

GLOBAL ASYMPTOTIC BEHAVIOR OF A CHEMOSTAT MODEL WITH TWO PERFECTLY COMPLEMENTARY RESOURCES AND DISTRIBUTED DELAY*

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Abstract. A model of the chemostat involving two species of microorganisms competing for two perfectly complementary, growth-limiting nutrients is considered. The model incorporates distributed time delay in the form of integral differential equations in order to describe the time involved in converting nutrient to biomass. The delays are included in the nutrient and species concentrations simultaneously. A general class of monotone increasing functions is used to describe nutrient uptake. Sufficient conditions based on biologically meaningful parameters in the model are given that predict competitive exclusion for certain parameter ranges and coexistence for others. We prove that the global asymptotic attractivity of steady states of the model is similar to that of the corresponding model without time delays. However, our results indicate that when the inherent delays are in fact large, ignoring them may result in incorrect predictions.

Key words. integral differential equations, distributed delays, perfectly complementary resources, competition, chemostat, competitive exclusion, coexistence, global asymptotic behavior

AMS subject classifications. 34D20, 34K20, 45M10, 92D25

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1. Introduction. The chemostat, a laboratory apparatus used for the continuous culture of microorganisms, has played an important role in microbiology and population biology (see, for example, Egli [18], Frederickson and Stephanopoulos [20], Herbert, Elsworth, and Telling [26], Novic and Sziliard [43], Smith and Waltman [51], Waltman [56], and Taylor and Williams [52]). It can be applied to increase our understanding of both environmental and industrial biotechnological processes. For an excellent review of mathematical results on the theory of the chemostat, see Smith and Waltman [51]. Some other very recent mathematical results can be found in Ballyk et al. [4], Li [35], Pilyugin and Waltman [45], and Wolkowicz, Xia, and Wu [62].

A derivation of the following model (1.1), which describes two populations of microorganisms competing for a single, essential, nonreproducing, growth-limiting nutrient in a chemostat, was given by Herbert, Elsworth, and Telling in [26].

$$(1.1) \quad \begin{aligned} S'(t) &= D(S^0 - S(t)) - \frac{x_1(t)}{y_{S_1}} p_1(S(t)) - \frac{x_2(t)}{y_{S_2}} p_2(S(t)), \\ x_1'(t) &= x_1(t)(-D + p_1(S(t))), \\ x_2'(t) &= x_2(t)(-D + p_2(S(t))). \end{aligned}$$

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In model (1.1), $S(t)$ denotes the concentration of the growth-limiting nutrient and $x_i(t)$ denotes the density of the i th population of microorganisms in the culture vessel at time t . The parameter $D = \frac{F}{V}$ is the dilution rate where V denotes the volume of the culture vessel and F denotes the input/output flow rate. The function $p_i(S(t))$ represents the growth rate of the i th species as a function of the limiting nutrient concentration. The ratio $p_i(S)/y_{S_i}$ denotes the uptake rate of the nutrient of the i th species; and so each y_{S_i} denotes a growth yield constant. S^0 denotes the concentration of the nutrient in the feed vessel. Here we assume that the growth vessel is well stirred, so that nutrients and microorganisms are removed in proportion to their concentrations. We also assume that the species-specific death rates are insignificant compared to the flow rate D and can be ignored.

Rigorous mathematical analysis of the chemostat model for an arbitrary number of competitors in this single limiting nutrient setting was carried out in Hsu, Hubbell, and Waltman [31] and Hsu [29], in the case in which the response functions were of the Michaelis–Menten form. In that case the model is known as the Monod model. The model with more general response functions was analyzed by Bush and Cook [9] in the case of only two competitors and by Armstrong and McGehee [1], Butler and Wolkowicz [10], Wolkowicz and Lu [59], and Li [35] for an arbitrary number of competitors. The mathematical results in all of these papers indicate that competitive exclusion holds. In fact, the model predicts that at most one population survives and that the population that survives can be predicted based on the relative values of the break-even concentrations, parameters that can be determined by growing each population alone in the chemostat and measuring the steady state concentration of the nutrient. For microorganisms such as *E. coli*, modeled well by the Monod model, the predictions of this model appear to agree with experiments (see Hansen and Hubbell [24]).

In order to identify the growth-limiting nutrient in ecosystems, specific nutrients are added to samples taken from the environment and then the stimulation in growth rate is measured. Apparently, the best stimulation of growth is commonly obtained when a combination of nutrients is supplied, rather than a single nutrient. When more than one nutrient is growth-limiting, one must consider how the nutrients, once consumed, interact to promote growth. Different classifications exist. At one extreme are compounds that represent alternative sources that serve the same physiological requirement, i.e., two different carbon sources. Such compounds are called perfectly substitutable by Leon and Tumpson [34], Rapport [47], and Tilman [54] and homologous by Harder and Dijkhuizen [25]. At the other extreme are compounds that serve different physiological requirements, such as a carbon source and a nitrogen source. Such compounds are classified as perfectly complementary by Leon and Tumpson [34], Rapport [47], and Baltzis and Fredrickson [7], as essential by Tilman [54], and as heterologous by Harder and Dijkhuizen [25].

Recently, there has been a lot of work, both experimental and theoretical, concerning growth of microorganisms on substitutable resources (see, for example, [42, 46, 55] and the references therein). For an excellent survey about growth on mixtures of substrates, in both the substitutable and the complementary cases, see Egli [18]. According to Egli [18], there are relatively few studies concerning growth on complementary nutrients. However, he cites many papers that give experimental evidence that dual nutrient limitation occurs. Theoretical references in the complementary nutrient case, besides the ones mentioned above, include [2, 3, 14, 44, 53, 63].

In this paper, we use the terminology of Leon and Tumpson [34] and restrict our

attention to perfectly complementary resources. The chemostat model in the case of complementary nutrients S and R , given in Leon and Tumpson [34], is

$$(1.2) \quad \begin{aligned} S'(t) &= (S^0 - S(t))D - \frac{x_1(t)}{y_{S_1}} f_1(S(t), R(t)) - \frac{x_2(t)}{y_{S_2}} f_2(S(t), R(t)), \\ R'(t) &= (R^0 - R(t))D - \frac{x_1(t)}{y_{R_1}} f_1(S(t), R(t)) - \frac{x_2(t)}{y_{R_2}} f_2(S(t), R(t)), \\ x'_i(t) &= x_i(t)(f_i(S(t), R(t)) - D), \quad i = 1, 2, \end{aligned}$$

where the same notation is used as in (1.1), with R^0 and y_{R_i} , $i = 1, 2$, denoting the concentration of nutrient R in the feed vessel and the yield constants, respectively. In (1.2),

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

where $p_i(S(t))$ ($q_i(R(t))$) represents the growth rate of the i th population as a function of nutrient concentration.

Leon and Tumpson [34] found conditions for the existence of a locally asymptotically stable interior steady state and hence conditions for the coexistence of two competitors. Hsu, Cheng, and Hubbell [30] provided a complete global analysis of the model for the case in which $p_i(S)$ and $q_i(R)$ take Michaelis–Menten form. They concluded that “each of the four outcomes of classical Lotka–Volterra two-species competition theory has multiple mechanistic origins in terms of consumer resource interactions.” Another approach, used by Butler and Wolkowicz [11], works for both monotone and nonmonotone response functions. For other related work on competition for multiple resources see [5, 6, 23, 57, 58].

In (1.1) and (1.2), the use of ordinary differential equations carries the implication that the conversion of nutrient consumed to viable biomass occurs instantaneously. This is clearly an oversimplification. If discrete time delays are used to describe the time involved in the conversion process, the model with two populations competing for one limiting nutrient is given by

$$(1.3) \quad \begin{aligned} S'(t) &= (S^0 - S(t))D - \frac{x_1(t)}{y_{S_1}} p_1(S(t)) - \frac{x_2(t)}{y_{S_2}} p_2(S(t)), \\ x'_1(t) &= -Dx_1(t) + e^{-D\tau_1} x_1(t - \tau_1) p_1(S(t - \tau_1)), \\ x'_2(t) &= -Dx_2(t) + e^{-D\tau_2} x_2(t - \tau_2) p_2(S(t - \tau_2)), \end{aligned}$$

where the same notation is used as in (1.1). Here, τ_i represents the time involved by the i th population to convert nutrient, once consumed, into viable biomass. This model involves a delay term both in the nutrient variables and the population concentrations simultaneously. The washout factor $e^{-D\tau_i}$ represents the approximate proportion of individuals that remain in the chemostat during the conversion process (see MacDonald [38, 39]). The presence of such delays and their effect on microbial population dynamics is discussed in Caperon [12] and Droop [16]. Model (1.3) was studied in Freedman, So, and Waltman [21], Ellermeyer [19], Hsu, Waltman, and Ellermeyer [32], and Wolkowicz and Xia [60]. The global asymptotic behavior of (1.3) is fully understood. It was shown that the competitive exclusion again holds for any monotone growth response functions. As pointed out in Wolkowicz and Xia [60], due to the fact that the break-even concentrations, which completely determine competitive ability, depend on delays, including large delays may change the outcome of the competition.

If discrete delay is introduced into (1.2) to describe the delay in nutrient conversion, (1.2) could be modified as follows:

$$\begin{aligned}
 S'(t) &= (S^0 - S(t))D - \frac{x_1(t)}{y_{S_1}} f_1(S(t), R(t)) - \frac{x_2(t)}{y_{S_2}} f_2(S(t), R(t)), \\
 R'(t) &= (R^0 - R(t))D - \frac{x_1(t)}{y_{R_1}} f_1(S(t), R(t)) - \frac{x_2(t)}{y_{R_2}} f_2(S(t), R(t)), \\
 x'_1(t) &= -Dx_1(t) + e^{-D\tau_1} x_1(t - \tau_1) f_1(S(t - \tau_1), R(t - \tau_1)), \\
 x'_2(t) &= -Dx_2(t) + e^{-D\tau_2} x_2(t - \tau_2) f_2(S(t - \tau_2), R(t - \tau_2)),
 \end{aligned}
 \tag{1.4}$$

where τ_i denotes the specific-population time delay in nutrient conversion. In fact, the concentrations of nutrient S and R stored internally by population i are given by

$$Z_{S_i}(t) = \frac{1}{y_{S_i}} Z_i(t) \quad \text{and} \quad Z_{R_i}(t) = \frac{1}{y_{R_i}} Z_i(t),$$

respectively, where

$$Z_i(t) = \int_{t-\tau_i}^t e^{-D(t-u)} f_i(S, R) x_i du.$$

The exponential appearing in the above integrals accounts for stored nutrients that are washed out during the storage period.

Balancing input and output and nutrient consumption as well as growth and removal, we obtain

$$\begin{aligned}
 S(t) &= S(0) + \int_0^t D(S^0 - S) du - \int_0^t \frac{1}{y_{S_1}} f_1(S, R) x_1 du - \int_0^t \frac{1}{y_{S_2}} f_2(S, R) x_2 du, \\
 R(t) &= R(0) + \int_0^t D(R^0 - R) du - \int_0^t \frac{1}{y_{R_1}} f_1(S, R) x_1 du - \int_0^t \frac{1}{y_{R_2}} f_2(S, R) x_2 du, \\
 x_i(t) + Z_i(t) &= x_i(0) + Z_i(0) + \int_0^t f_i(S, R) x_i du - \int_0^t D[x_i(u) + Z_i(u)] du.
 \end{aligned}
 \tag{1.5}$$

Differentiating these equations yields system (1.4).

