DISCRETE AND CONTINUOUS
DYNAMICAL SYSTEMS SERIES S
Volume **7**, Number **6**, December **2014**

doi:10.3934/dcdss.2014.7.1259

pp. **1259–1285**

DYNAMICS OF TWO PHYTOPLANKTON SPECIES COMPETING FOR LIGHT AND NUTRIENT WITH INTERNAL STORAGE

Sze-Bi Hsu

Department of Mathematics
National Tsing Hua University
National Center of Theoretical Science, Hsinchu 300, Taiwan

Chiu-Ju Lin

Department of Mathematics
National Tsing Hua University
Hsinchu 300, Taiwan

Abstract. We analyze a competition model of two phytoplankton species for a single nutrient with internal storage and light in a well mixed aquatic environment. We apply the theory of monotone dynamical system to determine the outcomes of competition: extinction of two species, competitive exclusion, stable coexistence and bistability of two species. We also present the graphical presentation to classify the competition outcomes and to compare outcome of models with and without internal storage.

1. **Introduction.** Nutrients and light are essential resource for growth of phytoplankton. Competition for resources affects the composition of species in the ecosystem. When species compete for one single limiting nutrient, the species with the highest tolerance for nutrient conditions in the surrounding environment, hence the smallest break-even concentration, wins the competition [4, 5] and outcompetes the others. Similarly, when multiple species compete for light, the one with the highest tolerance for light environment, hence the lowest break-even light intensity, wins the competition [7]. These demonstrate competitive exclusion in ecosystems and preclude species coexistence. Nevertheless, competition for multiple resources may allow coexistence of species under certain conditions. For example, under the condition of trade-off in tolerance for different nutrients, two species coexist in the competition for two complementary nutrients [3]. Importance of trade-off in species coexistence was revealed in the competition model on resources of single nutrient and light [8]. The same conclusion has been demonstrated graphically by Tilman [14].

Resource competition model mentioned previously assumed constant yield for population dynamics. This implies no energy conservation from one stage to the next. Grover [2] suggested that storage of excess resource could lead to variable yield for converting nutrient into organism. Such storage results from surplus of one resource due to limited reproduction (population growth) restricted by the

2010 *Mathematics Subject Classification.* Primary: 58F15, 58F17; Secondary: 53C35.
Key words and phrases. Two species competition, Droop model, well-mixed water column, competitive exclusion, bistability, stable coexistence, Tilman's graph presentation.

other resource. This level of resource storage is called cell quota [1, 2]. In the model proposed Passarge et al. [11], cell quota from previous stage constrains nutrient uptake rate of phytoplankton and affect population growth. This may alter dynamics of species in competition and lead to different equilibrium statement for species coexistence. Yet no analytical work was done for the model to the best of our knowledge.

In this paper, we study a model of two phytoplankton species competing for two complementary resources. The model assumes internal storage of the first resource, nutrient, and no internal storage of the second resource, light, in a well-mixed aquatic environment. Moreover, we will compare our results with those of competitions for two nutrients in graphical illustration.

The paper is organized as following. In section two, we show the model and study the single species model. We present results and analyze the model of the competition of two species for single-nutrient and light in section three and four, respectively. In section five we discuss the graphical presentation for the two species competition model (2) with $n = 2$ or the system (13). The last section is the discussion. We compare the experimental results in [11] with our analytic results.

2. **Model and single species growth model.** Assume that species consumes nutrient and stores it into cell quota, and that the nutrient uptake rate increases with nutrient and decreases with cell quota. It is the Droop model [1] or the variable yield model. Assume that the light intensity changes in accordance with the Lambert-Beer's law (see the fourth equation in (DE_n) below). When species consumes nutrient and light, its growth function is modeled by Von Liebig's "Law of minimum" (see the first equation in (DE_n) below). We shall analyze the following n-species competition model which was proposed by J. Passarge et al [11]:

$$\begin{cases} N_i' = \Big[\min\{\mu_i(Q_i), \eta_i(I_{\text{out}})\} - D\Big] N_i, \\ Q_i' = \nu_i(R, Q_i) - \min\{\mu_i(Q_i), \eta_i(I_{\text{out}})\} Q_i, \\ R' = D(R_{\text{in}} - R) - \sum_{j=1}^n \nu_j(R, Q_j) N_j, \\ I_{\text{out}} = I_{\text{in}} \exp(-k_{\text{bg}} z_m - \sum_{j=1}^n k_j N_j z_m), \\ N_i(0) \geq 0,\ Q_i(0) \geq Q_i^{\min},\ R(0) \geq 0,\ i = 1, 2..., n. \end{cases} \tag{DE_n}$$

Here $N_i(t)$ is the population density of phytoplankton species i at time t, and $Q_i(t)$ is the intracellular nutrient content of species i, $Q_i^{\min}$ is the minimum cellular quota satisfying $\mu_i(Q_i^{\min}) = 0$, for $i = 1, 2, ..., n$. The variable $R(t)$ is the nutrient concentration in the water column, and $I_{\text{out}}(t)$ is the light penetration to the bottom of the water column. The parameter D is the dilution rate, R_{in} is the nutrient input concentration, and I_{in} is the incident light intensity at the water surface, k_{bg} is the background turbidity caused by water, k_j is the light attenuation coefficient of phytoplankton species j, and z_m is the total depth of the water column.

There are some properties for the related functions. The function $\mu_i(Q_i)$ is the growth rate of species i under nutrient limitation with

$$\mu_i(Q_i) \geq 0,\ \mu_i'(Q_i) > 0,\ \mu_i(Q_i^{\min}) = 0,$$

and is continuous for $Q_i \geq Q_i^{\min}$. For example, from Droop [1], $\mu_i(Q_i)$ takes the following forms

$$\mu_i(Q_i) = \mu_{i\infty}\left(1 - \frac{Q_i^{\min}}{Q_i}\right),$$

where $\mu_{i\infty}$ is some specific parameter. The function $\eta_i(I_{\text{out}})$ is the growth rate of species i under light limitation with $\eta_i(I_{\text{out}}) \geq 0$, $\eta_i'(I_{\text{out}}) > 0$ and is continuous for $I_{\text{out}} \geq 0$. For example, $\eta_i(I_{\text{out}})$ may satisfy Holling type II functional response with half-saturation constant a_i and maximal growth rate m_i for i-th species, respectively, it takes the form

$$\eta_i(I_{\text{out}}) = \frac{m_i I_{\text{out}}}{a_i + I_{\text{out}}}.$$

The function $\nu_i(R, Q_i)$ is the nutrient uptake rate of species i, and it satisfies

$$\nu_i(R, Q_i) \geq 0, \ \frac{\partial \nu_i}{\partial R} > 0, \ \frac{\partial \nu_i}{\partial Q_i} < 0, \ \nu_i \in C^1(\mathbb{R}_+ \times [Q_i^{\min}, \infty)). \tag{1}$$

Grover's paper [2] presented a classical nutrient uptake function.

By the scaling, we may assume $z_m = 1$. Denote $I(t)$ to be $I_{\text{out}}(t)$, $I_0 = I_{\text{in}} e^{-k_{\text{bg}}}$. Let $\sum = R + \sum_{j=1}^n N_j Q_j$, then $\sum' = D(R_{\text{in}} - \sum)$. Hence $\sum(t) \to R_{\text{in}}$ as $t \to \infty$. Then the limiting system of (DE_n) is:

$$\begin{cases} N_i' = \Big[\min\{\mu_i(Q_i), \eta_i(I)\} - D\Big] N_i, \\ Q_i' = \nu_i(R, Q_i) - \min\{\mu_i(Q_i), \eta_i(I)\} Q_i, \\ I = I_0 \exp(-\sum_{j=1}^n k_j N_j), \\ R = R_{\text{in}} - \sum_{j=1}^n N_j Q_j, \\ N_i(0) \geq 0, \ Q_i(0) \geq Q_i^{\min}, \ i = 1, 2 ..., n. \end{cases} \tag{2}$$

We define the following positive numbers σ_i, ξ_i and λ_i by the equilibrium analysis of (2)

$$\mu_i(\sigma_i) = D, \ \eta_i(\xi_i) = D, \ \nu_i(\lambda_i, \sigma_i) = D\sigma_i. \tag{3}$$

For simplicity, we assume the following hypothesis:

(H1) $\lambda_i \neq \lambda_j$ for $i \neq j$ and $\lambda_i \neq R_{\text{in}}$ for all i.
(H2) $0 < \xi_1 < \xi_2 < \xi_3 < ... < \xi_n$ and $\xi_i \neq I_0$ for all i.
(H3) $\mu_i(Q_i) \neq \eta_i(I)$ at equilibria for all i.

In this paper we restrict our attention to the case $n = 2$, the competition of two species for light and one single nutrient with internal storage.

To understand the system (2) with $n = 2$, the first step is to consider the single species model, which takes the form:

$$\begin{cases} N' = \Big[\min\{\mu(Q), \eta(I)\} - D\Big] N, \\ Q' = \nu(R, Q) - \min\{\mu(Q), \eta(I)\} Q, \\ R = R_{\text{in}} - NQ, \\ I = I_0 \exp(-kN), \\ N(0) \geq 0, \ Q(0) \geq Q^{\min}. \end{cases} \tag{4}$$

We define the following positive numbers λ, ξ, σ based on the equilibrium analysis of the system (4),

$$\mu(\sigma) = D, \ \eta(\xi) = D, \ \nu(\lambda, \sigma) = D\sigma. \tag{5}$$

Equilibrium analysis: There are two types of equilibria representing species extinction and survival. First, we consider the equilibrium of extinction type, $E_0 = (0, Q^0)$ where Q^0 satisfies

$$\nu(R_{\text{in}}, Q^0) = \min\{\mu(Q^0), \eta(I_0)\} Q^0. \tag{6}$$

For the survival type, $E_c = (N_c, Q_c)$, $N_c > 0$. From the first equation in (4), we have either $\mu(Q_c) = D$ or $\eta(I_c) = D$ where $I_c = I_0 \exp(-kN_c)$. From the basic assumption (H3), there are two possible cases. In the first case, we have $\mu(Q_c) = D$ and $\eta(I_c) > D$, and denote $E_c = E_R = (N_R, Q_R)$. In this case, we called that the species is R-limited. From (5), we obtain that $Q_R = \sigma$ and $R_c = \lambda$, $N_R = (R_{\text{in}} - \lambda)/\sigma > 0$, denote $I_c = I_R = I_0 \exp(-kN_R) > \xi$. Thus E_R exists if and only if

$$R_{\text{in}} > \lambda,\ I_0 > \xi,\ \frac{\ln I_0 - \ln \xi}{R_{\text{in}} - \lambda} > \frac{k}{\sigma}. \tag{7}$$

In the second case, we have $\eta(I_c) = D$ and $\mu(Q_c) > D$, and denote $E_c = E_I = (N_I, Q_I)$, we say that the species is I-limited. From (5), we have that $I_c = \xi$ and $N_I = (\ln I_0 - \ln \xi)/k$. In this case, we denote $R = R_I$. From (1), there exists a unique $Q_I > 0$ satisfies $\nu(R_{\text{in}} - N_I Q_I, Q_I) = DQ_I$, then $R_I = R_{\text{in}} - N_I Q_I > 0$. From the fact $\mu(Q_I) > D$, we have $Q_I > \sigma$ and

$$\nu(R_I, Q_I) = DQ_I > D\sigma = \nu(\lambda, \sigma) > \nu(\lambda, Q_I).$$

Then we have $R_I > \lambda$, and $R_{\text{in}} - \lambda > R_{\text{in}} - R_I = Q_I N_I > \sigma N_I$, which implies that

$$\frac{k}{\sigma} > \frac{\ln I_0 - \ln \xi}{R_{\text{in}} - \lambda}.$$

Hence E_I exists if and only if

$$R_{\text{in}} > \lambda,\ I_0 > \xi,\ \frac{\ln I_0 - \ln \xi}{R_{\text{in}} - \lambda} < \frac{k}{\sigma}. \tag{8}$$

From (7) and (8), we conclude that if $R_{\text{in}} > \lambda$ and $I_0 > \xi$, then E_c exists and E_c is either E_R or E_I exclusively.

