otherwise, there exists a unique one-species survival equilibrium that is globally asymptotically stable. Next we considered the two-species competition model in this setting. In Table 2, we summarize the criteria for existence of the equilibria in the nonnegative cone, as well as the criteria that guarantee local asymptotic stability of these equilibria. For the two-species competition model, if $\mathcal{G}_i(S^o, R^o) < D_i$ for i = 1 and 2, then E_0 , the washout equilibrium, is globally asymptotically stable. On the other hand, $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) > D_1$ and $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) > D_2$ is necessary and sufficient for solutions of the twospecies competition model to be uniformly persistent, thus ensuring that both species survive in the presence of competition, regardless of the (positive) initial concentrations.

Next, in this setting, we compare the dynamics of growth on perfectly complementary resources with the dynamics of growth on perfectly substitutable resources. In both cases either the wash out equilibrium is globally asymptotically stable and hence the carrying capacity of the

Summary of Local Stability Analysis of (3.1)				
Critical point	Existence criteria	Criteria for asymptotic stability		
E_{0}	Always exists	$\mathscr{G}_1(S^o, R^o) < D_1 / V$ and $\mathscr{G}_2(S^o, R^o) < D_2 / V$		
E_1	$\mathcal{G}_1(S^o, R^o) > D_1 / V$	$\mathcal{G}_2(\overline{S}_1, \overline{R}_1) < D_2 / V$		
E_2	$\mathcal{G}_2(S^o, R^o) > D_2 / V$	$\mathcal{G}_1(\vec{S}_2, \vec{R}_2) < D_1 / V$		
E^* (not necessarily	(i) $\mathscr{G}_1(\overline{S}_2, \varphi_2(\overline{S}_2)) < D_1 / V$	(ii) holds, and either		
unique)	and $\mathscr{G}_2(\overline{S}_1, \varphi_1(\overline{S}_1)) < D_2 / V$	$ \varphi_1'(S^*) > \varphi_2'(S^*) $		
	or	if $\overline{S}_1 < \overline{S}_2$		
	(ii) $\mathscr{G}_1(\overline{S}_2, \varphi_2(\overline{S}_2)) > D_1 / V$	or $ \varphi_1'(S^*) < \varphi_2'(S^*) $		
	and $\mathcal{G}_2(\overline{S}_1, \varphi_1(\overline{S}_1)) > D_2 / V$	if $\overline{S}_1 > \overline{S}_2$.		

TABLE 2

Summary of Local Stability Analysis of (3.1)^a

^a $\mathscr{S}_{i}(S,R) = p_{i}(S)$ for all $R \ge 0$; $\mathscr{R}_{i}(S,R) = q_{i}(R)$ for all $S \ge 0$.

environment is zero, or there exists a one-species survival equilibrium that is globally asymptotically stable, and the species component of the equilibrium gives the carrying capacity of the environment. The major difference in the criterion that determines whether the species will survive or wash out is precisely as expected. For perfectly complementary resources, both resources must be above some threshold (see Table 3 of Butler and Wolkowicz [5]), whereas for perfectly substitutable resources, the threshold (see Theorem 3.10) depends on the combined amount of the resources. The classical, or logistic, model due to Verhulst predicts that as long as the initial population is positive, the population size will approach the carrying capacity of the environment, which must be known in advance because it is a parameter in the model that is always assumed to be positive. Thus an advantage of both of the resource-based growth models over the classical model is that they predict the carrying capacity of the environment.

Using graphical techniques to examine the local stability properties of two-species competition for two resources, Tilman [28] conjectured that the type of resources for which competition occurs will not lead to major, qualitative differences in the ecological patterns that can result from competition between two species for two resources. Butler and Wolkowicz [5], who extended the work of León and Tumpson [17], in the perfectly complementary resource case, found that in the case of monotone response functions, each of the outcomes of the classical theory for two-species competition is possible. We have shown that each of the outcomes for perfectly complementary resources is also possible in the perfectly substitutable case. Competition-independent extinction, an impossibility in the classical model, can occur in resource-based models. Both for perfectly complementary resources and in the classical model, coexistence always occurs at a globally asymptotically stable critical point. For perfectly substitutable resources in this setting, we were only able to show uniform persistence. (Note that uniform persistence of a system implies that at least one coexistence equilibrium exists.) In fact, multiple interior equilibria are possible, and so coexistence need not always occur at a globally asymptotically stable equilibrium. It is even possible for the outcome to be initial condition dependent in the sense that for certain initial conditions there is coexistence whereas for others there is competitive dominance, that is, one population drives the other population to extinction.