Distributed delay models have been used in biological systems (see Scudo and Ziegler [50] and MacDonald [36, 37]), and are often considered to be more realistic than discrete models (see Caperon [12], Caswell [13], and May [40]). When distributed delays are used to describe the delay involved in the process of conversion of nutrient consumed into viable cells, model (1.1) can be modified as in Wolkowicz, Xia, and Ruan [61] to obtain

$$\begin{aligned}
 S'(t) &= (S^0 - S(t))D - \frac{x_1(t)}{y_{S_1}} p_1(S(t)) - \frac{x_2(t)}{y_{S_2}} p_2(S(t)), \\
 x'_1(t) &= -Dx_1(t) + \int_{-\infty}^t x_1(\theta) p_1(S(\theta)) e^{-D(t-\theta)} K_1(t - \theta) d\theta, \\
 x'_2(t) &= -Dx_2(t) + \int_{-\infty}^t x_2(\theta) p_2(S(\theta)) e^{-D(t-\theta)} K_2(t - \theta) d\theta,
 \end{aligned}
 \tag{1.6}$$

where the delay kernels take the form of Gamma distributions

$$(1.7) \quad K_i(u) = \frac{\alpha_i^{r_i+1} u^{r_i}}{r_i!} e^{-\alpha_i u}, \quad i = 1, 2.$$

In the above formula, $\alpha_i > 0$ are constant and $r_i \geq 0$ are integers. r_i is called the order of the delay kernel K_i and the mean delay corresponding to the K_i is

$$(1.8) \quad \tau_i = \int_0^\infty u K_i(u) du = \frac{r_i + 1}{\alpha_i}$$

(see MacDonald [36]). The kernels $K_i(u)$ with $r_i = 0$ and $r_i = 1$ are often called the weak and strong kernels, respectively, and are frequently used in biological modeling (see Cushing [15] and MacDonald [37]). The discrete delay model (1.3) can be viewed as a limiting case of model (1.6) by letting r_i go to infinity while the mean delays $\frac{r_i+1}{\alpha_i}$ are fixed. See Wolkowicz, Xia, and Ruan [61], who gave a complete global analysis of (1.6) and showed that competitive exclusion still holds and that the global asymptotic behavior is fully determined by the relative values of the break-even concentrations.

The purpose of this paper is to study the chemostat model with two populations of microorganisms competing for two perfectly complementary nutrients when distributed delays are involved. To the best of our knowledge, this paper is the first one on the analysis of a chemostat model involving two nutrients and delay. We determine the global asymptotic behavior of the model by using the linear chain trick technique (see MacDonald [37]) and the fluctuation lemma (see Hirsch, Hanisch, and Gabriel [28]). We avoid local stability analysis which is very complicated due to the two delays that are involved.

This paper is organized as follows. The model is presented in section 2. In section 3 the main results are stated. The proofs are given in section 4. We conclude the paper with a discussion in section 5.

2. The model and preliminary results. As done in [61] in the single resource case, we modify the dual resource model (1.2) by including distributed delays to describe the time taken by each population of microorganisms to convert the nutrient consumed into viable cells. The model takes the form

$$(2.1) \quad \begin{aligned} S'(t) &= (S^0 - S(t))D - \frac{x_1(t)}{y_{S_1}} f_1(S(t), R(t)) - \frac{x_2(t)}{y_{S_2}} f_2(S(t), R(t)), \\ R'(t) &= (R^0 - R(t))D - \frac{x_1(t)}{y_{R_1}} f_1(S(t), R(t)) - \frac{x_2(t)}{y_{R_2}} f_2(S(t), R(t)), \\ x_1'(t) &= -Dx_1(t) + \int_{-\infty}^t x_1(\theta) f_1(S(\theta), R(\theta)) e^{-D(t-\theta)} K_1(t-\theta) d\theta, \\ x_2'(t) &= -Dx_2(t) + \int_{-\infty}^t x_2(\theta) f_2(S(\theta), R(\theta)) e^{-D(t-\theta)} K_2(t-\theta) d\theta, \end{aligned}$$

where the same notation is used as in (1.1), (1.2), and (1.6). As in (1.2), in this model

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

where $p_i(S)$ ($q_i(R)$) represents the per capita growth rate of the i th population when nutrient S is limiting (nutrient R is limiting). In (2.1), we assume, as in (1.7), that

the delay kernels take the form of Gamma distributions

$$(2.2) \quad K_i(u) = \frac{\alpha_i^{r_i+1} u^{r_i}}{r_i!} e^{-\alpha_i u}, \quad i = 1, 2.$$

We make the following assumptions on the response functions p_i and q_i , $i = 1, 2$:

$$(2.3) \quad p_i, q_i : R_+ \rightarrow R_+ \text{ are monotone increasing and locally Lipschitz with } p_i(0) = 0, q_i(0) = 0;$$

and there exist positive extended real numbers λ_{S_i} and λ_{R_i} such that

$$(2.4) \quad \begin{aligned} p_i(S) &< D \left(\frac{D + \alpha_i}{\alpha_i} \right)^{r_i+1} && \text{for } S \in (0, \lambda_{S_i}), \\ p_i(S) &> D \left(\frac{D + \alpha_i}{\alpha_i} \right)^{r_i+1} && \text{for } S \in (\lambda_{S_i}, +\infty), \\ q_i(R) &< D \left(\frac{D + \alpha_i}{\alpha_i} \right)^{r_i+1} && \text{for } R \in (0, \lambda_{R_i}), \\ q_i(R) &> D \left(\frac{D + \alpha_i}{\alpha_i} \right)^{r_i+1} && \text{for } R \in (\lambda_{R_i}, +\infty). \end{aligned}$$

In the case where $p_i(S) < D \left(\frac{D + \alpha_i}{\alpha_i} \right)^{r_i+1}$ ($q_i(R) < D \left(\frac{D + \alpha_i}{\alpha_i} \right)^{r_i+1}$) for all $S > 0$ ($R > 0$), we set $\lambda_{S_i} = +\infty$ ($\lambda_{R_i} = +\infty$).

Note that these parameters can be measured by growing each population alone in the chemostat. We will show that the outcome of competition between populations can be predicted, based on the relative values of the parameters in the model.

Following Hsu, Cheng, and Hubbell [30], we define

$$(2.5) \quad C_i = y_{S_i}/y_{R_i}, \quad i = 1, 2.$$

The parameter C_i denotes the ratio of the yield constants in (units of R consumed)/(units of S consumed) for species i growing on R and S .

Let

$$(2.6) \quad T_i = \frac{R^0 - \lambda_{R_i}}{S^0 - \lambda_{S_i}}, \quad i = 1, 2,$$

and

$$(2.7) \quad T^* = \frac{R^0 - \lambda_{R_2}}{S^0 - \lambda_{S_1}} \quad \text{and} \quad T_* = \frac{R^0 - \lambda_{R_1}}{S^0 - \lambda_{S_2}}.$$

Parameter T_i represents the ratio in which nutrients R and S are externally regenerated under steady state consumption pressure from population i in the absence of the competitor population when the population is R -limited versus S -limited. By comparing T_i and C_i one can determine whether population i is S -limited or R -limited. If $T_i > C_i$, population i is S -limited because S is regenerating at a steady state more slowly than R with respect to the required consumption ratio of population i . Similarly $T_i < C_i$ implies that population i is R -limited.

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

We make the following generic assumptions:

$$(2.8) \quad \begin{aligned} \lambda_{S_1} \text{ and } \lambda_{S_2} \text{ are distinct from each other,} \\ \lambda_{R_1} \text{ and } \lambda_{R_2} \text{ are distinct from each other,} \end{aligned}$$

and

$$(2.9) \quad T^* \text{ and } T_* \text{ are distinct from } C_1 \text{ and } C_2.$$

To ensure that the critical points are all isolated we assume

$$(2.10) \quad C_1 \neq C_2.$$

To ensure that if $(\bar{S}, \bar{R}, \bar{x}_1, \bar{x}_2)$ is a critical point, then $p_i(\bar{S}) \neq q_i(\bar{R})$ for $i = 1, 2$, we also assume that

$$(2.11) \quad T_i \neq C_j, \quad i, j = 1, 2.$$

The washout steady state for (2.1) is denoted by

$$E_0 = (S^0, R^0, 0, 0).$$

There are four possible steady states involving only one species each, denoted by

$$E_{S_1} = (\lambda_{S_1}, R^0 - C_1(S^0 - \lambda_{S_1}), y_{S_1} \left(\frac{\alpha_1}{D + \alpha_1} \right)^{r_1+1} (S^0 - \lambda_{S_1}), 0),$$

$$E_{S_2} = (\lambda_{S_2}, R^0 - C_2(S^0 - \lambda_{S_2}), 0, y_{S_2} \left(\frac{\alpha_2}{D + \alpha_2} \right)^{r_2+1} (S^0 - \lambda_{S_2})),$$

$$E_{R_1} = \left(S^0 - \frac{(R^0 - \lambda_{R_1})}{C_1}, \lambda_{R_1}, y_{R_1} \left(\frac{\alpha_1}{D + \alpha_1} \right)^{r_1+1} (R^0 - \lambda_{R_1}), 0 \right),$$

and

$$E_{R_2} = \left(S^0 - \frac{(R^0 - \lambda_{R_2})}{C_2}, \lambda_{R_2}, 0, y_{R_2} \left(\frac{\alpha_2}{D + \alpha_2} \right)^{r_2+1} (R^0 - \lambda_{R_2}) \right).$$

There are two possible steady states involving both species x_1 and x_2 , denoted by

$$E_{12} = \left(\lambda_{S_1}, \lambda_{R_2}, \bar{x}_1 \left(\frac{\alpha_1}{D + \alpha_1} \right)^{r_1+1}, \bar{x}_2 \left(\frac{\alpha_2}{D + \alpha_2} \right)^{r_2+1} \right),$$

where

$$(2.12) \quad \begin{aligned} \bar{x}_1 &= y_{S_1} y_{R_1} \frac{y_{S_2}(S^0 - \lambda_{S_1}) - y_{R_2}(R^0 - \lambda_{R_2})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}}, \\ \bar{x}_2 &= y_{S_2} y_{R_2} \frac{y_{R_1}(R^0 - \lambda_{R_2}) - y_{S_1}(S^0 - \lambda_{S_1})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}}, \end{aligned}$$

TABLE 1
Summary of steady states.

Steady state	Criteria for existence
E_0	always exists
E_{S_i}	$\lambda_{S_i} < S^0$, $\lambda_{R_i} < R^0$, and $T_i > C_i$
E_{R_i}	$\lambda_{S_i} < S^0$, $\lambda_{R_i} < R^0$, and $T_i < C_i$
E_{12}	$\lambda_{S_2} < \lambda_{S_1} < S^0$ and $\lambda_{R_1} < \lambda_{R_2} < R^0$ and $\min\{C_1, C_2\} < T^* < \max\{C_1, C_2\}$
E_{21}	$\lambda_{S_1} < \lambda_{S_2} < S^0$ and $\lambda_{R_2} < \lambda_{R_1} < R^0$ and $\min\{C_1, C_2\} < T_* < \max\{C_1, C_2\}$

and

$$E_{21} = \left(\lambda_{S_2}, \lambda_{R_1}, \bar{x}_1 \left(\frac{\alpha_1}{D + \alpha_1} \right)^{r_1+1}, \bar{x}_2 \left(\frac{\alpha_2}{D + \alpha_2} \right)^{r_2+1} \right),$$

whereas

$$(2.13) \quad \begin{aligned} \bar{x}_1 &= y_{S_1} y_{R_1} \frac{y_{S_2}(S^0 - \lambda_{S_2}) - y_{R_2}(R^0 - \lambda_{R_1})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}}, \\ \bar{x}_2 &= y_{S_2} y_{R_2} \frac{y_{R_1}(R^0 - \lambda_{R_1}) - y_{S_1}(S^0 - \lambda_{S_2})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}}, \end{aligned}$$

respectively.

In order for a steady state to be biologically reasonable, all of its components must be nonnegative. For any steady state (\bar{S}, \bar{R}) , since $f_i(\bar{S}, \bar{R}) = \min(p_i(\bar{S}), q_i(\bar{R}))$, if $f_i(\bar{S}, \bar{R}) = p_i(\bar{S})$, then $\bar{R} > \lambda_{R_i}$, and so S is limiting for population x_i , whereas if $f_i(\bar{S}, \bar{R}) = q_i(\bar{R})$, then $\bar{S} > \lambda_{S_i}$, and instead R is limiting.

In particular, for the single species steady states, E_{S_i} , since $f_i(\bar{S}, \bar{R}) = p_i(\lambda_{S_i})$, S is limiting for species i , and so $\bar{R} > \lambda_{R_i}$ must hold. A similar observation holds for the single species steady states of the form E_{R_i} .

For the coexistence steady states E_{ij} , $f_i(\bar{S}, \bar{R}) = p_i(\lambda_{S_i})$ and $f_j(\bar{S}, \bar{R}) = q_j(\lambda_{R_j})$, and so S is limiting for population i and R is limiting for population j . Therefore, $p_i(\lambda_{S_i}) < q_i(\lambda_{R_j})$ and so $\lambda_{R_j} > \lambda_{R_i}$ must hold. Similarly, $\lambda_{S_i} > \lambda_{S_j}$ must hold.

Table 1 summarizes the conditions required for each of the steady states above to be defined.