Stability analysis of E_0 , E_R and E_I: Consider the Jacobian of the system (4) evaluated at $E_0 = (0, Q^0)$, the washout equilibrium,

$$J(E_0) = \begin{bmatrix} \min\{\mu(Q^0), \eta(I_0)\} - D & 0 \\ -[\frac{\partial \nu}{\partial R}(R_{\text{in}}, Q^0) + \Delta_N(Q^0, I_0)]Q^0 & m_{44} \end{bmatrix}$$
$$m_{44} = \frac{\partial \nu}{\partial Q}(R_{\text{in}}, Q^0) - \min\{\mu(Q^0), \eta(I_0)\} - \Delta_Q(Q^0, I_0)Q^0,$$

where $\Delta_N(Q, I)$, $\Delta_Q(Q, I)$ are functions of Q, I and

$$\Delta_N(Q^0, I_0) = \frac{\partial}{\partial N} \min\{\mu(Q), \eta(I)\}\Big|_{(Q,I)=(Q^0,I_0)} = \begin{cases} 0 & \text{if } \mu(Q^0) < \eta(I_0), \\ -kI_0\eta'(I_0) & \text{if } \mu(Q^0) > \eta(I_0). \end{cases}$$

$$\Delta_Q(Q^0, I_0) = \frac{\partial}{\partial Q} \min\{\mu(Q), \eta(I)\}\Big|_{(Q,I)=(Q^0,I_0)} = \begin{cases} \mu'(Q^0) & \text{if } \mu(Q^0) < \eta(I_0), \\ 0 & \text{if } \mu(Q^0) > \eta(I_0). \end{cases}$$

The eigenvalues of $J(E_0)$ are:

$$\min\{\mu(Q^0), \eta(I_0)\} - D,\ \frac{\partial \nu}{\partial Q}(R_{\text{in}}, Q^0) - \min\{\mu(Q^0), \eta(I_0)\} - \Delta_Q(Q^0, I_0)Q^0.$$

From (1), $\frac{\partial}{\partial Q}\nu(R_{\text{in}}, Q^0) < 0$, it follows that E_0 is locally asymptotically stable if and only if $\min\{\mu(Q^0), \eta(I_0)\} < D$, i.e. $Q^0 < \sigma$ or $I_0 < \xi$. It is trivial that if $I_0 \geq \xi$, then we have that $Q^0 < \sigma$ if and only if $R_{\text{in}} < \lambda$. Therefore, we conclude that E_0 is locally asymptotically stable if and only if $I_0 < \xi$ or $R_{\text{in}} < \lambda$.

If the species N is R-limited, at the neighborhood of E_R, the system (4) becomes

$$\begin{cases} N' = \Big[\mu(Q) - D\Big]N, \\ Q' = \nu(R,Q) - \mu(Q)Q, \\ R = R_{\text{in}} - NQ. \end{cases} \tag{9}$$

The Jacobian of the system (9) evaluated at E_R is

$$J(E_R) = \begin{bmatrix} 0 & \mu'(Q_R)N_R \\ -Q_R\frac{\partial\nu}{\partial R}(\lambda, Q_R) & -N_R\frac{\partial\nu}{\partial R}(\lambda, Q_R) + \frac{\partial\nu}{\partial Q}(\lambda, Q_R) - \mu(Q_R) - \mu'(Q_R)Q_R \end{bmatrix}$$

The eigenvalues ρ of $J(E_R)$ satisfies

$$\rho^2 + \rho[N_R\frac{\partial\nu}{\partial R}(\lambda, Q_R) - \frac{\partial\nu}{\partial Q}(\lambda, Q_R) + \mu(Q_R) + \mu'(Q_R)Q_R] + \mu'(Q_R)N_RQ_R\frac{\partial\nu}{\partial R}(\lambda, Q_R) = 0$$

From (1) and Roth-Hurwitz criteria, the equilibrium E_R is locally asymptotically stable.

If the species N is I-limited, at the neighborhood of E_I, the system (4) becomes

$$\begin{cases} N' = \Big[\eta(I) - D\Big]N, \\ Q' = \nu(R,Q) - \eta(I)Q, \\ R = R_{\text{in}} - NQ, \\ I = I_0\exp(-kN). \end{cases} \tag{10}$$

The Jacobian of the system (10) evaluated at E_I is

$$J(E_I) = \begin{bmatrix} -k\xi\eta'(\xi)N_I & 0 \\ -Q_I\frac{\partial\nu}{\partial R}(R_I, Q_I) + k\xi\eta'(\xi)Q_I & -N_I\frac{\partial\nu}{\partial R}(R_I, Q_I) + \frac{\partial\nu}{\partial Q}(R_I, Q_I) - \eta(\xi) \end{bmatrix}$$

The eigenvalues are $-k\xi\eta'(\xi)N_I < 0$ and $-N_I\frac{\partial\nu}{\partial R}(R_I, Q_I) + \frac{\partial\nu}{\partial Q}(R_I, Q_I) - \eta(\xi) < 0$. Hence the equilibrium E_I is locally asymptotically stable.

The following theorem describes the global dynamics of system (4).

Theorem 2.1. *The following holds.*

(i) If $R_{\text{in}} < \lambda$ or $I_0 < \xi$, then E_0 is the only equilibrium and

$$\lim_{t\to\infty}(N(t), Q(t)) = E_0.$$

(ii) If $R_{\text{in}} > \lambda$ and $I_0 > \xi$, then E_0 is unstable and E_c exists, and either $E_c = E_R$ or $E_c = E_I$ exclusively. If species N is R-limited (I-limited) then for $N(0) > 0$

$$\lim_{t\to\infty}(N(t), Q(t)) = E_R\ (E_I).$$

Proof. Let $U = NQ$, then we convert system (4) into the following equations

$$\begin{cases} N' = \Big[\min\{\mu(\frac{U}{N}), \eta(I)\} - D\Big]N, \\ U' = \nu(R, \frac{U}{N})N - DU, \\ R = R_{\text{in}} - U, \\ I = I_0\exp(-kN), \\ N(0) \geq 0,\ U(0) \geq 0. \end{cases} \tag{11}$$

Note that $U = 0$ when $N = 0$ and the system (11) is dissipative.

The isoclines of N are $N = 0$ and

$$\min\{\mu(\frac{U}{N}), \eta(I)\} = D. \tag{12}$$

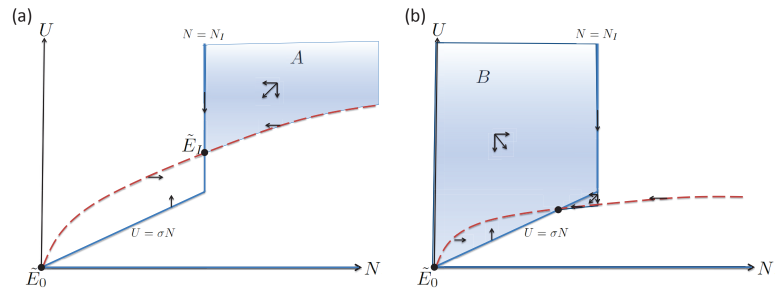

FIGURE 1. The phase plane (N, U) of system (11) in case (ii). Solid lines indicate the isoclines of N. Dashed line indicates the isocline of U. The vectors indicate the vector field of system (11). The set A in case (a) and the set B in case (b) are positively invariant sets.

Note that, if $\mu(\frac{U}{N}) = D$, then $\frac{U}{N} = \sigma$; if $\eta(I) = D$, then $I = I_0 e^{-kN} = \xi$ and $N = \frac{\ln I_0 - \ln \xi}{k} = N_I$ for $I_0 > \xi$. Hence the equation (12) implies that

$$U = \sigma N \text{ for } 0 \le N \le N_I, \quad \text{and } N = N_I \text{ for } U \ge \sigma N_I \text{ if } I_0 > \xi.$$

Next, we shall describe the isocline of U. Let the function $F(N, U)$ be defined by

$$F(N, U) = \nu(R_{\text{in}} - U, \frac{U}{N})N - DU.$$

Note that $N = 0$ implies $U = 0$ and $Q = Q^0$, then $F(0, 0) = 0$. And

$$\frac{\partial F}{\partial U}(0, 0) = \frac{\partial \nu}{\partial Q}(R_{\text{in}}, Q^0) - D < 0.$$

By implicit function theorem, there exists $\tilde{U}(N)$, a function of N, which satisfies $\tilde{U}(0) = 0$, $F(N, \tilde{U}(N)) = 0$ and

$$\tilde{U}'(N) = -\frac{\frac{\partial F}{\partial N}(N, \tilde{U})}{\frac{\partial F}{\partial U}(N, \tilde{U})} = \frac{-\frac{\partial \nu}{\partial Q}(R_{\text{in}} - \tilde{U}, \frac{\tilde{U}}{N})\frac{\tilde{U}}{N} + \nu(R_{\text{in}} - \tilde{U}, \frac{\tilde{U}}{N})}{\frac{\partial \nu}{\partial R}(R_{\text{in}} - \tilde{U}, \frac{\tilde{U}}{N})N - \frac{\partial \nu}{\partial Q}(R_{\text{in}} - \tilde{U}, \frac{\tilde{U}}{N}) + D} > 0.$$

(i) If $R_{\text{in}} < \lambda$ or $I_0 < \xi$, then $\min\{\mu(Q^0), \eta(I_0)\} < D$ and

$$\tilde{U}'(0) = -\frac{\frac{\partial F}{\partial N}(N, \tilde{U})}{\frac{\partial F}{\partial U}(N, \tilde{U})}\Big|_{(0,0)} = \frac{-\frac{\partial \nu}{\partial Q}(R_{\text{in}}, Q^0)Q^0 + \nu(R_{\text{in}}, Q^0)}{-\frac{\partial \nu}{\partial Q}(R_{\text{in}}, Q^0) + D}$$
$$< \frac{-\frac{\partial \nu}{\partial Q}(R_{\text{in}}, Q^0)\sigma + D\sigma}{-\frac{\partial \nu}{\partial Q}(R_{\text{in}}, Q^0) + D} = \sigma,$$

from the equation (6) the inequality holds. Hence $\tilde{E}_0 := (0, 0)$ is the only equilibrium of system (11) and it is locally asymptotically stable. Hence there is no periodic solutions, by Poincare-Bendixson theorem, and all solutions converge to $\tilde{E}_0$. Therefore, all solutions of system (4) converge to E_0.