4.2. MODEL (3.1)

While Tilman's conjecture appears to be true for the most part, there seems to a be a wider range of possible dynamics in the perfectly substitutable case. What also seems to make a difference is the strategy used for consumption—in particular, whether or not the concentration of each resource affects the amount of the other resource consumed. We extended model I of León and Tumpson to incorporate handling time in the sense of Holling [12] and hence allow the concentration of one resource to act as a competitive inhibitor on the consumption of the other resource [see assumptions (3.5)-(3.15)]. Here it becomes important to consider the relative values of m_{S_1} and m_{R_2} , the maximal growth rates on resource S and R, respectively, and D_i , the combined washout and specific death rate. When the maximal growth rate of population x_i on one resource, say resource S, is larger than the maximal growth rate of population x_i on the other resource, then there is a threshold, S_i^c , for resource S. (See Figure 1.) If the concentration of resource S is below this threshold, increasing the concentration of either resource is beneficial to that population. However, once the concentration of resource S is above this threshold, so that the maximal growth rate on resource Ris exceeded by consuming only resource S, increasing resource S is beneficial, but the presence of resource R becomes detrimental to that population.

In this setting, we again considered the one-species growth model. As in model I of León and Tumpson, we found that $\mathscr{G}_i(S^o, R^o) > D_i$ is necessary and sufficient for this model to be uniformly persistent, regardless of the relative values of m_{S_i} , m_{R_i} , and D_i . If $m_{S_i} \ge D_i$ and $m_{R_i} \ge D_i$, so the rate of removal from competition does not exceed the maximal growth rate for each resource, then if $\mathscr{G}_i(S^o, R^o) < D_i$, the environment is not rich enough to support population x_i , and it is driven to extinction. On the other hand, $\mathscr{G}_i(S^o, R^o) > D_i$ is a necessary and sufficient condition to ensure that a unique one-species survival equilibrium E_i exists. We have only shown that the criteria for the local asymptotic stability of E_i (see Table 2) apply under the added assumption that $\mathscr{G}_i(S^o, R^o) \leq 2D$. However, if the intrinsic death rate is assumed to be insignificant compared to the dilution rate $(D_i = D)$, then E_i is globally asymptotically stable with respect to the interior of (S, R, x_i) space.

The growth model exhibits more unusual dynamics when $m_{S_i} < D_i < m_{R_i}$ or $m_{R_i} < D_i < m_{S_i}$. If, in addition, $\mathcal{G}_i(S^o, R^o) < D_i$, there may or may not exist a one-species survival equilibrium, and if one exists it need not be unique. In fact, we provide an example (see Remark 3 following Theorem 3.7) in which $m_{R_i} < D_i < m_{S_i}$, and $\mathcal{G}_i(S^o, R^o) < D_i$ so the washout equilibrium is locally asymptotically stable. By treating the ratio of the growth yield constants, ξ_i / η_i , as a bifurcation parameter while fixing all of the other parameters in the model, one can obtain either zero, one, or two one-species survival equilibria. In this example, for at least one one-species survival equilibrium to exist, ξ_i / η_i must be sufficiently large. To see this, consider all concentrations $\overline{S}, \overline{R}$ of resources S and R satisfying $\mathcal{G}_i(\overline{S}, \overline{R}) = D_i$. Since the concentration \overline{S} of resource S is above the threshold S_i^c , resource R is detrimental. One would expect that the faster resource R is depleted the better. If the ratio ξ_i / η_i is too small, then

$$\frac{(R^{\circ} - \overline{R})D/V}{(S^{\circ} - \overline{S})D/V} > \frac{(1/\eta_i)\mathscr{R}_i(\overline{S}, \overline{R})}{(1/\xi_i)\mathscr{S}_i(\overline{S}, \overline{R})},$$
(4.1)

and so the ratio of the net supply rate of resource R to that of resource S exceeds the ratio of the consumption rate of resource R to that of resource S. As species x_i cannot deplete resource R quickly enough, no one-species survival equilibrium exists. In this example, if at least one one-species equilibrium exists, then at least one of them is locally asymptotically stable, and so whether the species survives or washes out depends on the initial conditions. Multiple one-species survival equilibria and initial condition dependent survival is not possible in any of the other growth models discussed in this paper.