Let BC_+^3 denote the Banach space of bounded continuous functions mapping $(-\infty, 0]$ to \mathbb{R}^3 . From the general theory of integral differential equations (see Burton [8] and Miller [41]), for any initial data $\phi = (\phi_S, \phi_R, \phi_1, \phi_2) \in BC_+^3$, there exists a unique solution $\pi(\phi, t) := (S(\phi, t), R(\phi, t), x_1(\phi, t), x_2(\phi, t))$ for all $t \geq 0$ and $\pi(\phi; \cdot)|_{(-\infty, 0]} = \phi$. Throughout this paper, we also use $(S(t), R(t), x_1(t), x_2(t))$ to denote the solution $\pi(\phi, t)$ with $\phi \in BC_+^3$. By a positive solution of (2.1), we mean each component of the solution is positive for all $t > 0$.

Let $(S(t), R(t), x_1(t), x_2(t))$ be an arbitrarily fixed positive solution of (2.1). We use the linear chain trick (see MacDonald [37]). Define

$$(2.14) \quad y_i = \int_{-\infty}^t x_1(\theta) f_1(S(\theta), R(\theta)) G^i_{D, \alpha_1}(t - \theta) d\theta, \quad i = 0, 1, \dots, r_1,$$

$$(2.15) \quad z_j = \int_{-\infty}^t x_2(\theta) f_1(S(\theta), R(\theta)) G^j_{D, \alpha_2}(t - \theta) d\theta, \quad j = 0, 1, \dots, r_2,$$

where

$$G^i_{D, \alpha_i} = \frac{\alpha_i^{k+1}}{k!} t^k e^{-(D+\alpha_i)t}, \quad i = 1, 2 \quad \text{and} \quad k = 0, 1, \dots, \max(r_1, r_2).$$

Note that for $k \geq 1$, $i = 1, 2$,

$$\frac{d}{dt} G^k_{D, \alpha_i}(t) = \alpha_i G^{k-1}_{D, \alpha_i}(t) - (D + \alpha_i) G^k_{D, \alpha_i}(t),$$

$$\frac{d}{dt} G^0_{D, \alpha_i}(t) = -(D + \alpha_i) G^0_{D, \alpha_i}(t).$$

It follows that

$$(2.16) \quad \begin{aligned} S' &= (S^0 - S)D - \sum_{i=1}^2 \frac{x_i}{y_{S_i}} f_i(S, R), \\ R' &= (R^0 - R)D - \sum_{i=1}^2 \frac{x_i}{y_{R_i}} f_i(S, R), \\ x'_1(t) &= -Dx_1(t) + y_{r_1}, \\ y'_0 &= -(D + \alpha_1)y_0 + \alpha_1 x_1 f_1(S, R), \\ y'_i &= -(D + \alpha_1)y_i + \alpha_1 y_{i-1}, \quad i = 1, 2, \dots, r_1, \\ x'_2(t) &= -Dx_2(t) + z_{r_2}, \\ z'_0 &= -(D + \alpha_2)z_0 + \alpha_2 x_2 f_2(S, R), \\ z'_j &= -(D + \alpha_2)z_j + \alpha_2 z_{j-1}, \quad j = 1, 2, \dots, r_2. \end{aligned}$$

Set

$$W(t) = S^0 - S(t) - \frac{1}{y_{S_1}} \sum_{i=1}^{r_1} \frac{y_i(t)}{\alpha_1} - \frac{1}{y_{S_2}} \sum_{j=1}^{r_2} \frac{z_j(t)}{\alpha_2} - \frac{x_1}{y_{S_1}} - \frac{x_2}{y_{S_2}}$$

and

$$V(t) = R^0 - R(t) - \frac{1}{y_{R_1}} \sum_{i=1}^{r_1} \frac{y_i(t)}{\alpha_1} - \frac{1}{y_{R_2}} \sum_{j=1}^{r_2} \frac{z_j(t)}{\alpha_2} - \frac{x_1}{y_{R_1}} - \frac{x_2}{y_{R_2}}.$$

It follows from (2.16) that $W'(t) = -DW(t)$ and $V'(t) = -DV(t)$ for all $t \geq 0$ and consequently

$$(2.17) \quad S(t) + \frac{1}{y_{S_1}} \sum_{i=1}^{r_1} \frac{y_i(t)}{\alpha_1} + \frac{1}{y_{S_2}} \sum_{j=1}^{r_2} \frac{z_j(t)}{\alpha_2} + \frac{x_1}{y_{S_1}} + \frac{x_2}{y_{S_2}} = S^0 + \epsilon_S(t), \quad t \geq 0,$$

and

$$(2.18) \quad R(t) + \frac{1}{y_{R_1}} \sum_{i=1}^{r_1} \frac{y_i(t)}{\alpha_1} + \frac{1}{y_{R_2}} \sum_{j=1}^{r_2} \frac{z_j(t)}{\alpha_2} + \frac{x_1}{y_{R_1}} + \frac{x_2}{y_{R_2}} = R^0 + \epsilon_R(t), \quad t \geq 0,$$

where $\epsilon_S(t) \rightarrow 0$ and $\epsilon_R(t) \rightarrow 0$ exponentially as $t \rightarrow \infty$.

The following lemma states that the solutions of (2.1) are positive and bounded.

LEMMA 2.1. *For any $\phi \in BC_+^3$ with $\phi_S(0) \geq 0$, $\phi_R(0) \geq 0$, and $\phi_i(0) > 0$, $i = 1, 2$, the solution $\pi(\phi; t)$ is positive and bounded for all $t > 0$.*

Proof. The proof for the positivity of $\pi(\phi; t)$ is similar to that of Lemma 2.1 in [61] and is omitted here. It follows from (2.14) and (2.15) that $y_i(t)$ and $z_i(t)$ are all positive for $t > 0$. The boundedness of the solution $(S(t), R(t), x_1(t), x_2(t))$ then follows immediately from (2.17) and (2.18). \square

3. Statement of results. The main results are presented in this section. The first result states that if λ_{S_i} or λ_{R_i} is larger than the respective input nutrient concentration, then that population will die out, not due to competition, but rather because the nutrient supply is inadequate.

THEOREM 3.1. *Let $\pi(\phi; t)$ be any positive solution of (2.1). If $\lambda_{S_i} \geq S^0$ or $\lambda_{R_i} \geq R^0$ for some $i \in \{1, 2\}$, then $\lim_{t \rightarrow \infty} x_i(\phi; t) = 0$.*

The next result follows immediately from Theorem 3.1 and indicates that neither population can survive in the chemostat if the nutrient supply is inadequate.

THEOREM 3.2. *If for each $i = 1, 2$, $\lambda_{S_i} \geq S^0$ or $\lambda_{R_i} \geq R^0$, then $\lim_{t \rightarrow \infty} \pi(\phi; t) = E_0$ for every positive solution $\pi(\phi; t)$ of (2.1).*

The following two results describe conditions where one population survives but the other one dies out, indicating that the model can exhibit competitive exclusion.

THEOREM 3.3. *Assume that one of the following holds:*

(1) $\lambda_{S_1} < S^0$, $\lambda_{R_1} < R^0$, and either $\lambda_{S_2} \geq S^0$ or $\lambda_{R_2} \geq R^0$;

(2) $\lambda_{S_1} < \lambda_{S_2} < S^0$, and either $\lambda_{R_1} < \lambda_{R_2} < R^0$, or $R^0 > \lambda_{R_1} > \lambda_{R_2}$ and $T_* > \max\{C_1, C_2\}$;

(3) $S^0 > \lambda_{S_1} > \lambda_{S_2}$, $\lambda_{R_1} < \lambda_{R_2} < R^0$, and $T_* < \min\{C_1, C_2\}$.

If $T_1 > C_1$ ($T_1 < C_1$), then $\lim_{t \rightarrow \infty} \pi(\phi; t) = E_{S_1}$ (E_{R_1}) for every positive solution $\pi(\phi; t)$ of (2.1).

THEOREM 3.4. *Assume that one of the following holds:*

(1) $\lambda_{S_2} < S^0$, $\lambda_{R_2} < R^0$, and either $\lambda_{S_1} \geq S^0$ or $\lambda_{R_1} \geq R^0$;

(2) $\lambda_{S_2} < \lambda_{S_1} < S^0$, and either $\lambda_{R_2} < \lambda_{R_1} < R^0$, or $R^0 > \lambda_{R_2} > \lambda_{R_1}$ and $T_* > \max\{C_1, C_2\}$;

(3) $S^0 > \lambda_{S_2} > \lambda_{S_1}$, $\lambda_{R_2} < \lambda_{R_1} < R^0$, and $T_* < \min\{C_1, C_2\}$.

If $T_2 > C_2$ ($T_2 < C_2$), then $\lim_{t \rightarrow \infty} \pi(\phi; t) = E_{S_2}$ (E_{R_2}) for every positive solution $\pi(\phi; t)$ of (2.1).

The most interesting question is whether both populations coexist and, if so, under what conditions. Conditions guaranteeing coexistence are given in the next two theorems.

THEOREM 3.5. *Assume $\lambda_{S_1} < \lambda_{S_2} < S^0$, $\lambda_{R_2} < \lambda_{R_1} < R^0$, and $C_1 > T_* > C_2$. Then $\lim_{t \rightarrow \infty} \pi(\phi; t) = E_{21}$ for every positive solution $\pi(\phi; t)$ of (2.1).*

THEOREM 3.6. *Assume $\lambda_{S_2} < \lambda_{S_1} < S^0$, $\lambda_{R_1} < \lambda_{R_2} < R^0$, and $C_1 < T_* < C_2$. Then $\lim_{t \rightarrow \infty} \pi(\phi; t) = E_{12}$ for every positive solution $\pi(\phi; t)$ of (2.1).*

4. Proofs of the results. We shall use the following lemma due to Barbălat throughout this section. For a proof, see Gopalsamy [22].

LEMMA 4.1 (Barbălat lemma). *Let a be a finite number and $f: [a, +\infty) \rightarrow R$ be a differentiable function. If $\lim_{t \rightarrow \infty} f(t)$ exists (finite) and f' is uniformly continuous on $(a, +\infty)$, then $\lim_{t \rightarrow \infty} f'(t) = 0$.*

We shall also need the following lemma due to Hirsh, Hanisch, and Gabriel [28].

LEMMA 4.2 (fluctuation lemma). *Let a be a finite number and $f: [a, +\infty) \rightarrow R$ be a differentiable function. If $\liminf_{t \rightarrow \infty} f(t) < \limsup_{t \rightarrow \infty} f(t)$, then there exist*

sequences $\{t_m\} \uparrow \infty$ and $\{s_m\} \uparrow \infty$ such that

$$\lim_{m \rightarrow \infty} f(t_m) = \limsup_{t \rightarrow \infty} f(t), \quad f'(t_m) = 0,$$

$$\lim_{m \rightarrow \infty} f(s_m) = \liminf_{t \rightarrow \infty} f(t), \quad f'(s_m) = 0.$$

Proof of Theorem 3.1. This proof is basically similar to the proof of Theorem 3.1 in [61] but is included here for completeness.

We provide only the proof for the case of $\lambda_{S_1} \geq S^0$ or $\lambda_{R_1} \geq R^0$. For $\lambda_{S_2} \geq S^0$ or $\lambda_{R_2} \geq R^0$, the proof is similar. Set

$$(4.1) \quad w(t) = \frac{1}{y_{S_1}} \sum_{i=0}^{r_1} \frac{(D + \alpha_1)^i}{\alpha_1^{i+1}} y_i(t) + \frac{x_1(t)}{y_{S_1}} \left(\frac{D + \alpha_1}{\alpha_1} \right)^{r_1+1}, \quad t \geq 0.$$

It follows from (2.14), (2.15), (2.17), and (2.18) that $w(t)$ is positive and bounded for $t > 0$. By (4.1), we see that

$$(4.2) \quad w'(t) = \frac{x_1(t)}{y_{S_1}} \left[-D \left(\frac{D + \alpha_1}{\alpha_1} \right)^{r_1+1} + f_1(S(t), R(t)) \right].$$

From the first equation of (2.16) it follows that $S' < 0$ if $S \geq S^0$. We conclude that $S(t) < S^0$ for all large t , and hence from (4.2), $w'(t) < 0$ for all large t . Therefore $\lim_{t \rightarrow \infty} w(t)$ exists (finite). On the other hand, it follows from (2.16) that y'_i and x'_1 are all uniformly continuous, and hence w' is also uniformly continuous. By Lemma 4.1, $\lim_{t \rightarrow \infty} w'(t) = 0$, and thus

$$(4.3) \quad \lim_{t \rightarrow \infty} \frac{x_1(t)}{y_{S_1}} \left[-D \left(\frac{D + \alpha_1}{\alpha_1} \right)^{r_1+1} + f_1(S(t), R(t)) \right] = 0.$$

If $\limsup_{t \rightarrow \infty} x_1(t) > 0$, then $\lim_{t \rightarrow \infty} x_1(t_m) > 0$ for some sequence $\{t_m\} \uparrow \infty$ such that $\lim_{m \rightarrow \infty} x_1(t_m) > r$ for some $r > 0$. By (4.3), we have $\lim_{m \rightarrow \infty} S(t_m) = \lambda_{S_1}$ and $\lim_{m \rightarrow \infty} R(t_m) \geq \lambda_{R_1}$ or $\lim_{m \rightarrow \infty} R(t_m) = \lambda_{R_1}$ and $\lim_{m \rightarrow \infty} S(t_m) \geq \lambda_{S_1}$. Then from (2.17) and (2.18), we always have $\lim_{t \rightarrow \infty} x_1(t_m) = 0$, contradicting $r > 0$. Therefore $\limsup_{t \rightarrow \infty} x_1(t) = 0$. This completes the proof.