(ii) If $R_{\text{in}} > \lambda$ and $I_0 > \xi$, it implies that $\min\{\mu(Q^0), \eta(I_0)\} > D$ and $\tilde{U}'(0) > \sigma$. The nontrivial intersection of isoclines is either $\tilde{E}_R := (N_R, \sigma N_R)$ or $\tilde{E}_I := (N_I, \tilde{U}(N_I))$ (see the Figure 1). From the phase plane analysis, we know that the region A and B are positively invariant, where

$$A = \{(N, U) : N \ge N_I, \text{ and } U \ge \tilde{U}(N), \text{ for } N \ge N_I\}.$$

$$B = \{(N,U) : N \le N_I, \text{ and } U \ge \sigma N \text{ for } 0 \le N \le N_R, \\ U \ge \tilde{U}(N) \text{ for } N_R \le N \le N_I\}.$$

Hence there is no limit cycles, and by Poincare-Bendixon theorem the omega limit set of $(N(0), U(0))$, $\omega(N(0), U(0))$, is an equilibrium. We know that $\tilde{E}_0$ is unstable under the assumption of (ii). Therefore $\omega(N(0), U(0))$ is either $\tilde{E}_R$ or $\tilde{E}_I$ for $N(0) > 0$. Thus, for system (4), $\omega(N(0), Q(0)) = E_R$ or E_I for $N(0) > 0,\ Q(0) \ge Q^{\min}$.

□

3. **Two species model.** In this section we consider a model of two species competing for light and a single nutrient with internal storage. The model takes the form

$$\begin{cases} N_1' = \Big[\min\{\mu_1(Q_1), \eta_1(I)\} - D\Big] N_1, \\ Q_1' = \nu_1(R, Q_1) - \min\{\mu_1(Q_1), \eta_1(I)\} Q_1, \\ N_2' = \Big[\min\{\mu_2(Q_2), \eta_2(I)\} - D\Big] N_2, \\ Q_2' = \nu_2(R, Q_2) - \min\{\mu_2(Q_2), \eta_2(I)\} Q_2, \\ I = I_0 \exp(-k_1 N_2 - k_2 N_2), \\ R = R_{\text{in}} - N_1 Q_1 - N_2 Q_2, \\ N_i(0) \ge 0,\ Q_i(0) \ge Q_i^{\min},\ i = 1,2. \end{cases} \tag{13}$$

Let the set Ω be

$$\Omega = \{(N_1, Q_1, N_2, Q_2) : N_i(0) \ge 0,\ Q_i(0) \ge Q_i^{\min},\ i = 1,2\}.$$

First of all, we find all equilibria and classify the stability of them.

Equilibrium analysis: The extinction equilibrium is $E_0 = (0, Q_1^0, 0, Q_2^0)$ where Q_i^0 satisfies $\nu_i(R_{\text{in}}, Q_i^0) = \min\{\mu_i(Q_i^0), \eta_i(I_0)\} Q_i^0,\ i = 1,2$.

For the case of competitive exclusion, we have the following semi-trivial equilibria E_{Ri} and $E_{Ii},\ i = 1,2$, representing that the species i is R-limited and I-limited, respectively.

(1) $E_{R1} = (N_1^{R1}, Q_1^{R1}, 0, Q_2^{R1})$, where $Q_1^{R1} = \sigma_1,\ R^{R1} = \lambda_1$, $N_1^{R1} = \frac{R_{\text{in}} - \lambda_1}{\sigma_1}$, $I^{R1} = I_0 \exp(-k_1 N_1^{R1}),\ \nu_2(\lambda_1, Q_2^{R1}) = \min\{\mu_2(Q_2^{R1}), \eta_2(I^{R1})\} Q_2^{R1}$. Species 1 is R-limited if and only if

$$R_{\text{in}} > \lambda_1,\ I_0 > \xi_1,\ \frac{\ln I_0 - \xi_1}{R_{\text{in}} - \lambda_1} > \frac{k_1}{\sigma_1}.$$

(2) $E_{R2} = (0, Q_1^{R2}, N_2^{R2}, Q_2^{R2})$, where $Q_2^{R2} = \sigma_2,\ R^{R2} = \lambda_2$, $N_2^{R2} = \frac{R_{\text{in}} - \lambda_2}{\sigma_2}$, $I^{R2} = I_0 \exp(-k_2 N_2^{R2}),\ \nu_1(\lambda_2, Q_1^{R2}) = \min\{\mu_1(Q_1^{R2}), \eta_1(I^{R2})\} Q_1^{R2}$. Species 2 is R-limited if and only if

$$R_{\text{in}} > \lambda_2,\ I_0 > \xi_2,\ \frac{\ln I_0 - \xi_2}{R_{\text{in}} - \lambda_2} > \frac{k_2}{\sigma_2}.$$

(3) $E_{I1} = (N_1^{I1}, Q_1^{I1}, 0, Q_2^{I1})$, where $I^{I1} = \xi_1,$, $N_1^{I1} = \frac{\ln I_0 - \ln \xi_1}{k_1}$, Q_1^{I1} satisfies $\nu_1(R_{\text{in}} - N_1^{I1} Q_1^{I1}, Q_1^{I1}) = D Q_1^{I1},\ R^{I1} = R_{\text{in}} - N_1^{I1} Q_1^{I1}$, and Q_2^{I1} satisfies $\nu_2(R^{I1}, Q_2^{I1}) = \min\{\mu_2(Q_2^{I1}), \eta_2(\xi_1)\} Q_2^{I1}$. Species 1 is I-limited if and only if

$$R_{\text{in}} > \lambda_1,\ I_0 > \xi_1,\ \frac{\ln I_0 - \xi_1}{R_{\text{in}} - \lambda_1} < \frac{k_1}{\sigma_1}.$$

(4) $E_{I2}=(0,Q_1^{I2},N_2^{I2},Q_2^{I2})$, where $I^{I2}=\xi_2,$, $N_2^{I2}=\frac{\ln I_0-\ln\xi_2}{k_2}$, Q_2^{I2} satisfies

$$\nu_2(R_{\rm in}-N_2^{I2}Q_2^{I2},Q_2^{I2})=DQ_2^{I2}, \tag{14}$$

$R^{I2}=R_{\rm in}-N_2^{I2}Q_2^{I2}$, and Q_1^{I2} satisfies $\nu_1(R^{I2},Q_1^{I2})=\min\{\mu_1(Q_1^{I2}),\eta_1(\xi_2)\}Q_1^{I2}$. Species 2 is I-limited if and only if

$$R_{\rm in}>\lambda_2,\ I_0>\xi_2,\ \frac{\ln I_0-\xi_2}{R_{\rm in}-\lambda_2}<\frac{k_2}{\sigma_2}.$$

Next, we consider the coexistent equilibria. In this case, we must have that $\min\{\mu_i(Q_i),\eta_i(I)\}=D$, for all $i=1,2$. If $\mu_1(Q_1)=D$ and $\mu_2(Q_2)=D$, which implies that $Q_1=\sigma_1,\ Q_2=\sigma_2$, and $\nu_i(R,\sigma_i)=D\sigma_i$, for $i=1,2$. Hence $R=\lambda_1=\lambda_2$, a contrary to (H1). If $\eta_1(I)=D$ and $\eta_2(I)=D$, then $I=\xi_1=\xi_2$, a contrary to (H2). From above discussion, we know that the resource can not attain to the break-even concentration of each species at the same time. Hence the coexistent equilibria exist if one species induces $\mu_i(Q_i)=D$ and the other causes $\eta_j(I)=D$. Therefore we have exactly two types of coexistent equilibria.

(1) $E_c^{RI}=(N_1^{RI},Q_1^{RI},N_2^{RI},Q_2^{RI})$ where $Q_1^{RI}=\sigma_1,\ R^{RI}=\lambda_1,\ I^{RI}=\xi_2$. Note that $\eta_1(\xi_2)>D=\eta_1(\xi_1)$ then $\xi_2>\xi_1$. Q_2^{RI} satisfies $\nu_2(\lambda_1,Q_2^{RI})=DQ_2^{RI}$. From the fact $\eta_2(\xi_2)=D<\mu_2(Q_2^{RI})$, we have $Q_2^{RI}>\sigma_2$ and

$$\nu_2(\lambda_1,Q_2^{RI})=DQ_2^{RI}>D\sigma_2=\nu_2(\lambda_2,\sigma_2)>\nu_2(\lambda_2,Q_2^{RI}),$$

it follows that $\lambda_1>\lambda_2$. $N_1^{RI},\ N_2^{RI}$ is the intersection of following two lines

$$\begin{cases}\ln I_0-\ln\xi_2=k_1N_1^{RI}+k_2N_2^{RI},\\ R_{\rm in}-\lambda_1=\sigma_1N_1^{RI}+Q_2^{RI}N_2^{RI}.\end{cases} \tag{15}$$

We need assumption (H4):

(H4) Any two of $\dfrac{\ln I_0-\ln\xi_2}{R_{\rm in}-\lambda_1},\ \dfrac{k_1}{\sigma_1},\ \dfrac{k_2}{Q_2^{RI}}$ are not equal.

Then the solution $(N_1^{RI},\ N_2^{RI})$ of (15) exists and is unique if and only if

$$\frac{k_1}{\sigma_1}<\frac{\ln I_0-\ln\xi_2}{R_{\rm in}-\lambda_1}<\frac{k_2}{Q_2^{RI}}, \tag{16}$$

or

$$\frac{k_1}{\sigma_1}>\frac{\ln I_0-\ln\xi_2}{R_{\rm in}-\lambda_1}>\frac{k_2}{Q_2^{RI}}. \tag{17}$$

(2) $E_c^{IR}=(N_1^{IR},Q_1^{IR},N_2^{IR},Q_2^{IR})$ where $Q_2^{IR}=\sigma_2,\ R^{IR}=\lambda_2,\ I^{IR}=\xi_1,\ \eta_1(\xi_1)=D<\mu_1(Q_1^{IR}),\ Q_1^{IR}>\sigma_1$ and Q_1^{IR} satisfies $\nu_1(\lambda_2,Q_1^{IR})=DQ_1^{IR}$. And $N_1^{IR},\ N_2^{IR}$ satisfy

$$\begin{cases}\ln I_o-\ln\xi_1=k_1N_1^{IR}+k_2N_2^{IR},\\ R_{\rm in}-\lambda_2=Q_1^{IR}N_1^{IR}+\sigma_2N_2^{IR}.\end{cases} \tag{18}$$

Similarly, the existence of E_c^{IR} implies that $\xi_2>\xi_1$, $Q_1^{IR}>\sigma_1$, and $\lambda_2>\lambda_1$. The basic assumption is

(H5) Any two of $\dfrac{\ln I_0-\ln\xi_1}{R_{\rm in}-\lambda_2},\ \dfrac{k_2}{\sigma_2},\ \dfrac{k_1}{Q_1^{IR}}$ are not equal.

Under (H5) equation (18) has a unique positive solution (N_1^{IR},N_2^{IR}) if and only if

$$\frac{k_2}{\sigma_2}<\frac{\ln I_0-\ln\xi_1}{R_{\rm in}-\lambda_2}<\frac{k_1}{Q_1^{IR}},$$

or

$$\frac{k_2}{\sigma_2} > \frac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_2} > \frac{k_1}{Q_1^{IR}}.$$

We present the criterion of the existence of E_c^{RI} and E_c^{IR} in Table 1. Note that the assumption (H2) implies the nonexistence of E_c^{IR}.