We then considered the two-species competition model. If, for each species, either (both breakeven concentrations λ_i and μ_i are finite and $\mathscr{G}_i(S^o, R^o) < D_i$) or $(\lambda_i = \infty$ and $\mu_i \ge R^o)$ or $(\lambda_i \ge S^o$ and $\mu_i = \infty$), then E_0 , the washout equilibrium, is globally asymptotically stable; that is, both species become extinct. On the other hand, we found that if E_1

and E_2 are globally asymptotically stable in their respective three-dimensional subsystems, then a necessary and sufficient condition for the two-species competition model to be uniformly persistent is that $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) > D_1$ and $\mathscr{G}_2(\overline{S}_1, \overline{R}_1) > D_2$. We examined the existence and stability of coexistence equilibria under the assumption that $m_{s_i} \ge D_i$ and $m_R \ge D_i$ for i = 1 and 2. The results in this case are summarized in Table 2. [Note that the condition for the local asymptotic stability of E^* only ensures that the constant term in the characteristic equation of the variational matrix of (3.1) evaluated at E^* is positive.] We first showed that if a coexistence equilibrium exists, then E_1 and E_2 exist and are unique. We then characterized those resource concentrations that yield coexistence equilibria. Using this characterization, we proved that if E_1 and E_2 exist and either both repel into or both attract from the interior, then at least one coexistence equilibrium exists. We also showed that $\mathcal{G}_1(S,R)$ and $\mathcal{G}_2(S,R)$ can be chosen so that these conditions on the stability of E_1 and E_2 yield precisely one coexistence equilibrium. In particular, when the subsistence curves are linear, as in Waltman et al. [31], we found that if both E_1 and E_2 attract from the interior, then E^* is unique and unstable, and if both E_1 and E_2 repel into the interior, then E^* is unique and the condition for the local asymptotic stability of E^* , given in Table 2, is satisfied. Also, if E_1 and E_2 exist and one attracts and the other repels with respect to the interior, no coexistence equilibrium exists. However, if the subsistence curves are nonlinear, multiple coexistence equilibria are possible, and, as in model I of León and Tumpson, the outcome of competition may depend on the initial conditions.

As in the growth model, the competition model exhibits more unusual dynamics when $m_{S_i} < D_i < m_{R_i}$ or $m_{R_i} < D_i < m_{S_i}$ for at least one *i*. We provided an example (see the remark following Theorem 3.12) exhibiting the following characteristics. For population x_1 , $m_{R_1} < D_1 < m_{S_1}$, and the ratio ξ_1/η_1 is small enough that (4.1) holds. Therefore, in the absence of population x_2 , the washout equilibrium E_0 is globally attracting and population x_1 dies out. On the other hand, for population $x_2, m_{S_2} > D_2$ and $m_{R_2} > D_2$. Since $\mathscr{G}_2(S^o, R^o) > D_2$, E_0 is unstable, and there exists a unique one-species survival equilibrium of the form E_2 that is locally asymptotically stable with respect to (S, R, x_2) space. At the resource concentrations of E_2 , $\mathscr{G}_1(\overline{S}_2, \overline{R}_2) > D_1$, and so E_2 is unstable with respect to (S, R, x_1, x_2) -space. Also, $\lambda_1 < \lambda_2$, and so population x_1 would outcompete population x_2 , driving it to extinction if no resource R were available. Under these conditions, the subsistence curves intersect uniquely. To ensure that the corresponding solution of (3.37b) satisfies $x_1^* > 0$ and $x_2^* > 0$, so that a unique coexistence equilibrium E^* exists, the ratio ξ_2 / η_2 was chosen to satisfy

$$\frac{(1/\eta_2)\mathscr{R}_2(S^*, R^*)}{(1/\xi_2)\mathscr{S}_2(S^*, R^*)} > \frac{(R^o - R^*)D/V}{(S^o - S^*)D/V}.$$

Thus, population x_2 depletes resource R quickly enough that populations x_1 and x_2 coexist, even though population x_1 cannot survive in the absence of competitor population x_2 . Thus, in some circumstances it seems that a population can be better off with a competitor than without one.

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