Let

$$(4.4) \quad \begin{aligned} u_i(t) &= x_1(t) + \sum_{j=i}^{r_1} \frac{y_j(t)}{\alpha_1}, \quad i = 0, 1, 2, \dots, r_1 + 1, \\ v_i(t) &= x_2(t) + \sum_{j=i}^{r_2} \frac{z_j(t)}{\alpha_2}, \quad i = 0, 1, 2, \dots, r_2 + 1, \end{aligned}$$

where we use the convention that $\sum_{j=m}^n k_j = 0$ if $n < m$. Thus $x_1 = u_{r_1+1}$ and

$x_2 = v_{r_2+1}$. By using (2.16) and (4.4), we obtain a new system:

$$\begin{aligned}
 u'_0(t) &= -Du_0(t) \\
 &\quad + u_{r_1+1}(t)f_1 \left(S^0 - \frac{1}{y_{S_1}}u_0(t) - \frac{1}{y_{S_2}}v_0(t) + \epsilon_S(t), \right. \\
 &\quad \left. R^0 - \frac{1}{y_{R_1}}u_0(t) - \frac{1}{y_{R_2}}v_0(t) + \epsilon_R(t) \right), \\
 u'_i(t) &= -(D + \alpha_1)u_i(t) + \alpha_1u_{i-1}(t), \quad i = 1, 2, \dots, r_1 + 1, \\
 v'_0(t) &= -Dv_0(t) \\
 &\quad + v_{r_2+1}(t)f_2 \left(S^0 - \frac{1}{y_{S_1}}u_0(t) - \frac{1}{y_{S_2}}v_0(t) + \epsilon_S(t), \right. \\
 &\quad \left. R^0 - \frac{1}{y_{R_1}}u_0(t) - \frac{1}{y_{R_2}}v_0(t) + \epsilon_R(t) \right), \\
 v'_j(t) &= -(D + \alpha_2)v_j(t) + \alpha_2v_{j-1}(t), \quad j = 1, 2, \dots, r_2 + 1.
 \end{aligned}
 \tag{4.5}$$

If $(S(t), R(t), x_1(t), x_2(t))$ is a solution of (2.1), then by Lemma 2.1, (2.14)–(2.18), $u_i(t)$, and $v_j(t)$ are all positive and bounded. Therefore, the following numbers are well defined:

$$\begin{aligned}
 \delta_i &= \liminf_{t \rightarrow \infty} u_i(t), \quad \gamma_i = \limsup_{t \rightarrow \infty} u_i(t), \quad i = 0, 1, 2, \dots, r_1 + 1, \\
 a_j &= \liminf_{t \rightarrow \infty} v_j(t), \quad b_j = \limsup_{t \rightarrow \infty} v_j(t), \quad j = 0, 1, 2, \dots, r_2 + 1.
 \end{aligned}
 \tag{4.6}$$

Clearly, $0 \leq \delta_i \leq \gamma_i$ and $0 \leq a_j \leq b_j$ for $i \in \{0, 1, \dots, r_1 + 1\}$ and $j \in \{0, 1, \dots, r_2 + 1\}$, and $u_i(t)$, $v_j(t)$ and their derivatives $u'_i(t)$, $v'_j(t)$ are also uniformly continuous.

LEMMA 4.3.

$$\left(\frac{\alpha_1}{D + \alpha_1} \right)^i \delta_0 \leq \delta_i \leq \gamma_i \leq \left(\frac{\alpha_1}{D + \alpha_1} \right)^i \gamma_0, \quad i = 1, 2, \dots, r_1 + 1,
 \tag{4.7}$$

and

$$\left(\frac{\alpha_2}{D + \alpha_2} \right)^j a_0 \leq a_j \leq b_j \leq \left(\frac{\alpha_2}{D + \alpha_2} \right)^j b_0, \quad j = 1, 2, \dots, r_2 + 1.
 \tag{4.8}$$

The proof of Lemma 4.3 is basically the same as that of Lemma 4.3 in [61].

LEMMA 4.4. $\gamma_0 \leq \min\{y_{S_1}(S^0 - \min(S^0, \lambda_{S_1})), y_{R_1}(R^0 - \min(R^0, \lambda_{R_1}))\}$, and $b_0 \leq \min\{y_{S_2}(S^0 - \min(S^0, \lambda_{S_2})), y_{R_2}(R^0 - \min(R^0, \lambda_{R_2}))\}$.

Proof. We show that $\gamma_0 \leq \min\{y_{S_1}(S^0 - \min(S^0, \lambda_{S_1})), y_{R_1}(R^0 - \min(R^0, \lambda_{R_1}))\}$. The proof for $b_0 \leq \min\{y_{S_2}(S^0 - \min(S^0, \lambda_{S_2})), y_{R_2}(R^0 - \min(R^0, \lambda_{R_2}))\}$ is similar. We consider two cases.

Case 1. Either $\lambda_{S_1} \geq S^0$ or $\lambda_{R_1} \geq R^0$. It will suffice to show $\delta_0 = \gamma_0 = 0$. By Theorem 3.1, $\lim_{t \rightarrow \infty} x_1(t) = 0$. It follows from Lemma 4.1 that $\lim_{t \rightarrow \infty} x'_1(t) = 0$. Then from the third equation of (2.16), we have $\lim_{t \rightarrow \infty} y_{r_1}(t) = 0$. Repeating this argument, we have that $\lim_{t \rightarrow \infty} y_i(t) = 0$ for $i = 0, 1, 2, \dots, r_1 + 1$. Applying (4.4) yields $\lim_{t \rightarrow \infty} u_0(t) = 0$, i.e., $\delta_0 = \gamma_0 = 0$, as desired.

Case 2. $\lambda_{S_1} < S^0$ and $\lambda_{R_1} < R^0$. We consider two cases: $\delta_0 < \gamma_0$ and $\delta_0 = \gamma_0$.

If $\delta_0 < \gamma_0$, we apply Lemma 4.2 to obtain a sequence $\{t_m\} \uparrow \infty$ such that

$$\lim_{m \rightarrow \infty} u_0(t_m) = \gamma_0 > 0 \quad \text{and} \quad \lim_{m \rightarrow \infty} u'_0(t_m) = 0.$$

From (4.5) it follows that

$$\begin{aligned} D\gamma_0 &= \lim_{m \rightarrow \infty} Du_0(t_m) \\ &= \lim_{m \rightarrow \infty} \left[u_{r_1+1}(t_m) f_1 \left(S^0 - \frac{1}{y_{S_1}} u_0(t_m) - \frac{1}{y_{S_2}} v_0(t_m) + \epsilon_S(t_m), \right. \right. \\ &\quad \left. \left. R^0 - \frac{1}{y_{R_1}} u_0(t_m) - \frac{1}{y_{R_2}} v_0(t_m) + \epsilon_R(t_m) \right) \right] \\ &\leq \limsup_{m \rightarrow \infty} u_{r_1+1}(t_m) f_1 \left(S^0 - \frac{1}{y_{S_1}} u_0(t_m) + \epsilon_S(t_m), R^0 - \frac{1}{y_{R_1}} u_0(t_m) + \epsilon_R(t_m) \right) \\ &\leq \gamma_{r_1+1} f_1 \left(S^0 - \frac{1}{y_{S_1}} \gamma_0, R^0 - \frac{1}{y_{R_1}} \gamma_0 \right). \end{aligned} \tag{4.9}$$

Using Lemma 4.3 and (4.9), we obtain

$$D\gamma_0 \leq \left(\frac{\alpha_1}{D + \alpha_1} \right)^{r_1+1} \gamma_0 f_1 \left(S^0 - \frac{1}{y_{S_1}} \gamma_0, R^0 - \frac{1}{y_{R_1}} \gamma_0 \right).$$

Therefore

$$\lambda_{S_1} \leq S^0 - \frac{1}{y_{S_1}} \gamma_0 \quad \text{and} \quad \lambda_{R_1} \leq R^0 - \frac{1}{y_{R_1}} \gamma_0$$

or

$$\gamma_0 \leq y_{S_1} (S^0 - \lambda_{S_1}) \quad \text{and} \quad \gamma_0 \leq y_{R_1} (R^0 - \lambda_{R_1})$$

or

$$\gamma_0 \leq \min\{y_{S_1} (S^0 - \lambda_{S_1}), y_{R_1} (R^0 - \lambda_{R_1})\}$$

as desired.

If $\delta_0 = \gamma_0$, we apply Lemma 4.1 to obtain $\lim_{t \rightarrow \infty} u'_0(t) = 0 > 0$. Using the first equation of (4.5), we have

$$\begin{aligned} D\gamma_0 &= \lim_{t \rightarrow \infty} Du_0(t) \\ &= \lim_{t \rightarrow \infty} \left[u_{r_1+1}(t) f_1 \left(S^0 - \frac{1}{y_{S_1}} u_0(t) - \frac{1}{y_{S_2}} v_0(t) + \epsilon_S(t), \right. \right. \\ &\quad \left. \left. R^0 - \frac{1}{y_{R_1}} u_0(t) - \frac{1}{y_{R_2}} v_0(t) + \epsilon_R(t) \right) \right] \\ &\leq \limsup_{t \rightarrow \infty} u_{r_1+1}(t) f_1 \left(S^0 - \frac{1}{y_{S_1}} u_0(t) + \epsilon_S(t), R^0 - \frac{1}{y_{R_1}} u_0(t) + \epsilon_R(t) \right) \\ &\leq \gamma_{r_1+1} f_1 \left(S^0 - \frac{1}{y_{S_1}} \gamma_0, R^0 - \frac{1}{y_{R_1}} \gamma_0 \right), \end{aligned}$$

which also gives

$$\gamma_0 \leq \min\{y_{S_1}(S^0 - \lambda_{S_1}), y_{R_1}(R^0 - \lambda_{R_1})\}.$$

The proof is complete. \square

LEMMA 4.5. *If*

$$(4.10) \quad \begin{aligned} & \min\{y_{S_2}(S^0 - \min(S^0, \lambda_{S_2})), y_{R_2}(R^0 - \min(R^0, \lambda_{R_2}))\} \\ & < \min\{y_{S_2}(S^0 - \min(S^0, \lambda_{S_1})), y_{R_2}(R^0 - \min(R^0, \lambda_{R_1}))\}, \end{aligned}$$

then $\delta_i > 0$ for $i = 0, 1, 2, \dots, r_1 + 1$.

Proof. By (4.7), it suffices to show $\delta_0 > 0$. Note that condition (4.10) implies $\lambda_{S_1} < S^0$ and $\lambda_{R_1} < R^0$.