Table 1

Equilibrium	Existence criteria
E_c^{RI}	$\lambda_1 > \lambda_2,\ \xi_2 > \xi_1$
	either $\frac{k_1}{\sigma_1} < \frac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_1} < \frac{k_2}{Q_2^{RI}}$ or $\frac{k_1}{\sigma_1} > \frac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_1} > \frac{k_2}{Q_2^{RI}}$
E_c^{IR}	$\lambda_2 > \lambda_1,\ \xi_1 > \xi_2$
	either $\frac{k_2}{\sigma_2} < \frac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_2} < \frac{k_1}{Q_1^{IR}}$ or $\frac{k_2}{\sigma_2} > \frac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_2} > \frac{k_1}{Q_1^{IR}}$.

Stability analysis: The details of the local stability analysis of each equilibrium are presented in the Appendix. We denote $J(E)$ be the variational matrix of (13) evaluated at equilibrium E. The eigenvalues of $J(E_0)$ are three negative real values and $\min\{\mu_1(Q_1^0), \eta_1(I_0)\} - D$. It follows that E_0 is locally stable if $\min\{\mu_i(Q_i^0), \eta_i(I_0)\} < D$, equivalently $\xi_i > I_0$ or $\lambda_i > R_{\text{in}}$, for each $i = 1, 2$.

There are three eigenvalues of $J(E_{R1})$ with negative real part, E_{R1} is locally stable if $\min\{\mu_2(Q_2^{R1}), \eta_2(I^{R1})\} < D$, that is, $Q_2^{R1} < \sigma_2$ or $I^{R1} < \xi_2$. Hence E_{R1} is locally stable if

$$\lambda_1 < \lambda_2 \text{ or } \frac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_1} < \frac{k_1}{\sigma_1}.$$

Similarly, for equilibrium E_{R2}, there are three eigenvalues of $J(E_{R2})$ with negative real part and it is locally stable if

$$\lambda_2 < \lambda_1 \text{ or } \frac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_2} < \frac{k_2}{\sigma_2}.$$

There are three eigenvalues of $J(E_{I1})$ with negative real part, E_{I1} is locally stable if $\min\{\mu_2(Q_2^{I1}), \eta_2(\xi_1)\} < D$, i.e., $Q_2^{I1} < \sigma_1$ of $\xi_1 < \xi_2$. Hence E_{I1} is locally stable if

$$\frac{k_1}{Q_1^{I1}} < \frac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_2} \text{ or } \xi_1 < \xi_2.$$

Similarly, for equilibrium E_{I2}, there are three eigenvalues of $J(E_{I2})$ with negative real part and it is locally stable if

$$\frac{k_2}{Q_2^{I2}} < \frac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_1} \text{ or } \xi_2 < \xi_1.$$

We summarize the criteria for the existence and local stability of E_0, E_{R1}, E_{R2}, E_{I1}, E_{I2} in Table 2.

TABLE 2

Equilibrium	Existence	Stability criteria
E_0	Always exists	$R_{\text{in}} < \sigma_i$ or $I_0 < \xi_i$, for each $i = 1, 2$.
E_{R1}	$R_{\text{in}} > \lambda_1, I_0 > \xi_1$, $\dfrac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_1} > \dfrac{k_1}{\sigma_1}$	$\lambda_1 < \lambda_2$ or $\dfrac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_1} < \dfrac{k_1}{\sigma_1}$.
E_{R2}	$R_{\text{in}} > \lambda_2, I_0 > \xi_2$, $\dfrac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_2} > \dfrac{k_2}{\sigma_2}$	$\lambda_2 < \lambda_1$ or $\dfrac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_2} > \dfrac{k_2}{\sigma_2}$.
E_{I1}	$R_{\text{in}} > \lambda_1, I_0 > \xi_1$, $\dfrac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_1} < \dfrac{k_1}{\sigma_1}$	$\xi_1 < \xi_2$ or $\dfrac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_2} > \dfrac{k_1}{Q_1^{I1}}$.
E_{I2}	$R_{\text{in}} > \lambda_2, I_0 > \xi_2$, $\dfrac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_2} < \dfrac{k_2}{\sigma_2}$	$\xi_2 < \xi_1$ or $\dfrac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_1} > \dfrac{k_2}{Q_2^{I2}}$.

The stability of coexistent equilibrium is more complicated. We note that from assumption (H2) and Table 1, E_c^{RI} is the only coexistent equilibrium. Observing that the equilibrium E_c^{RI} is hyperbolic since the determinant of $J(E_c^{RI})$ is

$$\xi_2 N_1^{RI} N_2^{RI} \mu_1'(\sigma_1)\eta_2'(\xi_2)\frac{\partial \nu_1}{\partial R}(\lambda_1, \sigma_1)\Big(D - \frac{\partial \nu_2}{\partial Q_2}(\lambda_1, Q_2^{RI})\Big)(k_2\sigma_1 - k_1 Q_2^{RI}),$$

which is not zero by (H4).

We state the outcomes of competition in the following theorems, and the proofs are postponed to the next section.

Theorem 3.1. *If either $R_{\text{in}} < \lambda_i$ or $I_0 < \xi_i$ for some $i \in \{1, 2\}$, then* $\lim_{t\to\infty} N_i(t) = 0$.

For the rest of this section, we always assume that $R_{\text{in}} > \lambda_i,\ I_0 > \xi_i$ for $i = 1, 2$. We denote some important parameters as following:

$$T_1 = \frac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_1},\ C_1 = \frac{k_1}{\sigma_1},$$
$$T_2 = \frac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_2},\ C_2 = \frac{k_2}{\sigma_2},\ C_{I2} = \frac{k_2}{Q_2^{I2}},$$

and

$$T^* = \frac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_1}.$$

Theorem 3.2. *Assume* (H1)-(H3). *If $\lambda_1 < \lambda_2 < R_{\text{in}}$ and $\xi_1 < \xi_2 < I_0$, then for $N_1(0) > 0,\ N_2(0) > 0$,*

$$\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{R1}\ (E_{I1}),\ \text{if } T_1 > C_1\ (T_1 < C_1).$$

Theorem 3.3. *Assume* (H1)-(H4) *and $\lambda_2 < \lambda_1 < R_{\text{in}},\ \xi_1 < \xi_2 < I_0$.*

(i) If $T_1 < C_1,\ T_2 < C_2$, then $E_{I1},\ E_{I2}$ exist and E_{I1} is locally stable.

(a) If $T^* > C_{I2}$, then E_{I2} is locally stable and there exists a saddle equilibrium E_c^{RI}. The outcomes depend on initial conditions.

(b) If $T^* < C_{I2}$, then E_{I2} is unstable, and for $N_1(0) > 0,\ N_2(0) > 0$,

$$\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{I1}.$$

(ii) *If* $T_1 < C_1,\ T_2 > C_2$, *then* $E_{I1},\ E_{R2}$ *exist and both are locally stable and there exists a saddle equilibrium* E_c^{RI}. *The outcomes depend on initial conditions.*

(iii) *If* $T_1 > C_1,\ T_2 > C_2$, *then* $E_{R1},\ E_{R2}$ *exist and* E_{R2} *is locally stable.*

(a) *If* $T^* < C_1$, *then* E_{R1} *is locally stable and there exists a saddle equilibrium* E_c^{RI}. *The outcomes depend on initial conditions.*

(b) *If* $T^* > C_1$, *then* E_{R1} *is unstable and for* $N_1(0) > 0,\ N_2(0) > 0$,

$$\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{R2}.$$

(iv) *If* $T_1 > C_1,\ T_2 < C_2$, *then* $E_{R1},\ E_{I2}$ *exist.*

(a) *If* $T^* < C_1, C_{I2}$, *then* E_{R1} *is locally stable and* E_{I2} *is unstable, and for* $N_1(0) > 0,\ N_2(0) > 0$,

$$\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{R1}.$$

(b) *If* $C_1 < T^* < C_{I2}$, *then* E_{R1} *and* E_{I2} *are unstable and* E_c^{RI} *exists, and for* $N_1(0) > 0,\ N_2(0) > 0$,

$$\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_c^{RI}.$$

(c) *If* $C_{I2} < T^* < C_1$, *then* E_{R1} *and* E_{I2} *are both locally stable and there exists a saddle equilibrium* E_c^{RI}. *The outcomes depend on initial conditions.*

(d) *If* $C_1, C_{I2} < T^*$, *then* E_{R1} *is unstable and* E_{I2} *is locally stable, and for* $N_1(0) > 0,\ N_2(0) > 0$,

$$\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{I2}.$$

We note that $C_{I2} = \frac{k_2}{Q_2^{I2}} < \frac{k_2}{\sigma_2} = C_2$, where $Q_2^{I2} = Q_2^{I2}(R_{\text{in}}, I_0)$, a function of R_{in} and I_0, satisfies equation (14). For convenience, we consider $Q_2^{I2} = Q_2^{I2}(R_{\text{in}}, \ln I_0)$ as a function of R_{in} and $\ln I_0$. Therefore $C_{I2} = C_{I2}(R_{\text{in}}, \ln I_0)$ is also a function of R_{in} and $\ln I_0$. The following lemma describes the monotonicity of C_{I2}.

Lemma 3.4. $C_{I2}(R_{\text{in}}, \ln I_0)$ *is strictly decreasing in* R_{in} *and strictly increasing in* $\ln I_0$.

4. **The proofs.**

To prove the results in section 3, we need the following lemma and theorems. The lemma states the nonexistence of coexistent equilibrium. Note that assumption (H2), $\xi_1 < \xi_2$, implies that E_c^{IR} does not exist.

Lemma 4.1. *Assume the semi-trivial equilibria* E_{L1} *and* E_{L2} *exist,* $L \in \{R, I\}$. *If one of them is locally stable and the other is unstable, then* E_c^{RI} *does not exist.*

Proof. Assumption (H2) implies that E_{I1} is locally stable if it exists.

(1) For the case E_{R1} or E_{I1} is locally stable and E_{R2} is unstable, then the instability of E_{R2} implies $\lambda_1 < \lambda_2$, and it follows that E_c^{RI} does not exist.

(2) Assume E_{R1} is locally stable and E_{I2} is unstable, then the instability of E_{I2} implies that $Q_2^{I2} > \sigma_2$ if and only if $R^{I2} > \lambda_1$. Assume E_c^{RI} exists, then $\lambda_1 > \lambda_2$ and either

$$(16) \Leftrightarrow C_1 < T^* < \frac{k_2}{Q_2^{RI}} \text{ or}$$

$$(17) \Leftrightarrow C_1 > T^* > \frac{k_2}{Q_2^{RI}}$$

holds. The stable condition of E_{R1} implies $T^* < C_1$, then (16) does not hold. From (17), $N_2^{I2} = \frac{\ln(I_0)-\ln(\xi_2)}{k_2} > \frac{R_{\text{in}}-\lambda_1}{Q_2^{RI}} > \frac{R_{\text{in}}-R^{I2}}{Q_2^{RI}}$, which implies $Q_2^{RI} > \frac{R_{\text{in}}-R^{I2}}{N_2^{I2}} = Q_2^{I2}$. It follows that

$$\nu_2(\lambda_1, Q_2^{RI}) = DQ_2^{RI} > DQ_2^{I2} = \nu_2(R^{I2}, Q_2^{I2}) > \nu_2(R^{I2}, Q_2^{RI}),$$

and $\lambda_1 > R^{I2}$, a contradiction.