Let

$$(4.11) \quad \delta := \liminf_{t \rightarrow \infty} w(t),$$

where

$$(4.12) \quad w(t) = \alpha_1 u_0(t) + \sum_{j=1}^{r_1+1} D \left(\frac{D + \alpha_1}{\alpha_1} \right)^{j-1} u_j(t).$$

It follows from (4.5) that

$$(4.13) \quad \begin{aligned} w'(t) = -\alpha_1 u_{r_1+1}(t) & \left[D \left(\frac{D + \alpha_1}{\alpha_1} \right)^{r_1+1} - f_1 \left(S^0 - \frac{1}{y_{S_1}} u_0(t) - \frac{1}{y_{S_2}} v_0(t) + \epsilon_S(t), \right. \right. \\ & \left. \left. R^0 - \frac{1}{y_{R_1}} u_0(t) - \frac{1}{y_{R_2}} v_0(t) + \epsilon_R(t) \right) \right]. \end{aligned}$$

We prove $\delta > 0$. Suppose that $\delta = 0$. Then there is a sequence $\{s_m\} \uparrow \infty$ such that $\epsilon_S(s_m) > -\varepsilon/2$ and $\epsilon_R(s_m) > -\varepsilon/2$, where ε is an arbitrarily fixed small positive number, $w'(s_m) \leq 0$, and $\lim_{m \rightarrow \infty} w(s_m) = 0$. Then it follows from (4.13) that

$$\begin{aligned} \alpha_1 u_{r_1+1}(s_m) & \left[D \left(\frac{D + \alpha_1}{\alpha_1} \right)^{r_1+1} - f_1 \left(S^0 - \frac{1}{y_{S_1}} u_0(s_m) - \frac{1}{y_{S_2}} v_0(s_m) + \epsilon_S(s_m), \right. \right. \\ & \left. \left. R^0 - \frac{1}{y_{R_1}} u_0(s_m) - \frac{1}{y_{R_2}} v_0(s_m) + \epsilon_R(s_m) \right) \right] \geq 0. \end{aligned}$$

Since $u_{r_1+1}(s_m) > 0$, the above inequality implies that

$$\begin{aligned} D \left(\frac{D + \alpha_1}{\alpha_1} \right)^{r_1+1} - f_1 \left(S^0 - \frac{1}{y_{S_1}} u_0(s_m) - \frac{1}{y_{S_2}} v_0(s_m) + \epsilon_S(s_m), \right. \\ \left. R^0 - \frac{1}{y_{R_1}} u_0(s_m) - \frac{1}{y_{R_2}} v_0(s_m) + \epsilon_R(s_m) \right) \geq 0. \end{aligned}$$

Consequently, for all large m , either

$$(4.14) \quad S^0 - \frac{1}{y_{S_1}} u_0(s_m) - \frac{1}{y_{S_2}} v_0(s_m) + \epsilon_S(s_m) \leq \lambda_{S_1}$$

or

$$(4.15) \quad R^0 - \frac{1}{y_{R_1}}u_0(s_m) - \frac{1}{y_{R_2}}v_0(s_m) + \epsilon_R(s_m) \leq \lambda_{R_1}.$$

If (4.14) holds, then for sufficiently large m ,

$$\begin{aligned} v_0(s_m) &\geq y_{S_2} \left(S^0 - \lambda_{S_1} - \frac{1}{y_{S_1}}u_0(s_m) + \epsilon_S(s_m) \right) \\ &> y_{S_2}(S^0 - \lambda_{S_1} + \epsilon_S(s_m)), \end{aligned}$$

which indicates

$$(4.16) \quad b_0 \geq y_{S_2}(S^0 - \lambda_{S_1})$$

since $\lim_{m \rightarrow \infty} \epsilon_S(s_m) = 0$. Similarly, if (4.15) holds, then

$$(4.17) \quad b_0 \geq y_{R_2}(R^0 - \lambda_{R_1}).$$

However, using Lemma 4.4 we see that (4.16) and (4.17) both contradict (4.10). Therefore $\delta > 0$.

Next we show that $\delta_0 > 0$. Suppose, to the contrary, that $\delta_0 = 0$. Then from (4.4) it follows that there is a sequence $\{t_m\} \uparrow \infty$ such that $\lim_{m \rightarrow \infty} u_0(t_m) = 0$. Note that from (4.4),

$$u_0(t_m) = u_{r_1+1}(t_m) + \sum_{j=0}^{r_1} \frac{y_j(t_m)}{\alpha_1}.$$

Then it follows that

$$\lim_{m \rightarrow \infty} u_0(t_m) = \lim_{m \rightarrow \infty} u_{r_1+1}(t_m) = \lim_{m \rightarrow \infty} y_j(t_m) = 0, \quad j = 0, 1, 2, \dots, r_1.$$

Using (4.4) once more, we obtain $\lim_{m \rightarrow \infty} u_j(t_m) = 0$ for $j = 0, 1, 2, \dots, r_1 + 1$. Now (4.11) and (4.12) imply $\lim_{m \rightarrow \infty} w(t_m) = 0$, which yields $\delta = 0$, a contradiction. This completes the proof. \square

The proof of the following lemma is similar to that of Lemma 4.5.

LEMMA 4.6. *If*

$$(4.18) \quad \begin{aligned} &\min\{y_{S_1}(S^0 - \min(S^0, \lambda_{S_1})), y_{R_1}(R^0 - \min(R^0, \lambda_{R_1}))\} \\ &< \min\{y_{S_1}(S^0 - \min(S^0, \lambda_{S_2})), y_{R_1}(R^0 - \min(R^0, \lambda_{R_2}))\}, \end{aligned}$$

then $a_j > 0$ for $j = 0, 1, 2, \dots, r_2 + 1$.

LEMMA 4.7. *Assume that one of the following holds:*

- (1) $\lambda_{S_1} < S^0, \lambda_{R_1} < R^0$, and either $\lambda_{S_2} \geq S^0$ or $\lambda_{R_2} \geq R^0$;
- (2) $\lambda_{S_1} < \lambda_{S_2} < S^0$, and either $\lambda_{R_1} < \lambda_{R_2} < R^0$, or $R^0 > \lambda_{R_1} > \lambda_{R_2}$ and $T_* > C_1, C_2$;
- (3) $S^0 > \lambda_{S_1} > \lambda_{S_2}, \lambda_{R_1} < \lambda_{R_2} < R^0$, and $T^* < C_1, C_2$.

Then $a_j = b_j = 0$ for $j = 0, 1, 2, \dots, r_2 + 1$.

Proof. By (4.8), it suffices to show $a_0 = b_0 = 0$. If (1) holds, the conclusion follows from Theorem 3.1. We provide a proof for (2). The proof for (3) is similar.

We apply Lemmas 4.1 and 4.2 to $u_0(t)$ to obtain a sequence $\{t_m\} \uparrow \infty$ such that

$$\lim_{m \rightarrow \infty} u_0(t_m) = \delta_0 \quad \text{and} \quad \lim_{m \rightarrow \infty} u'_0(t_m) = 0.$$

It follows from (4.5) that

$$(4.19) \quad \lim_{m \rightarrow \infty} Du_0(t_m) = \lim_{m \rightarrow \infty} \left[u_{r_1+1}(t_m) f_1 \left(S^0 - \frac{1}{y_{S_1}} u_0(t_m) - \frac{1}{y_{S_2}} v_0(t_m) + \epsilon_S(t_m), \right. \right. \\ \left. \left. R^0 - \frac{1}{y_{R_1}} u_0(t_m) - \frac{1}{y_{R_2}} v_0(t_m) + \epsilon_R(t_m) \right) \right].$$

Let $\varepsilon > 0$ be given. We have $\epsilon_S(t_m) > -\varepsilon/2, \epsilon_R(t_m) > -\varepsilon/2, u_{r_1+1}(t_m) \geq \delta_{r_1+1} - \varepsilon$ and $v_0(t_m) \leq b_0 + \varepsilon/2$ for all large m . Then (4.19) implies that

$$\lim_{m \rightarrow \infty} Du_0(t_m) \geq \lim_{m \rightarrow \infty} (\delta_{r_1+1} - \varepsilon) f_1 \left(S^0 - \frac{1}{y_{S_1}} u_0(t_m) - \frac{1}{y_{S_2}} b_0 - \varepsilon, \right. \\ \left. R^0 - \frac{1}{y_{R_1}} u_0(t_m) - \frac{1}{y_{R_2}} b_0 - \varepsilon \right)$$

or

$$D\delta_0 \geq (\delta_{r_1+1} - \varepsilon) f_1 \left(S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} b_0 - \varepsilon, R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} b_0 - \varepsilon \right).$$

Since $\varepsilon > 0$ is arbitrary, we have

$$D\delta_0 \geq \delta_{r_1+1} f_1 \left(S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} b_0, R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} b_0 \right).$$

By Lemma 4.3, the above inequality leads to

$$D \left(\frac{D + \alpha_1}{\alpha_1} \right)^{r_1+1} \delta_{r_1+1} \geq f_1 \left(S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} b_0, R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} b_0 \right) \delta_{r_1+1}.$$

Note that (2) implies (4.10). By Lemma 4.5, $\delta_{r_1+1} > 0$. Then the above inequality yields

$$(4.20) \quad S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} b_0 \leq \lambda_{S_1} \quad \text{or} \quad R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} b_0 \leq \lambda_{R_1}.$$

Next we show that $b_0 = 0$. Suppose, to the contrary, that $b_0 > 0$. Let $\varepsilon > 0$ be given. Apply Lemmas 4.1 and 4.2 to obtain a sequence $\{t_m\} \uparrow \infty$ such that

$$\lim_{m \rightarrow \infty} v_0(t_m) = b_0 \quad \text{and} \quad \lim_{m \rightarrow \infty} v'_0(t_m) \leq 0, \quad \text{and} \\ v_{r_2+1}(t_m) \leq b_{r_2+1} + \varepsilon, \quad u_0(t_m) \geq \delta_0 - \varepsilon/2.$$

It follows from (4.5) that

$$\lim_{m \rightarrow \infty} Dv_0(t_m) \leq \lim_{m \rightarrow \infty} \left[v_{r_2+1}(t_m) f_2 \left(S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} v_0(t_m) + \epsilon_S(t), \right. \right. \\ \left. \left. R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} v_0(t_m) + \epsilon_R(t) \right) \right].$$

Then

$$Db_0 \leq (b_{r_2+1} + \varepsilon) f_2 \left(S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} b_0 + \varepsilon, \right. \\ \left. R^0 - \frac{1}{y_{R_1}} \delta_0(t) - \frac{1}{y_{R_2}} b_0 + \varepsilon \right).$$

Letting $\varepsilon \rightarrow 0$, we obtain

$$(4.21) \quad Db_0 \leq b_{r_2+1} f_2 \left(S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} b_0, R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} b_0 \right).$$

By (4.8), the above inequality leads to

$$D \left(\frac{D + \alpha_2}{\alpha_2} \right)^{r_2+1} b_{r_2+1} \leq f_2 \left(S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} b_0, R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} b_0 \right) b_{r_2+1}.$$

Again note that $b_{r_1+1} > 0$. Then the above inequality yields

$$(4.22) \quad S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} b_0 \geq \lambda_{S_2} \quad \text{and} \quad R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} b_0 \geq \lambda_{R_2}.$$

Since $\lambda_{S_1} < \lambda_{S_2}$, the first equation of (4.20) contradicts the first equation of (4.22). Therefore, we must have

$$S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} b_0 \geq \lambda_{S_2} \quad \text{and} \quad R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} b_0 \leq \lambda_{R_1}$$

or

$$\frac{1}{y_{S_1}(S^0 - \lambda_{S_2})} \delta_0 + \frac{1}{y_{S_2}(S^0 - \lambda_{S_2})} b_0 \leq 1 \quad \text{and} \quad \frac{1}{y_{R_1}(R^0 - \lambda_{R_1})} \delta_0 + \frac{1}{y_{R_2}(R^0 - \lambda_{R_1})} b_0 \geq 1,$$

which contradicts $T_* > C_1, C_2$. Therefore $b_0 = 0$ and hence $a_0 = b_0 = 0$. The proof is complete. \square

The proof of the following lemma is similar to that of Lemma 4.7.

LEMMA 4.8. *Assume that one of the following holds:*

- (1) $\lambda_{S_2} < S^0$, $\lambda_{R_2} < R^0$, and either $\lambda_{S_1} \geq S^0$ or $\lambda_{R_1} \geq R^0$;
- (2) $\lambda_{S_2} < \lambda_{S_1} < S^0$, and either $\lambda_{R_2} < \lambda_{R_1} < R^0$, or $R^0 > \lambda_{R_1} > \lambda_{R_2}$ and $T_* > C_1, C_2$;
- (3) $S^0 > \lambda_{S_2} > \lambda_{S_1}$, $\lambda_{R_2} < \lambda_{R_1} < R^0$, and $T_* < C_1, C_2$.

Then $\delta_j = \gamma_j = 0$ for $j = 0, 1, 2, \dots, r_1 + 1$.