(3) If E_{I1} is locally stable and E_{I2} is unstable, similarly, we have $R^{I2} > \lambda_1$, and the existence of E_{I1} implies $T_1 < C_1$. Assume E_c^{RI} exists, then $\lambda_1 > \lambda_2$ and either (16) or (17) holds. If (16) holds, then

$$\frac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_1} = T_1 < C_1 < T^* = \frac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_1}$$

implies that $\xi_2 < \xi_1$, a contradiction. Under assumption (H2) and instability of E_{I2}, $R^{I2} > \lambda_1$ implies $Q_2^{I2} > Q_2^{RI}$. If (17) holds,

$$N_2^{I2} = \frac{R_{\text{in}} - R^{I2}}{Q_2^{I2}} < \frac{R_{\text{in}} - \lambda_1}{Q_2^{RI}} < \frac{\ln I_0 - \ln \xi_2}{k_2} = N_2^{I2},$$

a contradiction.

(4) If E_{R2} is locally stable and E_{R1} is unstable, then $\lambda_1 > \lambda_2$ and

$$\frac{\ln I_0 - \ln \xi_1}{R_{\text{in}} - \lambda_2} < C_2 < \frac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_2}.$$

Hence $\xi_1 > \xi_2$, it implies the nonexistence of E_c^{RI}.

(5) If E_{I2} is locally stable and E_{R1} is unstable, then $\lambda_1 > \lambda_2$ and $T^* > C_1,\ C_{I2}$. Assume E_c^{RI} exists, then (16) holds. E_{I2} is locally stable means that $Q_2^{I2} < \sigma_2 < Q_2^{RI}$. Thus $T^* > C_{I2} > \frac{k_2}{Q_2^{RI}}$, a contradiction to (16). □

By changing variables, we transform the system (13) into a monotone system, and apply monotone dynamical theory to obtain the global asymptotic behavior of the solutions. Let $U_i = N_i Q_i$, $i = 1, 2$, then we have the following equations.

$$\begin{cases} N_1' = \Big[\min\{\mu_1(\frac{U_1}{N_1}), \eta_1(I)\} - D\Big] N_1, \\ U_1' = \nu_1(R, \frac{U_1}{N_1}) N_1 - DU_1, \\ N_2' = \Big[\min\{\mu_2(\frac{U_2}{N_2}), \eta_2(I)\} - D\Big] N_2, \\ U_2' = \nu_2(R, \frac{U_2}{N_2}) N_2 - DU_2, \\ I = I_0 \exp(-k_1 N_1 - k_2 N_2),\ R = R_{\text{in}} - U_1 - U_2, \\ N_i(0) \ge 0,\ U_i(0) \ge 0,\ i = 1, 2. \end{cases} \tag{19}$$

Let the biological relevant domain be

$$\tilde{\Omega} = \{(N_1, U_1, N_2, U_2) \in \mathbb{R}_+^4 : U_1 + U_2 \le R_{\text{in}}, \\ Q_i^{\min} \le \frac{U_i}{N_i},\ N_i = 0 \Rightarrow U_i = 0,\ i = 1, 2\}.$$

Then $\tilde{\Omega}$ is positively invariant for (19), and the forward orbit of (19) have compact closure in $\tilde{\Omega}$.

We denote $\widetilde{E}_0$, $\widetilde{E}_{R1}$, $\widetilde{E}_{I1}$, $\widetilde{E}_{R2}$, $\widetilde{E}_{I2}$, $\widetilde{E}_c^{RI}$, be the associated equilibria of system (19) with respect to the equilibria of system (13), and their stability are the same as in system (13). Let $X_i = (N_i, U_i) \in \mathbb{R}^2$, $X_i^+ = \{(N_i, U_i) : N_i \ge 0, U_i \ge 0\}$ be the positive cone of X_i for $i = 1, 2$. Let the space $X = X_1 \times X_2$, the positive cone be $X^+ = X_1^+ \times X_2^+$, the cone $K = X_1^+ \times (-X_2^+)$. We can define an order by cone K, denoted by $\leq_K$, and $(N_1, U_1, N_2, U_2) \leq_K (\bar{N}_1, \bar{U}_1, \bar{N}_2, \bar{U}_2)$ means that $N_1 \leq \bar{N}_1$, $U_1 \leq \bar{U}_1$, and $N_2 \geq \bar{N}_2$, $U_2 \geq \bar{U}_2$. Define $\Phi_t : X^+ \to X^+$ for $t \geq 0$ by that $\Phi_t(N_1(0), U_1(0), N_2(0), U_2(0))$ is the solution flow of (19) with initial condition $(N_1(0), U_1(0), N_2(0), U_2(0))$ which belongs to $\tilde{\Omega} \subset X^+$. Then the flow Φ_t is strongly monotone with respect to $<_K$.

Theorem 4.2. *If either $R_{\text{in}} < \lambda_i$ or $I_0 < \xi_i$ for each $i = 1, 2$, then E_0 is the only equilibrium of system* (13) *and* $\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_0$.

Proof. From Table 2, E_0 is the only equilibrium of system (13), then $\widetilde{E}_0$ is also the only equilibrium of system (19). Since

$$(0, 0, N_2(0), U_2(0)) \leq_K (N_1(0), U_1(0), N_2(0), U_2(0)) \leq_K (N_1(0), U_1(0), 0, 0),$$

and Φ_t is monotone, we have that for $t \geq 0$

$$\Phi_t(0, 0, N_2(0), U_2(0)) \leq_K \Phi_t(N_1(0), U_1(0), N_2(0), U_2(0)) \leq_K \Phi_t(N_1(0), U_1(0), 0, 0). \tag{20}$$

From Theorem 2.1, $\Phi_t(0, 0, N_2(0), U_2(0))$ and $\Phi_t(N_1(0), U_1(0), 0, 0)$ tend to $\tilde{E}_0$ as t goes to infinity. Then the equation (20) implies that

$$\lim_{t\to\infty} \Phi_t(N_1(0), U_1(0), N_2(0), U_2(0)) = \tilde{E}_0.$$

Furthermore, for system (13) every trajectory tends to E_0. ∎

Theorem 4.3. *The following holds.*

(i) If $R_{\text{in}} > \lambda_1$ and $I_0 > \xi_1$, and either $R_{\text{in}} < \lambda_2$ or $I_0 < \xi_2$, then E_0 and $E_{R1}(E_{I1})$ exist, and for $N_1(0) > 0$,

$$\lim_{t\to\infty} (N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{R1}\ (E_{I1}), \text{ if } T_1 > C_1\ (T_1 < C_1).$$

(ii) If $R_{\text{in}} > \lambda_2$ and $I_0 > \xi_2$, and either $R_{\text{in}} < \lambda_1$ or $I_0 < \xi_1$, then E_0 and $E_{R2}(E_{I2})$ exist, and for $N_2(0) > 0$,

$$\lim_{t\to\infty} (N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{R2}\ (E_{I2}), \text{ if } T_2 > C_2\ (T_2 < C_2).$$

Proof. We focus on case (i), the proof of case (ii) is similar.

From assumption and Table 2, it follows that E_0, $E_{R1}(E_{I1})$ exist in system (13), and E_0 is unstable. Similarly, $\widetilde{E}_0$, $\widetilde{E}_{R1}(\widetilde{E}_{I1})$ exist in system (19) and $\widetilde{E}_0$ is unstable. It is similar to the proof of Theorem 4.2, we will use the monotonicity of Φ_t. Consider the initial condition $(N_1(0), U_1(0), N_2(0), U_2(0))$, then equation (20) holds. From Theorem 2.1, $\Phi_t(N_1(0), U_1(0), 0, 0)$ tends to $\widetilde{E}_{R1}$ or $\widetilde{E}_{I1}$ as t goes to infinity for $N_1(0) > 0$, and $\widetilde{E}_0$ is unstable in (N_1, Q_1) direction. Hence for the system (13) with initial condition $N_1(0) > 0$, the desired results hold. ∎

From now on, we assume that (H1)-(H4) hold and $R_{\text{in}} > \lambda_i$ and $I_0 > \xi_i$, for all $i = 1, 2$. From Table 2, E_0 is a repelling in system (13), so is $\widetilde{E}_0$ in system (19). Note that

$$\Phi_t(X_1^+ \times \{0\}) \subset X_1^+ \times \{0\},\ \Phi_t(\{0\} \times X_2^+) \subset \{0\} \times X_2^+,$$

and Theorem 2.1 tells us that the omega limit set $\omega(x_1, 0) = \widetilde{E}_{R1}$ or $\widetilde{E}_{I1}$ for $x_1 \in X_1^+ \setminus \{0\}$, $\omega(0, x_2) = \widetilde{E}_{R2}$ or $\widetilde{E}_{I2}$ for $x_2 \in X_2^+ \setminus \{0\}$.

By Theorem B in [6] or Theorem 2.4.1 in [16], we have the following results.

Theorem 4.4. *Let $S = [\widetilde{E}_{L2}, \widetilde{E}_{L1}]_K$, $L \in \{R, I\}$. Then S is positively invariant and the omega limit set of every orbit in X^+ is contained in S and exactly one of the following holds:*

(i) There exists a positive equilibrium $\widetilde{E}_c^{RI}$ of Φ_t in S;
(ii) $\omega(x) = \widetilde{E}_{L1}$ for every $x = (x_1, x_2) \in S$ with $x_i \neq 0$, $i = 1, 2$.
(iii) $\omega(x) = \widetilde{E}_{L2}$ for every $x = (x_1, x_2) \in S$ with $x_i \neq 0$, $i = 1, 2$.

Finally, if (ii) or (iii) hold, $x = (x_1, x_2) \in X^+ \setminus S$ and with $x_i \neq 0$, $i = 1, 2$, then either $\Phi_t(x) \to \widetilde{E}_{L1}$ or $\Phi_t(x) \to \widetilde{E}_{L2}$ as $t \to \infty$.

Theorem 4.5. *If E_{Li} is locally stable and E_{Lj} is unstable for $i, j \in \{1, 2\}$, $i \neq j$, $L \in \{R, I\}$, then $\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{Ri}(E_{Ii})$, for $N_i(0) > 0$.*

Proof. From Lemma 4.1, we know that the coexistent equilibrium E_c^{RI} does not exist in system (13), and neither do $\widetilde{E}_c^{RI}$. The assumption implies that $\widetilde{E}_{Li}$ is locally stable and $\widetilde{E}_{Lj}$ is unstable for system (19). By Theorem 4.4 then $\omega(x) = \tilde{E}_{Li}$ for every $x \in X^+$ with $N_i(0) > 0$. Hence for system (13), we proves the desired results. □

Theorem 4.6. *If both E_{L1} and E_{L2} are unstable, $L \in \{R, I\}$, then E_c^{RI} exists and $\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_c^{RI}$, for $N_1(0) > 0$, $N_2(0) > 0$.*

Proof. From assumption, we have that $\widetilde{E}_{L1}$, $\widetilde{E}_{L2}$ are unstable. By Theorem 4.4, $\omega(x) \neq \widetilde{E}_{L1}$, $\widetilde{E}_{L2}$ for all $x \in S$, then there exists $\widetilde{E}_c^{RI}$.

The result of Theorem 4.4 (ii) does not hold, which implies that E_{L1} is not locally attractive from below. Similarly, Theorem 4.4 (iii) does not hold implies that E_{L2} is not attractive from above.

By Theorem 2 of [12], and the fact that the coexistent equilibrium is unique, then for $x \in [\tilde{E}_c^{RI}, \tilde{E}_{L1}]_K \cup [\tilde{E}_{L2}, \tilde{E}_c^{RI}]_K := M$, $\omega(x) = \tilde{E}_c^{RI}$. We denote $\tilde{E}_c^{RI} := (\widetilde{N}_1, \widetilde{Q}_1, \widetilde{N}_2, \widetilde{Q}_2)$. Next, we consider $x = (x_1, x_2) \in S \setminus M$, if $x_i \geq (\widetilde{N}_i, \widetilde{Q}_i)$ for $i = 1, 2$ then there exist $\bar{x}_1 < x_1$, $\bar{x}_2 < x_2$ such that $(\bar{x}_1, x_2)$, $(x_1, \bar{x}_2) \in M$ and $(\bar{x}_1, x_2) <_K (x_1, x_2) <_K (x_1, \bar{x}_2)$. Since $\omega(\bar{x}_1, x_2) = \tilde{E}_c^{RI}$ and $\omega(x_1, \bar{x}_2) = \tilde{E}_c^{RI}$, we have that $\omega(x_1, x_2) = \tilde{E}_c^{RI}$. It is similar for the case $x_i \leq (\widetilde{N}_i, \widetilde{Q}_i)$ for $i = 1, 2$. Hence for $x \in S$, $\omega(x) = \tilde{E}_c^{RI}$, and $\tilde{E}_c^{RI}$ is a global attractor. Thus for system (13), we gives the desired results. □

Theorem 4.7. *If both E_{L1} and E_{L2} are locally stable, $L \in \{R, I\}$, we denote $B_i = \{x \in S : \omega(x) = E_{Li}\}$ be the basin of attracting of E_{Li}, for $i = 1, 2$, then E_c^{RI} exists and $\omega(x) = E_c^{RI}$ for $x \in Q = \Omega \setminus (B_1 \cup B_2)$ where Q is an unordered and positively invariant sub-manifold with codimension one.*

Proof. From assumption, we have that $\widetilde{E}_{L1}$, $\widetilde{E}_{L2}$ are also locally stable. From Theorem 4.4, $\omega(x) \neq \widetilde{E}_{L1}$, $\widetilde{E}_{L2}$ for all $x \in S$, then there exists $\widetilde{E}_c^{RI}$.

The assumption (H3) implies that Φ_t is continuously differentiable near the equilibrium $\tilde{E}_c^{RI}$. By [13] Theorem E.1, the spectral radius $r(D_x\Phi_t(\tilde{E}_c^{RI})) > 1$. By [9], we have that $\tilde{Q} = X^+ \setminus \{\tilde{B}_1 \cup \tilde{B}_2\}$ is an unordered and positively invariant sub-manifold with codimension one. Note that $\tilde{E}_0$ and $\tilde{E}_c^{RI}$ belong to the set $\tilde{Q}$. Since $\tilde{Q}$ is positively invariant, there is a heteroclinic orbit connecting $\tilde{E}_0$ and $\tilde{E}_c^{RI}$. In fact, the set $\tilde{Q}$ is the stable manifold of $\tilde{E}_c^{RI}$. Hence, for $x \notin \tilde{Q}$, either $\omega(x) = \widetilde{E}_{L1}$ or $\omega(x) = \widetilde{E}_{L2}$. The outcomes depend on initial conditions. □

Proof of Theorem 3.1. The assumption $R_{\text{in}} < \lambda_i$ or $I_0 < \xi_i$, by Theorem 4.2 or Theorem 4.3, we know that $N_i(t) \to 0$ as $t \to \infty$. $\square$

Proof of Theorem 3.2. The assumption implies that E_{R1} (or E_{I1}) is locally asymptotically stable if it exists, and the coexistent equilibrium E_c^{RI} does not exist. Assume that E_{R2} (or E_{I2}) is also locally asymptotically stable, from Theorem 4.7, E_c^{RI} exists, a contradiction. Thus E_{R2} (or E_{I2}) is unstable if it exists. By Theorem 4.5, the conclusion of this theorem holds. $\square$

Proof of Theorem 3.3. Note that, under the assumption $\lambda_2 < \lambda_1$ and $\xi_1 < \xi_2$, we have that $T_1 > T^* > T_2$. Table 2 tells us that $E_{R2},\ E_{I1}$ are locally asymptotically stable if they exist; $T^* < C_1$ if and only if E_{R1} is locally asymptotically stable; $T^* > C_{I2}$ if and only if E_{I2} is locally stable.

(i) If $T_1 < C_1,\ T_2 < C_2$, then $E_{I1},\ E_{I2}$ exists and E_{I1} is locally stable. We know that the stability of E_{I2} affects the global behavior of system (13). Hence there are two subcases:
  (a) If $T^* > C_{I2}$, then E_{I2} is locally stable. Hence, by Theorem 4.7, the outcomes depend on initial conditions.
  (b) If $T^* < C_{I2}$, then E_{I2} is unstable. Hence, by Theorem 4.5, $\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{I1}$, for $N_1(0) > 0,\ N_2(0) > 0$.

(ii) If $T_1 < C_1,\ T_2 > C_2$, then $E_{I1},\ E_{R2}$ exist and they are locally stable. Hence, by Theorem 4.7, the outcomes depend on initial conditions.

(iii) If $T_1 > C_1,\ T_2 > C_2$, then $E_{R1},\ E_{R2}$ exist and E_{R2} is locally stable. Similarly, we will consider the following subcases.
  (a) If $T^* < C_1$, then E_{R1} is locally stable, and by Theorem 4.7, the outcomes depend on initial conditions.
  (b) If $T^* > C_1$, then E_{R1} is unstable, by Theorem 4.5, $\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{R2}$, for $N_1(0) > 0,\ N_2(0) > 0$.

(iv) If $T_1 > C_1,\ T_2 < C_2$, then $E_{R1},\ E_{I2}$ exist. Similarly, we will consider the stability of $E_{R1},\ E_{I2}$.
  (a) If $T^* < C_1, C_{I2}$, then E_{R1} is locally stable and E_{I2} is unstable. Hence, by Theorem 4.5, $\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{R1}$, for $N_1(0) > 0,\ N_2(0) > 0$.
  (b) If $C_1 < T^* < C_{I2}$, then E_{R1} and E_{I2} are unstable and E_c^{RI} exists, since Theorem 4.4. Hence, by Theorem 4.6, $\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_c^{RI}$, for $N_1(0) > 0,\ N_2(0) > 0$.
  (c) If $C_{I2} < T^* < C_1$, then E_{R1} and E_{I2} are locally stable. Hence, by Theorem 4.7, the outcomes depend on initial conditions.
  (d) If $C_1, C_{I2} < T^*$, then E_{R1} is unstable and E_{I2} is locally stable. Hence, by Theorem 4.5, $\lim_{t\to\infty}(N_1(t), Q_1(t), N_2(t), Q_2(t)) = E_{I2}$, for $N_1(0) > 0,\ N_2(0) > 0$. $\square$

Proof of Lemma 3.4. From (14), we have

$$\nu_2(R_{\text{in}} - N_2^{I2} Q_2^{I2}, Q_2^{I2}) = D Q_2^{I2}, \tag{21}$$

where $N_2^{I2} = N_2^{I2}(\ln I_0) = \frac{\ln I_0 - \ln \xi_2}{k_2},\ Q_2^{I2} = Q_2^{I2}(R_{\text{in}}, \ln I_0)$. Note that

$$\frac{d}{d \ln I_0} N_2^{I2}(\ln I_0) = \frac{1}{k_2}.$$

Differentiating the equation (21) with respect to R_{in}, then

$$\frac{\partial \nu_2}{\partial R}(R_{\text{in}} - N_2^{I2}Q_2^{I2}, Q_2^{I2})(1 - N_2^{I2}\frac{\partial Q_2^{I2}}{\partial R_{\text{in}}}) + \frac{\partial \nu_2}{\partial Q}(R_{\text{in}} - N_2^{I2}Q_2^{I2}, Q_2^{I2})\frac{\partial Q_2^{I2}}{\partial R_{\text{in}}} = D\frac{\partial Q_2^{I2}}{\partial R_{\text{in}}}.$$

Hence

$$\frac{\partial Q_2^{I2}}{\partial R_{\text{in}}} = \frac{\frac{\partial \nu_2}{\partial R}(R_{\text{in}} - N_2^{I2}Q_2^{I2}, Q_2^{I2})}{\frac{\partial \nu_2}{\partial R}(R_{\text{in}} - N_2^{I2}Q_2^{I2}, Q_2^{I2})N_2^{I2} - \frac{\partial \nu_2}{\partial Q}(R_{\text{in}} - N_2^{I2}Q_2^{I2}, Q_2^{I2}) + D} > 0$$

Similarly, differentiating (21) with respective to $\ln I_0$, we have

$$\frac{\partial \nu_2}{\partial R}(R_{\text{in}} - N_2^{I2}Q_2^{I2}, Q_2^{I2})(-\frac{Q_2^{I2}}{k_2} - N_2^{I2}\frac{\partial Q_2^{I2}}{\partial \ln I_0}) + \frac{\partial \nu_2}{\partial Q}(R_{\text{in}} - N_2^{I2}Q_2^{I2}, Q_2^{I2})\frac{\partial Q_2^{I2}}{\partial \ln I_0} = D\frac{\partial Q_2^{I2}}{\partial \ln I_0}.$$

Hence

$$\begin{aligned}\frac{\partial Q_2^{I2}}{\partial \ln I_0} &= \frac{-\frac{Q_2^{I2}}{k_2}\frac{\partial \nu_2}{\partial R}(R_{\text{in}} - N_2^{I2}Q_2^{I2}, Q_2^{I2})}{\frac{\partial \nu_2}{\partial R}(R_{\text{in}} - N_2^{I2}Q_2^{I2}, Q_2^{I2})N_2^{I2} - \frac{\partial \nu_2}{\partial Q}(R_{\text{in}} - N_2^{I2}Q_2^{I2}, Q_2^{I2}) + D} \\ &= -\frac{Q_2^{I2}}{k_2}\frac{\partial Q_2^{I2}}{\partial R_{\text{in}}} < 0\end{aligned}$$

Therefore,

$$\frac{\partial C_{I2}}{\partial R_{\text{in}}} = -\frac{k_2\frac{\partial Q_2^{I2}}{\partial R_{\text{in}}}}{(Q_2^{I2})^2} < 0, \ \frac{\partial C_{I2}}{\partial \ln I_0} = -\frac{k_2\frac{\partial Q_2^{I2}}{\partial \ln I_0}}{(Q_2^{I2})^2} > 0.$$

□

5. **Graphical presentation.** In this section we demonstrate the graphical presentation of the two species competition for light and single nutrient with internal storage under the assumption $\lambda_i < R_{\text{in}}$, $\xi_i < I_0$ for all $i = 1, 2$. First of all, we consider the identities for resources R and I in (13) that is

$$R_{\text{in}} - R = Q_1N_1 + Q_2N_2, \tag{22}$$
$$\ln I_0 - \ln I = k_1N_1 + k_2N_2, \tag{23}$$

Here we rewrite the identity of $I(t)$ in (13) as equation (23). Note that (22), (23) imply that the supply resource is equal to all consumption. We can rewrite (22), (23) in the form

$$\begin{bmatrix} R_{\text{in}} - R \\ \ln I_0 - \ln I \end{bmatrix} = \begin{bmatrix} Q_1 \\ k_1 \end{bmatrix} N_1 + \begin{bmatrix} Q_2 \\ k_2 \end{bmatrix} N_2. \tag{24}$$

We called the vector in the left hand side of (24) the supply vector, and called the right hand side the consumption vector. We can use graphical presentation to predict the outcomes of competition, the method is similar to [14].