LEMMA 4.9. *If $\delta_0 > 0$ and $a_0 = b_0 = 0$, then either $\delta_i = \gamma_i = y_{S_1} \left(\frac{\alpha_1}{D + \alpha_1} \right)^i (S^0 - \lambda_{S_1})$ for all $i = 0, 1, 2, \dots, r_1 + 1$, or $\delta_i = \gamma_i = y_{R_1} \left(\frac{\alpha_1}{D + \alpha_1} \right)^i (R^0 - \lambda_{R_1})$ for all $i = 0, 1, 2, \dots, r_1 + 1$.*

Proof. We first show that $\delta_0 = \gamma_0$. Suppose, to the contrary, that $\delta_0 < \gamma_0$. By Lemma 4.2, there is a sequence $\{s_m\} \uparrow \infty$ such that

$$\lim_{m \rightarrow \infty} u_0(s_m) = \delta_0 \quad \text{and} \quad u'_0(s_m) = 0 \quad \text{for all } m.$$

By (4.5),

$$Du_0(s_m) = u_{r_1+1}(s_m) f_1 \left(S^0 - \frac{1}{y_{S_1}} u_0(s_m) - \frac{1}{y_{S_2}} v_0(s_m) + \epsilon_S(s_m), \right. \\ \left. R^0 - \frac{1}{y_{R_1}} u_0(s_m) - \frac{1}{y_{R_2}} v_0(s_m) - \epsilon_R(s_m) \right).$$

Letting $m \rightarrow \infty$ in the above equation and using (4.7), we obtain

$$\begin{aligned}
 D\delta_0 &= \lim_{m \rightarrow \infty} u_{r_1+1}(s_m) f_1 \left(S^0 - \frac{1}{y_{S_1}} \delta_0, R^0 - \frac{1}{y_{R_1}} \delta_0 \right) \\
 &\geq \delta_{r_1+1} f_1 \left(S^0 - \frac{1}{y_{S_1}} \delta_0, R^0 - \frac{1}{y_{R_1}} \delta_0 \right) \\
 (4.23) \quad &\geq \left(\frac{\alpha_1}{D + \alpha_1} \right)^{r_1+1} \delta_0 f_1 \left(S^0 - \frac{1}{y_{S_1}} \delta_0, R^0 - \frac{1}{y_{R_1}} \delta_0 \right).
 \end{aligned}$$

Canceling δ_0 in (4.23), we obtain

$$S^0 - \frac{1}{y_{S_1}} \delta_0 \leq \lambda_{S_1} \quad \text{or} \quad R^0 - \frac{1}{y_{R_1}} \delta_0 \leq \lambda_{R_1}$$

or equivalently

$$\delta_0 \geq y_{S_1}(S^0 - \lambda_{S_1}) \quad \text{or} \quad \delta_0 \geq y_{R_1}(R^0 - \lambda_{R_1}),$$

which, by Lemma 4.4, leads to $\delta_0 \geq \gamma_0$, a contradiction. Therefore, $\delta_0 = \gamma_0$. Since $\lim_{t \rightarrow \infty} u_0(t)$ exists, by (4.7) it follows that $\lim_{t \rightarrow \infty} u_i(t) = \delta_i = \gamma_i$ exists for every $i = 1, 2, \dots, r_1 + 1$. By Lemma 4.1, $\lim_{t \rightarrow \infty} u'_0(t) = 0$. It follows from (4.5) and (4.7) that

$$(4.24) \quad D\delta_0 \geq \left(\frac{\alpha_1}{D + \alpha_1} \right)^{r_1+1} \delta_0 f_1 \left(S^0 - \frac{1}{y_{S_1}} \delta_0, R^0 - \frac{1}{y_{R_1}} \delta_0 \right).$$

Since $\delta_0 > 0$, canceling δ_0 in (4.24) yields

$$\delta_0 \geq y_{S_1}(S^0 - \lambda_{S_1}) \quad \text{or} \quad \delta_0 \geq y_{R_1}(R^0 - \lambda_{R_1}).$$

By Lemma 4.4, this implies that either $\delta_0 = \gamma_0 = y_{S_1}(S^0 - \lambda_{S_1})$ or $\delta_0 = \gamma_0 = y_{R_1}(R^0 - \lambda_{R_1})$, as desired. The rest of the proof follows immediately from (4.7). \square

The proof of the following lemma is similar to that of Lemma 4.9.

LEMMA 4.10. *If $a_0 > 0$ and $\delta_0 = \gamma_0 = 0$, then either $a_i = b_i = y_{S_2} \left(\frac{\alpha_2}{D + \alpha_2} \right)^i (S^0 - \lambda_{S_2})$ for all $i = 0, 1, 2, \dots, r_2 + 1$, or $a_i = b_i = y_{R_2} \left(\frac{\alpha_2}{D + \alpha_2} \right)^i (R^0 - \lambda_{R_2})$ for all $i = 0, 1, 2, \dots, r_2 + 1$.*

LEMMA 4.11. *If $\lambda_{S_1} < \lambda_{S_2} < S^0$, $\lambda_{R_2} < \lambda_{R_1} < R^0$, and $C_1 > T_* > C_2$, then*

$$\delta_0 = \gamma_0 = y_{S_1} y_{R_1} \frac{y_{S_2}(S^0 - \lambda_{S_2}) - y_{R_2}(R^0 - \lambda_{R_1})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}}$$

and

$$a_0 = b_0 = y_{S_2} y_{R_2} \frac{y_{R_1}(R^0 - \lambda_{R_1}) - y_{S_1}(S^0 - \lambda_{S_2})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}},$$

$\delta_i = r_i = \left(\frac{\alpha_1}{D + \alpha_1} \right)^i \delta_0$ for $i = 1, 2, \dots, r_1 + 1$, and $a_i = b_i = \left(\frac{\alpha_2}{D + \alpha_2} \right)^i a_0$ for $i = 1, 2, \dots, r_2 + 1$.

Proof. First note that $C_1 > T_* > C_2$ is equivalent to

$$y_{R_1}(R^0 - \lambda_{R_1}) < y_{S_1}(S^0 - \lambda_{S_2}) \quad \text{and} \quad y_{S_2}(S^0 - \lambda_{S_2}) < y_{R_2}(R^0 - \lambda_{R_1}).$$

On the other hand, since $\lambda_{S_1} < \lambda_{S_2}$, $\lambda_{R_2} < \lambda_{R_1}$ it follows that

$$y_{S_1}(S^0 - \lambda_{S_1}) > y_{S_1}(S^0 - \lambda_{S_2}) \quad \text{and} \quad y_{R_1}(R^0 - \lambda_{R_2}) > y_{R_1}(R^0 - \lambda_{R_1}).$$

It follows that (4.10) and (4.18) hold. From Lemmas 4.5 and 4.6, it follows that $\delta_0 > 0$ and $a_0 > 0$. Since $\delta_0 > 0$, we can apply Lemmas 4.1 and 4.2 to $u_0(t)$, and use the same argument as in the proof of Lemma 4.9, to obtain either

$$(4.25) \quad S^0 - \frac{1}{y_{S_1}}\delta_0 - \frac{1}{y_{S_2}}b_0 \leq \lambda_{S_1}$$

or

$$(4.26) \quad R^0 - \frac{1}{y_{R_1}}\delta_0 - \frac{1}{y_{R_2}}b_0 \leq \lambda_{R_1}.$$

Similarly, since $a_0 > 0$, we can apply Lemmas 4.1 and 4.2 to $v_0(t)$ to obtain either

$$(4.27) \quad S^0 - \frac{1}{y_{S_1}}\gamma_0 - \frac{1}{y_{S_2}}a_0 \leq \lambda_{S_2}$$

or

$$(4.28) \quad R^0 - \frac{1}{y_{R_1}}\gamma_0 - \frac{1}{y_{R_2}}a_0 \leq \lambda_{R_2}.$$

Since $\gamma_0 > 0$, we can apply Lemmas 4.1 and 4.2 to $u_0(t)$, and use the same argument as in the proof of Lemma 4.9, to obtain

$$(4.29) \quad S^0 - \frac{1}{y_{S_1}}\gamma_0 - \frac{1}{y_{S_2}}a_0 \geq \lambda_{S_1}$$

and

$$(4.30) \quad R^0 - \frac{1}{y_{R_1}}\gamma_0 - \frac{1}{y_{R_2}}a_0 \geq \lambda_{R_1}.$$

Similarly, since $b_0 > 0$, by applying Lemmas 4.1 and 4.2 to $v_0(x)$, one can obtain

$$(4.31) \quad S^0 - \frac{1}{y_{S_1}}\delta_0 - \frac{1}{y_{S_2}}b_0 \geq \lambda_{S_2}$$

and

$$(4.32) \quad R^0 - \frac{1}{y_{R_1}}\delta_0 - \frac{1}{y_{R_2}}b_0 \geq \lambda_{R_2}.$$

Since $\lambda_{S_1} < \lambda_{S_2}$ and $\lambda_{R_2} < \lambda_{R_1}$, it follows from (4.31) and (4.30) that neither (4.25) nor (4.28) is possible. Let $\Delta_1 = \gamma_0 - \delta_0$ and $\Delta_2 = b_0 - a_0$. Clearly $\Delta_1 \geq 0$ and $\Delta_2 \geq 0$. Combining (4.26) and (4.30) it follows that

$$\Delta_2 \geq \frac{y_{R_2}}{y_{R_1}} \Delta_1.$$

Combining (4.27) and (4.31) it follows that

$$\Delta_1 \geq \frac{y_{S_1}}{y_{S_2}} \Delta_2.$$

Therefore

$$\Delta_1 \geq \frac{y_{S_1} y_{R_2}}{y_{S_2} y_{R_1}} \Delta_1.$$

Note that $C_1 > C_2$ or $\frac{y_{S_1} y_{R_2}}{y_{S_2} y_{R_1}} > 1$. It follows that $\Delta_1 = 0$, and thus $\Delta_2 = 0$. Therefore, $\gamma_0 = \delta_0$ and $b_0 = a_0$. Since $\lim_{t \rightarrow \infty} u_0(t)$ and $\lim_{t \rightarrow \infty} v_0(t)$ exist, from (4.5) it follows that $\lim_{t \rightarrow \infty} u_i(t) = \delta_i = \gamma_i$ exists for every $i = 1, 2, \dots, r_1 + 1$, and $\lim_{t \rightarrow \infty} v_i(t) = a_i = b_i$ exists for every $i = 1, 2, \dots, r_2 + 1$.

Applying Lemma 4.1 to $u_0(t)$,

$$(4.33) \quad D\delta_0 = \left(\frac{\alpha_1}{D + \alpha_1} \right)^{r_1+1} \delta_0 f_1 \left(S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} a_0, R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} a_0 \right).$$

Since $\delta_0 > 0$, canceling δ_0 in (4.33) yields either

$$(4.34) \quad S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} a_0 = \lambda_{S_1}$$

or

$$(4.35) \quad R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} a_0 = \lambda_{R_1}.$$

Similarly, applying Lemma 4.1 to $v_0(t)$, we obtain either

$$(4.36) \quad S^0 - \frac{1}{y_{S_1}} \delta_0 - \frac{1}{y_{S_2}} a_0 = \lambda_{S_2}$$

or

$$(4.37) \quad R^0 - \frac{1}{y_{R_1}} \delta_0 - \frac{1}{y_{R_2}} a_0 = \lambda_{R_2}.$$

By the hypotheses of Lemma 4.11, (4.30), and (4.31), we see that only (4.35) and (4.36) can hold. Solving (4.35) and (4.36), we have

$$\delta_0 = \gamma_0 = y_{S_1} y_{R_1} \frac{y_{S_2}(S^0 - \lambda_{S_2}) - y_{R_2}(R^0 - \lambda_{R_1})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}}$$

and

$$a_0 = y_{S_2} y_{R_2} \frac{y_{R_1}(R^0 - \lambda_{R_1}) - y_{S_1}(S^0 - \lambda_{S_2})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}},$$

as desired. The rest of the proof follows immediately by Lemma 4.3. \square

The proof of the following lemma is similar to that of Lemma 4.11.

LEMMA 4.12. *If $\lambda_{S_2} < \lambda_{S_1} < S^0$, $\lambda_{R_1} < \lambda_{R_2} < R^0$, and $C_1 < T^* < C_2$, then*

$$\delta_0 = \gamma_0 = y_{S_1} y_{R_1} \frac{y_{S_2}(S^0 - \lambda_{S_1}) - y_{R_2}(R^0 - \lambda_{R_2})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}},$$

$$a_0 = b_0 = y_{S_2} y_{R_2} \frac{y_{R_1}(R^0 - \lambda_{R_2}) - y_{S_1}(S^0 - \lambda_{S_1})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}},$$

$\delta_i = r_i = \left(\frac{\alpha_1}{D+\alpha_1}\right)^i \delta_0$ for $i = 1, 2, \dots, r_1 + 1$, and $a_i = b_i = \left(\frac{\alpha_2}{D+\alpha_2}\right)^i a_0$ for $i = 1, 2, \dots, r_2 + 1$.