See Figure 2, if the slope of supply vector at the corner of isocline of species 1 is larger than $C_1 = \frac{k_1}{\sigma_1}$, then species 1 is R-limited (region A), that means $T_1 = \frac{\ln I_0 - \xi_1}{R_{\text{in}} - \lambda_1} > C_1$. On the other hand, if $T_1 < C_1$ then species 1 is I-limited (region B) and the slope of consumption vector is $C_{I1} = \frac{k_1}{Q_1^{I1}}$. For the case of species 2,

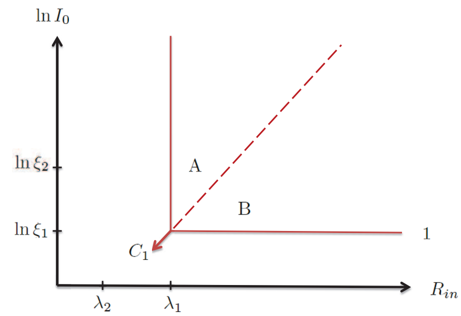

FIGURE 2. The isocline of N_1 is right-angled. In region A, $T_1 > C_1$ and species 1 is R-limited; in region B, $T_1 < C_1$ and species 1 is I-limited.

we have similar results, that is, when $T_2 = \frac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_2} < C_2 = \frac{k_2}{\sigma_2}$, then species 2 is R-limited; when $T_2 < C_2$, then species 2 is I-limited and the slope of consumption vector is $C_{I2} = \frac{k_2}{Q_2^{I2}}$. From Lemma 3.4, we know that C_{I2} is strictly decreasing in R_{in} and strictly increasing in $\ln I_0$, and so is C_{I1}.

We assume that (H2) $\xi_1 < \xi_2$ always holds. If $\lambda_1 < \lambda_2$, then species 1 is better competitor in nutrient and light. Hence species 1 will out-compete species 2.

TABLE 3

Case	Condition	States	Stability
(I)	$T_1 < C_1$ $T_2 < C_2$	$E_{I1},\ E_{I2}$	(I.a) $T^* > C_{I2}$, bistability happens. (I.b) $T^* < C_{I2}$, E_{I1} is G.A.S.
(II)	$T_1 < C_1$ $T_2 > C_2$	$E_{I1},\ E_{R2}$	Bi-stability happens.
(III)	$T_1 > C_1$ $T_2 > C_2$	$E_{R1},\ E_{R2}$	(III.a) $T^* < C_1$, bistability happens. (III.b) $T^* > C_1$, E_{R2} is G.A.S.
(IV)	$T_1 > C_1$ $T_2 < C_2$	$E_{R1},\ E_{I2}$	(IV.a) $T^* < C_1,\ C_{I2}$, E_{R1} is G.A.S. (IV.b) $C_1 < T^* < C_{I2}$, E_c^{RI} is G.A.S. (IV.c) $C_1 > T^* > C_{I2}$, bistability happens. (IV.d) $T^* > C_1,\ C_{I2}$, E_{I2} is G.A.S.

G.A.S. means globally asymptotically stable.

Assume $\lambda_1 > \lambda_2$ and (H2) hold, then species 1 is better competitor in light and species 2 is better competitor in nutrient. There are four possibilities in the following (see also Table 3):

(I) Species 1 is I-limited and species 2 is I-limited, that is $T_1 < C_1,\ T_2 < C_2$. Because species 1 is better competitor in light, then E_{I1} is locally asymptotically stable.

The fact that

$$\min\{\mu_1(Q_1^{I2}), \eta_1(\xi_2)\} - D < 0 \tag{25}$$

implies that

$$\frac{N_1'}{N_1}\Big|_{(N_1,Q_1,N_2,Q_2)=E_{I2}} < 0,$$

and species 1 can not invade when the resident species attains the amount N_2^{I2} with cell quota Q_2^{I2}. Hence E_{I2} is locally asymptotically stable. On the other hand, if $\min\{\mu_1(Q_1^{I2}), \eta_1(\xi_2)\} - D > 0$ then species 1 invade successfully and E_{I2} is unstable. Note that, under assumption (H2), (25) means that $Q_1^{I2} < \sigma_1$, which is equivalent to $R^{I2} < \lambda_1$. From the fact

$$R^{I2} = R_{\text{in}} - N_2^{I2}Q_2^{I2} = R_{\text{in}} - \frac{\ln I_1 - \ln \xi_2}{k_2} Q_2^{I2} < \lambda_1,$$

we have

$$T^* = \frac{\ln I_1 - \ln \xi_2}{R_{\text{in}} - \lambda_1} > \frac{k_2}{Q_2^{I2}} = C_{I2}.$$

Hence E_{I2} is locally asymptotically stable if and only if $T^* > C_{I2}$. Therefore, we have the following two cases.

(I.a) If $T^* > C_{I2}$ then E_{I1} and E_{I2} are locally stable, hence the outcome depends on initial population, it is a bistable case;

(I.b) If $T^* < C_{I2}$, then E_{I2} is unstable. Hence E_{I1} is globally stable and species 1 competitively excludes species 2.

(II) Species 1 is I-limited and species 2 is R-limited, that is $T_1 < C_1,\ T_2 > C_2$. We know that species 1 is better competitor in light and species 2 is better competitor in nutrient, hence E_{I1} and E_{R2} are locally asymptotically stable. Therefore, it is bistable and the outcome depends on initial population.

(III) Species 1 is R-limited and species 2 is R-limited, that is $T_1 > C_1,\ T_2 > C_2$. We know that species 2 is better competitor in nutrient, hence E_{R2} is locally asymptotically stable.

Note that

$$\min\{\mu_2(Q_2^{R1}), \eta_2(I^{R1})\} - D < 0 \tag{26}$$

implies that

$$\frac{N_2'}{N_2}\Big|_{(N_1,Q_1,N_2,Q_2)=E_{R1}} < 0,$$

and species 2 can not invade when the resident species attains the amount N_1^{R1} with cell quota Q_1^{R1}. Hence E_{R1} is locally asymptotically stable. On the other hand, if $\min\{\mu_2(Q_2^{R1}), \eta_2(I^{R1})\} - D > 0$ then species 2 invade successfully and E_{R1} is unstable. Under the assumption $\lambda_1 > \lambda_2$, the inequality (26) implies that $Q_2^{R1} > \sigma_2$. If not, then

$$\nu_2(\lambda_1, Q_2^{R1}) < DQ_2^{R1} \le D\sigma_2 = \nu_2(\lambda_2, \sigma_2) \le \nu_2(\lambda_2 Q_2^{R1}),$$

and $\lambda_1 \le \lambda_2$, a contradiction. Hence the assumption $\lambda_1 > \lambda_2$ implies that (26) holds if and only if $I^{R1} < \xi_2$, that is

$$I^{R1} = I_0 \exp(-k_1 \frac{R_{\text{in}} - \lambda_1}{\sigma_1}) < \xi_2,$$

i.e.,

$$T^* = \frac{\ln I_0 - \ln \xi_2}{R_{\text{in}} - \lambda_1} < \frac{k_1}{\sigma_1} = C_1.$$

Hence E_{R1} is locally asymptotically stable if and only if $T^* < C_1$.

(III.a) If $T^* < C_1$ then E_{R1} and E_{R2} are locally asymptotically stable, hence the outcome depends on initial population, it is a bistable case;

(III.b) If $T^* > C_1$, then E_{R1} is unstable. Hence E_{R2} is globally stable and species 2 competitively excludes species 1.

(IV) Species 1 is R-limited and species 2 is I-limited, that is $T_1 > C_1,\ T_2 < C_2$. From the stability of E_{R1} and E_{I2} which were discussed in (I) and (III), we have the following subcases:

(IV.a) If $T^* < C_1,\ C_{I2}$, then E_{I2} is unstable and E_{R1} is locally asymptotically stable. Hence E_{R1} is globally stable and species 1 competitively excludes species 2;

(IV.b) If $C_1 < T^* < C_{I2}$, then E_{R1} and E_{I2} are unstable, then there exists an coexistent equilibrium E_c^{RI} and it is globally stable;

(IV.c) If $C_{I2} < T^* < C_1$, then E_{R1} and E_{I2} are locally asymptotically stable. Hence the outcome depends on initial population, it is a bistable case;

(IV.d) If $C_1,\ C_{I2} < T^*$, then E_{R1} is unstable and E_{I2} is locally asymptotically stable. Hence E_{I2} is globally stable and species 2 competitively excludes species 1.

We summarize all possible outcomes in Table 3 and present the relations in Figure 3. From calculation in the Appendix, we know that the curve $T^* = C_{I2}$ is a straight line.

We also draw the graphs, Figure 4, of the model in [10], which is two species $(x_1,\ x_2)$ competition for two resources R and S with internal storage. We follow the notations and results in [10], and demonstrate the competition outcomes graphically. We assume $0 < \lambda_{R2} < \lambda_{R1} < R^0,\ 0 < \lambda_{S1} < \lambda_{S2} < S^0$ and denote

$$T_1 = \frac{S^0 - \lambda_{S1}}{R^0 - \lambda_{R1}},\ C_1 = \frac{\sigma_{S1}}{\sigma_{R1}},\ C_{R1} = \frac{Q_{S1}^{R1}}{\sigma_{R1}}$$
$$T_2 = \frac{S^0 - \lambda_{S2}}{R^0 - \lambda_{R2}},\ C_2 = \frac{\sigma_{S2}}{\sigma_{R2}},\ C_{S2} = \frac{\sigma_{S2}}{Q_{R2}^{S2}},$$

and

$$T^* = \frac{S^0 - \lambda_{S2}}{R^0 - \lambda_{R1}}.$$

Note that $Q_{S1}^{R1} > \sigma_{S1}$ and $Q_{R2}^{S2} > \sigma_{R2}$ which implies that $C_{R1} > C_1$ and $C_{S2} < C_2$. From calculation in the Appendix, we know that $T^* = C_{R1}$ and $T^* = C_{S2}$ are two straight lines. We summarize all possible outcomes of competition in Table 4 and illustrate in Figure 4.