We are now ready to prove Theorems 3.3–3.6.

Proof of Theorem 3.3. First note that by Lemma 4.7, $a_j = b_j = 0$ for $j = 0, 1, 2, \dots, r_2 + 1$. It follows from Lemma 4.5 that $\delta_0 > 0$. Then by Lemma 4.9, either

$$(4.38) \quad \delta_0 = \gamma_0 = y_{S_1}(S^0 - \lambda_{S_1}), \quad \delta_{r_1+1} = \gamma_{r_1+1} = y_{S_1} \left(\frac{\alpha_1}{D + \alpha_1}\right)^{r_1+1} (S^0 - \lambda_{S_1})$$

or

$$(4.39) \quad \delta_0 = \gamma_0 = y_{R_1}(R^0 - \lambda_{R_1}), \quad \delta_{r_1+1} = \gamma_{r_1+1} y_{R_1} \left(\frac{\alpha_1}{D + \alpha_1}\right)^{r_1+1} (R^0 - \lambda_{R_1}).$$

If (4.38) holds, from (2.17) we have

$$\begin{aligned} \lim_{t \rightarrow \infty} (S^0 - S(t) + \epsilon_S(t)) &= \lim_{t \rightarrow \infty} \left[\frac{1}{y_{S_1}} \sum_{i=1}^{r_1} \frac{y_i(t)}{\alpha_1} + \frac{1}{y_{S_2}} \sum_{j=1}^{r_2} \frac{y_j(t)}{\alpha_2} + \frac{x_1}{y_{S_1}} + \frac{x_2}{y_{S_2}} \right] \\ &= \lim_{t \rightarrow \infty} \left[\frac{1}{y_{S_1}} u_0(t) + \frac{1}{y_{S_2}} v_0(t) \right] \\ &= \frac{1}{y_{S_1}} \gamma_0 + \frac{1}{y_{S_2}} b_0 \\ &= S^0 - \lambda_{S_1}. \end{aligned}$$

This leads to $\lim_{t \rightarrow \infty} S(t) = \lambda_{S_1}$, and

$$(4.40) \quad \lim_{t \rightarrow \infty} \pi(\phi; t) = \lim_{t \rightarrow \infty} (S(t), u_{r_1+1}, v_{r_2+1}(t)) = E_{\lambda_{S_1}}.$$

Similarly, if (4.39) holds, one can show that

$$(4.41) \quad \lim_{t \rightarrow \infty} \pi(\phi; t) = E_{\lambda_{R_1}}.$$

One can check that if $T_1 > C_1$, then (4.41) is impossible and (4.40) must hold, but if $T_1 < C_1$, then (4.40) is impossible and (4.41) must hold. This completes the proof. \square

The proof of Theorem 3.4 is similar to that of Theorem 3.3.

Proof of Theorem 3.5. By Lemma 4.11,

$$(4.42) \quad \begin{aligned} \delta_0 = \gamma_0 &= y_{S_1} y_{R_1} \frac{y_{S_2}(S^0 - \lambda_{S_2}) - y_{R_2}(R^0 - \lambda_{R_1})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}}, \\ \delta_{r_1+1} = \gamma_{r_1+1} &= \left(\frac{\alpha_1}{D + \alpha_1}\right)^{r_1+1} \delta_0, \end{aligned}$$

and

$$(4.43) \quad \begin{aligned} a_0 = b_0 &= y_{S_2} y_{R_2} \frac{y_{R_1}(R^0 - \lambda_{R_1}) - y_{S_1}(S^0 - \lambda_{S_2})}{y_{S_2} y_{R_1} - y_{S_1} y_{R_2}}, \\ a_{r_2+1} = b_{r_2+1} &= \left(\frac{\alpha_2}{D + \alpha_2}\right)^{R_2+1} a_0. \end{aligned}$$

It follows from (2.17) that

$$\begin{aligned} \lim_{t \rightarrow \infty} (S^0 - S(t) + \epsilon_S(t)) &= \lim_{t \rightarrow \infty} \left[\frac{1}{y_{S_1}} \sum_{i=1}^{r_1} \frac{y_i(t)}{\alpha_1} + \frac{1}{y_{S_2}} \sum_{j=1}^{r_2} \frac{y_j(t)}{\alpha_2} + \frac{x_1}{y_{S_1}} + \frac{x_2}{y_{S_2}} \right] \\ &= \lim_{t \rightarrow \infty} \left[\frac{1}{y_{S_1}} u_0(t) + \frac{1}{y_{S_2}} v_0(t) \right] \\ &= \frac{1}{y_{S_1}} \gamma_0 + \frac{1}{y_{S_2}} b_0 \\ &= S^0 - \lambda_{S_2}, \end{aligned}$$

and

$$\begin{aligned} \lim_{t \rightarrow \infty} (R^0 - R(t) + \epsilon_R(t)) &= \lim_{t \rightarrow \infty} \left[\frac{1}{y_{R_1}} \sum_{i=1}^{r_1} \frac{y_i(t)}{\alpha_1} + \frac{1}{y_{R_2}} \sum_{j=1}^{r_2} \frac{z_j(t)}{\alpha_2} + \frac{x_1}{y_{R_1}} + \frac{x_2}{y_{R_2}} \right] \\ &= \lim_{t \rightarrow \infty} \left[\frac{1}{y_{R_1}} u_0(t) + \frac{1}{y_{R_2}} v_0(t) \right] \\ &= \frac{1}{y_{R_1}} \gamma_0 + \frac{1}{y_{R_2}} b_0 \\ &= R^0 - \lambda_{R_1}. \end{aligned}$$

This leads to $\lim_{t \rightarrow \infty} S(t) = \lambda_{S_2}$, $\lim_{t \rightarrow \infty} R(t) = \lambda_{R_1}$,

$$(4.44) \quad \lim_{t \rightarrow \infty} \pi(\phi; t) = \lim_{t \rightarrow \infty} (S(t), u_{r_1+1}, v_{r_2+1}(t)) = E_{12}.$$

The proof is complete. \square

The proof of Theorem 3.6 is similar to that of Theorem 3.5.

5. Discussion. In this paper, we studied system (2.1), a mathematical model describing two populations of microorganisms competing for two perfectly complementary nutrients in a chemostat, and we determined the global dynamics. The model involves integral differential equations to model the time lag involved in the conversion of nutrient to new cells as a distributed delay. Our analysis relied heavily on the linear chain technique and the fluctuation lemma. Sufficient conditions were obtained in terms of biologically meaningful parameters in the model, which guarantee competitive exclusion for certain parameter ranges and coexistence of the two populations for other parameter ranges in the form of globally attracting steady states.

It appears that the global attractivity results for model (2.1) are similar to those for the corresponding ODEs model (1.2) (see [11, 30]). However, it should be remembered that the values of the break-even concentrations λ_{S_i} and λ_{R_i} play an important role in predicting the asymptotic outcome of the model. These parameters depend not only on D , the flow rate of the chemostat, as in the ODEs model, but also on

the parameters in the specific delay kernel chosen. Therefore, including delays in the model may change the relative values of the λ 's, and hence the prediction of the outcome, in particular, whether there is coexistence or competitive exclusion, and in the case of competitive exclusion, which of the two competitors is the sole survivor. To see this note that by (2.4)

$$(5.1) \quad \begin{aligned} \lambda_{S_i}(\alpha_i, r_i) &= p_i^{-1} \left(D \left(\frac{D + \alpha_i}{\alpha_i} \right)^{r_i+1} \right), \\ \lambda_{R_i}(\alpha_i, r_i) &= q_i^{-1} \left(D \left(\frac{D + \alpha_i}{\alpha_i} \right)^{r_i+1} \right). \end{aligned}$$

Let $\lambda_{S_i}(0)$ and $\lambda_{R_i}(0)$, $i = 1, 2$, denote the values of break-even concentrations for the ODEs model (1.2). If, for example,

$$\lambda_{S_1}(0) < \lambda_{S_2}(0) < S^0 \quad \text{and} \quad \lambda_{R_1}(0) < \lambda_{R_2}(0) < R^0,$$

then model (1.2) predicts that population x_1 survives and population x_2 dies out. (The limiting value of x_1 depends on whether x_1 is S -limited or R -limited at the steady state.) It follows from (5.1) that if the mean delay τ_i is sufficiently small (e.g., let $\alpha_i \rightarrow \infty$ with $\tau_i \rightarrow 0$), $i = 1, 2$, then

$$\lambda_{S_1}(\alpha_1, r_1) < \lambda_{S_2}(\alpha_2, r_2) < S^0 \quad \text{and} \quad \lambda_{R_1}(\alpha_1, r_1) < \lambda_{R_2}(\alpha_2, r_2) < R^0.$$

By Theorem 3.3, x_1 survives and x_2 dies out as in the ODEs case, i.e., small mean delays do not affect the qualitative behavior of the model and therefore can be neglected. However, if the mean delay τ_1 is significant, the above inequalities may be reversed. For instance, if for a relatively large τ_1 , instead

$$\lambda_{S_2}(\alpha_2, r_2) < \lambda_{S_1}(\alpha_1, r_1) < S^0 \quad \text{and} \quad \lambda_{R_1}(\alpha_1, r_1) < \lambda_{R_2}(\alpha_2, r_2) < R^0,$$

then there are at least two other possibly outcomes: (1) x_2 survives and x_1 dies out (Theorem 3.4); (2) both x_1 and x_2 coexist (Theorem 3.6) depending on the relative values of the λ 's with respect to S^0 and R^0 , as well as the yield constants y_{S_i} and y_{R_i} , $i = 1, 2$. As a consequence, compared with the ODEs model, the distributed delay model (2.1) may give completely different predictions about the outcome of the competition. We observe that the yield constants y_{S_i} and y_{R_i} cannot all be scaled out (as can be done in the case of one limiting nutrient). In fact, these parameters play an important role in the prediction of the outcome of the competition as shown in Theorems 3.3–3.6.

In practice, the actual form of the delay kernels is not known precisely. Readers may have the impression that the delay kernels used were simply chosen so that the linear chain trick could be used. However, as proved in [61], both the discrete delay model (1.3) and the ODEs model (1.1) are limiting cases of the distributed delay model (1.6) with this choice of kernel. A similar argument can be used to show that the ODEs model (1.2) and the discrete delay model (1.4) are limiting cases of the distributed delay model (2.1). Replacing $\left(\frac{D+\alpha_i}{\alpha_i}\right)^{r_i+1}$ by $e^{D\tau_i}$ in (2.4) as well as in $E_{\lambda_{S_i}}, E_{\lambda_{R_i}}$, $i = 1, 2$, E_{12} and E_{21} , and handling the problem in a much simpler fashion than the analysis in this paper, one can show that Theorems 3.1–3.6 are indeed still valid for the discrete model (1.4). In Hines [27], some theoretical evidence is provided for selecting unimodal-type delay kernels in integral delay differential equations. However, it would

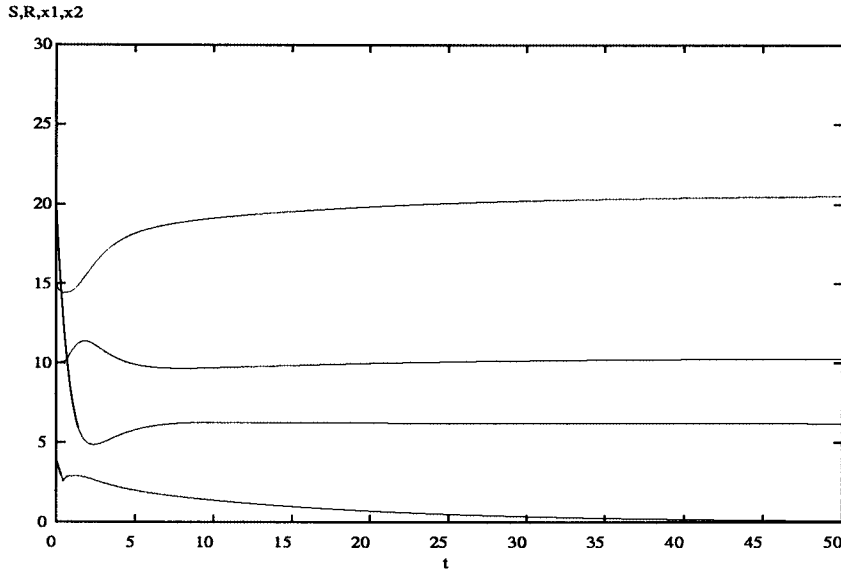


FIG. 1. This figure shows that for initial data $(S(\theta), R(\theta), x_1(\theta), x_2(\theta)) = (20, 15, 4, 10), \theta \in [-\max\{\tau_1, \tau_2\}, 0]$, the solution tends to E_{S_2} . x_2 wins.

still be of interest to investigate the global dynamics for more general kernels. We leave this problem for future investigation.

Note also that our formulation of the model involves delay kernels that require that initial conditions be specified on $(-\infty, 0)$. Obviously, in practical applications it is not usually possible to know the entire past history as required. However, note that the predictions for the outcome of the competition in the cases we considered indicate global attractivity and hence show that in these cases the outcome should be totally independent of the initial conditions.

In this paper we did not consider two cases: (1) $\lambda_{S_1} < \lambda_{S_2} < S^0, \lambda_{R_2} < \lambda_{R_1} < R^0$, and $C_1 < T_* < C_2$; (2) $\lambda_{S_2} < \lambda_{S_1} < S^0, \lambda_{R_1} < \lambda_{R_2} < R^0$, and $C_1 > T_* > C_2$. As a matter of fact, for the ODEs model (1.2), in case (1) (case (2)) the coexistence steady state E_{21} (E_{12}) is a saddle, and each nonsteady state positive solution approaches a boundary steady state, depending on the initial conditions. Our extensive simulation work indicates that this bistability is maintained when discrete delays are introduced (as in model (1.4)). We speculate that this is also true for model (2.1) as well as for other types of distributed delays.

As pointed out earlier, it is difficult to provide initial conditions for model (2.1) in order to carry out meaningful simulations. For simulations of the integral differential equations model (1.6) that show the effect of varying the parameters in the kernel as well as the initial data, see [61]. Since model (1.4) is a limiting case of model (2.1), and since the simulations of (1.6) in [61] (see in particular their Figure 1) seem to indicate that there should be very little difference between the simulations of the discrete delay model and those for the integral differential equation model for kernels of sufficiently high order (e.g., $r_i \geq 40$), instead we carried out extensive simulation work on model (1.4). These simulations confirm our theoretical findings and complement our work where theoretical results are absent.

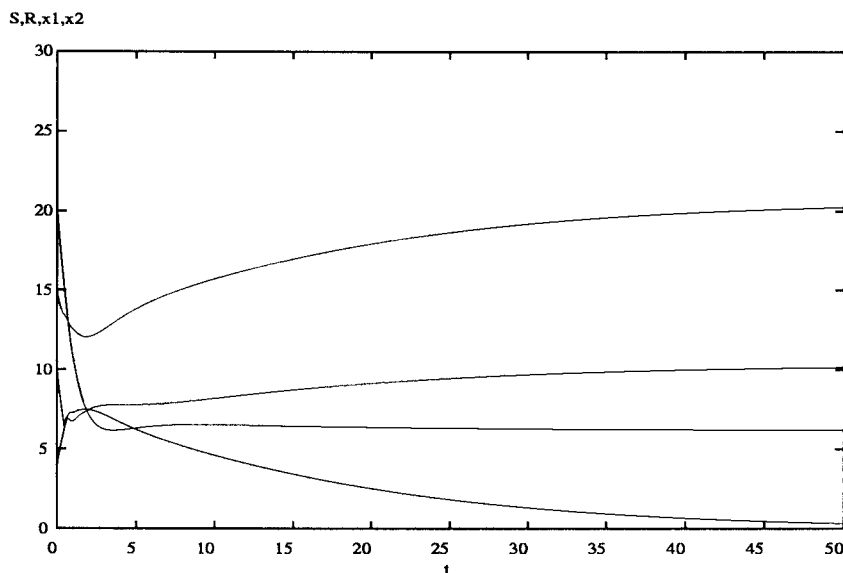


FIG. 2. This figure shows that for initial data $(S(\theta), R(\theta), x_1(\theta), x_2(\theta)) = (20, 15, 10, 4), \theta \in [-\max\{\tau_1, \tau_2\}, 0]$, the solution tends to E_{R_1} . x_2 loses.

For example, let

$$p_i(S) = \frac{m_i S}{a_i + S}, \quad q_i(R) = \frac{n_i R}{b_i + R},$$

and $\tau_1 = 0.4, \tau_2 = 0.6, D = 1, S^0 = 25, R^0 = 30, a_1 = 3, m_1 = 2, a_2 = 4, m_2 = 3, b_1 = 5, n_1 = 4, b_2 = 9, n_2 = 3.6, y_{S_1} = y_{R_2} = 2, y_{R_1} = y_{S_2} = 1$. Then

$$\lambda_{S_1} = 8.8064, \lambda_{S_2} = 6.1876, \lambda_{R_1} = 2.9738, \lambda_{R_2} = 9.2237, C_1 = 2, C_2 = 0.5, T^* = 1.283.$$

So, the criteria for case (2) hold. Figure 1 shows that for initial data

$$(S(\theta), R(\theta), x_1(\theta), x_2(\theta)) = (20, 15, 4, 10), \theta \in [-\max\{\tau_1, \tau_2\}, 0],$$

the solution tends to the boundary steady state of the form $E_{S_2} = (S_2^*, R_2^*, 0, x_2^*)$, where for $i = 1, 2$,

$$De^{D\tau_i} = \min \left\{ \frac{m_i S_i^*}{a_i + S_i^*}, \frac{n_i R_i^*}{b_i + R_i^*} \right\}, \quad (S^0 - S_i^*)D = \frac{x_i^*}{y_{S_i}} De^{D\tau_i}, \quad (R^0 - R_i^*)D = \frac{x_i^*}{y_{R_i}} De^{D\tau_i}. \tag{5.2}$$

Indeed, it can be shown that $E_{S_2} = (\lambda_{S_2}, R^0 - C_2(S^0 - \lambda_{S_2}), 0, e^{-D\tau_2} y_{S_2}(S^0 - \lambda_{S_2}))$. The difference between the expression for E_{S_2} here and that given in section 2 is due to the difference between models (1.4) and (2.1).

Figure 2 shows that for the same set of parameters, but different initial data

$$(S(\theta), R(\theta), x_1(\theta), x_2(\theta)) = (20, 15, 10, 4), \theta \in [-\max\{\tau_1, \tau_2\}, 0],$$

the solution tends to the boundary steady state of the form $E_{R_1} = (S_1^*, R_1^*, x_1^*, 0) = (S^0 - (R^0 - \lambda_{R_1})/C_1, \lambda_{R_1}, e^{-D\tau_1} y_{R_1}(R^0 - \lambda_{R_1}), 0)$.

We conclude by considering the effect of enriching the environment. First we consider the growth model. In experiments it has been demonstrated that in certain cases enriching by increasing the feed concentration of both resources simultaneously (i.e., increasing both S^0 and R^0 simultaneously) can enhance the growth of a population of microorganisms more than by just enriching by increasing the feed concentration of a single resource. See, for example, [17, 48, 49]. Although in model (2.1) we are assuming that only one resource is limiting to a particular population at a time, the model still seems to capture this phenomenon to some extent. For example, assume that $x_2(t) \equiv 0$ so that we are considering the growth of population x_1 . Suppose also that before enrichment $T_1 > C_1$ so that population x_1 is S limited. If $y_{S_1} > y_{R_1}$, if the feed concentration of each resource is simultaneously increased by the same fixed amount η where η is larger than $\frac{y_{R_1}(R^0 - \lambda_{R_1}) - y_{S_1}(S^0 - \lambda_{S_1})}{y_{S_1} - y_{R_1}}$, then population x_1 does better than if the feed concentration of either resource alone was increased by any amount. Alternatively, regardless of the relative values of y_{S_1} and y_{R_1} , if S^0 is increased by μ where μ is larger than $\frac{y_{R_1}(R^0 - \lambda_{R_1}) - y_{S_1}(S^0 - \lambda_{S_1})}{y_{S_1}}$ and R^0 is increased by any amount, then again population x_1 does better than if the feed concentration of either resource alone was increased by any amount. In fact, our model suggests that it is most efficient to enhance the growth rate, by increasing the input concentration of both resources simultaneously in such a way as to keep T_1 as close to C_1 as possible. Note also that, due to the distributed delay in the model, the transition from limitation of the population by one resource to limitation by the other, after a change in the feed concentrations of both resources (as indicated above), may actually appear to pass through a region of simultaneous limitation rather than to proceed stepwise.

Our results seem to indicate that instead of increasing the feed concentration of both resources simultaneously, a better test of whether there can actually be limitation by two resources at the same time would be to perform the following experiment. Set up two chemostats under the same operating parameters with the same microbial populations under steady state conditions where one suspects that both resources are limiting at the same time. In one chemostat increase only the feed concentration of one resource and in the other chemostat (all else being the same) increase only the feed concentration of the other resource. If growth is enhanced in both cases, then this would indicate that both resources are in fact limiting at the same time.

Finally we consider enrichment of the competition model. For the sake of discussion, we assume that $\lambda_{S_2} < \lambda_{S_1} < S^0$ and $\lambda_{R_1} < \lambda_{R_2} < R^0$. Then, it follows easily that $T_1 > T^*$, $T_1 > T_*$, $T_2 < T^*$, and $T_2 < T_*$, and these inequalities remain unchanged if we increase R^0 . We assume also that $C_1 < C_2$. Suppose to begin with that $T^* < T_1 < C_1$. Then, by Theorem 3.3(3) E_{R_1} is the global attractor (with respect to initial data in the positive cone) and so competitive exclusion holds with x_1 the sole survivor, R limited. If R^0 is increased until $T^* < C_1 < T_1$, by Theorem 3.3(3) E_{S_1} becomes the global attractor and so competitive exclusion still holds but with x_1 the sole survivor S limited. Increasing R^0 even more so that $C_1 < T^* < C_2$, by Theorem 3.6, E_{12} is the global attractor and so there is coexistence with x_1 S limited and x_2 R limited. Increasing R^0 even more, so that $T_2 < C_2 < T^*$ (recalling that we are assuming that $T_2 < T^*$), by Theorem 3.4(2) E_{R_2} becomes the global attractor and so once again there is competitive exclusion but now with x_2 the sole survivor, R limited. Increasing R^0 so that $C_2 < T_2 < T^*$, by Theorem 3.4(2) E_{S_2} becomes the global attractor, with x_2 the sole survivor being S limited. Thus enrichment can change the predicted outcome from competitive exclusion to coexistence or from coexistence to competitive exclusion, or from competitive exclusion to competitive exclusion but a

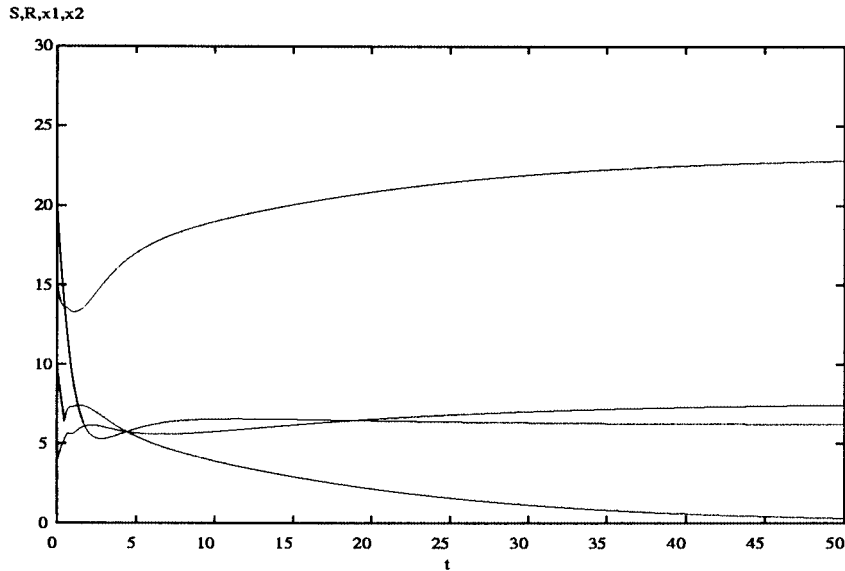


FIG. 3. This figure shows that for the same parameters (except for S^0) and initial data as in Figure 2, when S^0 decreases from 25 to 20, x_2 wins.

change in the winner, or it can have no effect on the predicted outcome. Note also that decreasing S^0 instead of increasing R^0 would have the same effect (Figure 3).

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