Table 4

Case	Condition	States	Stability
(I)	$T_1 < C_1$	$E_{S1},\ E_{S2}$	(I.a) $T^* > C_{S2}$, bistability happens.
	$T_2 < C_2$		(I.b) $T^* < C_{S2}$, E_{R1} is G.A.S.
(II)	$T_1 < C_1$	$E_{S1},\ E_{R2}$	Bistability happens.
	$T_2 > C_2$		
(III)	$T_1 > C_1$	$E_{R1},\ E_{R2}$	(III.a) $T^* < C_{R1}$, bistability happens.
	$T_2 > C_2$		(III.b) $T^* > C_{R1}$, E_{R2} is G.A.S.
(IV)	$T_1 > C_1$	$E_{R1},\ E_{S2}$	(IV.a) $T^* < C_{R1},\ C_{S2}$, E_{R1} is G.A.S.
	$T_2 < C_2$		(IV.b) $C_{R1} < T^* < C_{S2}$, E_c^{RS} is G.A.S.
			(IV.c) $C_{R1} > T^* > C_{S2}$, bistability happens.
			(IV.d) $T^* > C_{R1},\ C_{S2}$, E_{S2} is G.A.S.

G.A.S. means globally asymptotically stable.

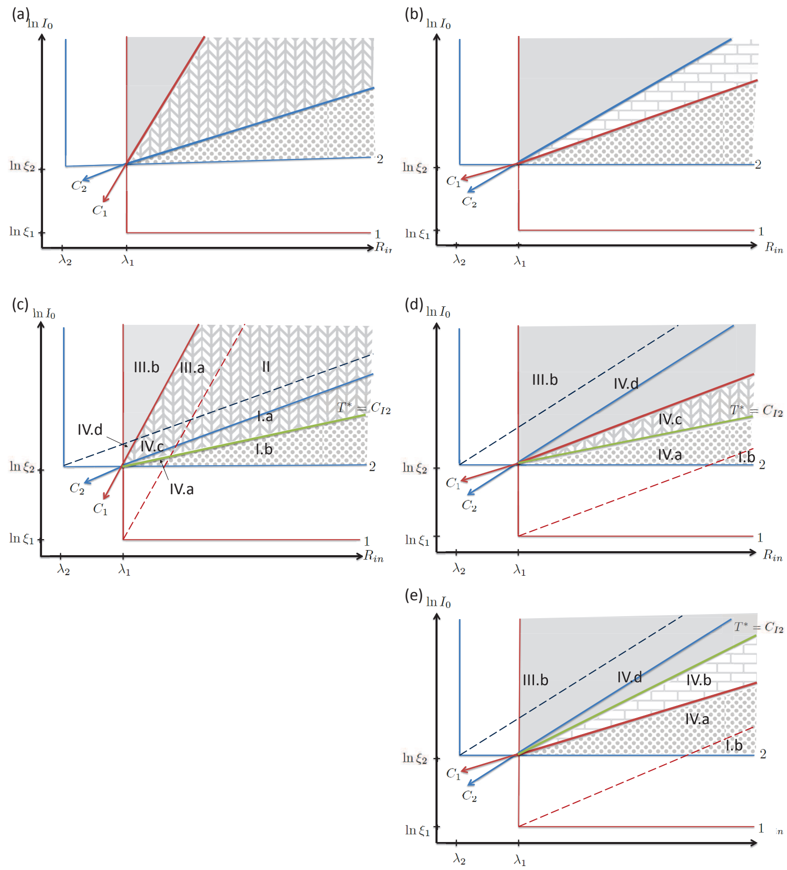

FIGURE 3. (a) and (b) are modified from Figure 1 in Passarge et al. [11]. (c)-(e) illustrate outcomes of our model. The isoclines of N_1 and N_2 are right-angled and denoted by graphs 1 and 2, respectively. In dotted region, species 1 wins; species 2 wins in gray region; the feathered region indicates bistable case; the brick region represents species coexistence. The case $C_2 < C_1$ are (a) and (c); The case $C_1 < C_2$ are (b), (d), (e) where $C_{I2} < C_1$ in (d) and $C_{I2} > C_1$ in (e).

6. **Discussion.** We analyze a competition model of two phytoplankton species for a single nutrient with internal storage and light in a well mixed aquatic environment. The results show that extinction, coexistence and bistability are predictable in this model. First, while the input concentration of nutrient is less than the break-even amount of each species, or when the input light intensity is lower than the basic need of each species, both species extinct (Theorem 3.1). Secondly, when the input concentrations of nutrient and light are higher than break-even concentration of all species, the outcomes vary as following. If the species i, $i \in \{1, 2\}$, has lowest break-even concentration of nutrient and light, then it competitively excludes the other (Theorem 3.2). If the semitrivial equilibrium E_i, $i \in \{1, 2\}$, is locally stable and E_j, $j \neq i$, is unstable, then coexistence is impossible (Lemma 3.4) and E_i is globally stable (Theorem 4.5). If both E_i and E_j are unstable, then coexistence is possible,

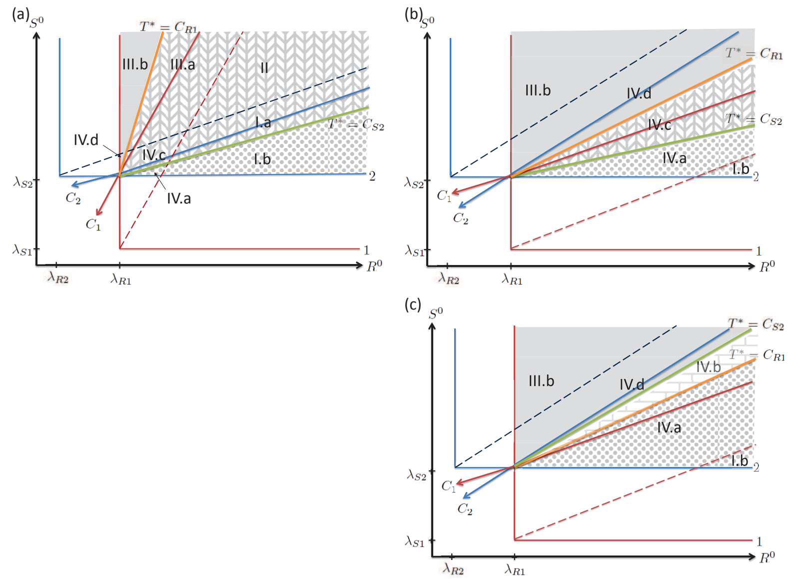

FIGURE 4. The isoclines of N_1 and N_2 are right-angled and denoted by graphs 1 and 2, respectively. In dotted region, species 1 wins; species 2 wins in gray region; the feathered region indicates bistable case; the brick region represents species coexistent. (a) The case $C_2 < C_1$; (b) The case $C_1 < C_2$ with $C_{S2} < C_1$; (c) The case $C_1 < C_2$ with $C_{S2} > C_1$.

i.e., the coexistent equilibrium E_c^{RI} exists and it is globally stable (Theorem 4.6). If both E_i and E_j are locally stable, then the outcome of competition is bistability of two species (Theorem 4.7).

In the graphical presentation, our results (Figure 3cde) are compared with results modified from Passarge et al. [11] (Figure 3ab), in which they considered two species competition for light and nutrient without internal storage. For the case $C_1 > C_2$, bistability of two species occurs in Figure 3a and our model (Figure 3c); however, the bistable region is broader from our model. For the case $C_1 < C_2$, coexistence occurs in Figure 3b; however, our model indicates coexistence or bistability of the two species (Figure 3d and 3e).

We apply graphic approach for the model in [10] and show the results in Figure 4. We demonstrate two species competition for two complementary nutrients, both exhibit internal storage. We compare Figure 4 with the result in Tilman [14], which consider the model without any internal storage. Similar to the comparison beween our model (13) and that of Passarge et al. [11], Figure 4 presents the additional prediction of bistability in the case $C_1 < C_2$, and the enlarged bistable region in the case $C_1 > C_2$. From the comparison of models with and without internal storage, we obtain that bistability occurs in the case $C_1 > C_2$ of those four models. The models with internal storage do not change the outcome qualitatively; namely, they only enlarge the bistable region. In the case $C_1 < C_2$, the outcome of the model without internal storage is either coexistence or competitive exclusion. Model with internal storage predicts an additional region of bistability for the two species.

In Passarge et al. [11], they carried out monoculture experiments for five freshwater phytoplankton species competing for phosphorus and light. The results show that the species with the lowest break-even concentration of nutrient happens to have the lowest break-even light intensity, and competitively excludes others as the case in Theorem 3.2. The analytical result does not match the outcome of the experiment in Passarge et al. [11]. We owe this to the violation on the assumption of trade-off between competitive ability for phosphorus and light in the focal species in Passarge et al. [11]. Without the trade-off, the competitive exclusion will occur.

In reality, a large number of phytoplankton species coexist in competing for multiple nutrients and light. In this paper we consider only two species compete for a limiting single-nutrient with internal storage and light and obtain the possible outcomes that are classified in graphical presentation. To explore the mechanism promoting biodiversity in more realistic conditions, we will expand the model for multiple species with the assumption of internal storage for our future work. In addition, we will consider heterogeneity for light environment as suggested by Yoshiyama et al. [15]. We trust such expansion in the model shall bring fruitful and insightful knowledge to such system.

7. Appendix.

A. Local stability of equilibria. For equilibrium $E_0 = (0, Q_1^0, 0, Q_2^0)$,

$$J(E_0) = \begin{bmatrix} m_{11} & 0 & 0 & 0 \\ m_{21} & m_{22} & m_{23} & 0 \\ 0 & 0 & m_{33} & 0 \\ m_{41} & 0 & m_{43} & m_{44} \end{bmatrix},$$

where

$$m_{11} = \min\{\mu_1(Q_1^0), \eta_1(I_0)\} - D,\ m_{21} = -\frac{\partial \nu_1}{\partial R}(R_{\text{in}}, Q_1^0)Q_1^0 - \Delta_{N_1}^1(Q_1^0, I_0)Q_1^0,$$

$$m_{22} = \frac{\partial \nu_1}{\partial Q_1}(R_{\text{in}}, Q_1^0) - \min\{\mu_1(Q_1^0), \eta_1(I^0)\} - \Delta_{Q_1}^1(Q_1^0, I_0)Q_1^0,$$

$$m_{23} = -\frac{\partial \nu_1}{\partial R}(R_{\text{in}}, Q_1^0)Q_2^0 - \Delta_{N_2}^1(Q_1^0, I_0)Q_1^0,\ m_{33} = \min\{\mu_2(Q_2^0), \eta_2(I^0)\} - D,$$

$$m_{41} = -\frac{\partial \nu_2}{\partial R}(R_{\text{in}}, Q_2^0)Q_1^0 - \Delta_{N_1}^2(Q_2^0, I_0)Q_2^0,$$

$$m_{43} = -\frac{\partial \nu_2}{\partial R}(R_{\text{in}}, Q_2^0)Q_2^0 - \Delta_{N_2}^2(Q_2^0, I_0)Q_2^0,$$

$$m_{44} = \frac{\partial \nu_2}{\partial Q_2}(R_{\text{in}}, Q_2^0) - \min\{\mu_2(Q_2^0), \eta_2(I^0)\} - \Delta_{Q_2}^2(Q_2^0, I_0)Q_2^0,$$

where $\Delta_{N_1}^1(Q_1, I)$, $\Delta_{N_2}^1(Q_1, I)$, $\Delta_{Q_1}^1(Q_1, I)$ are functions of Q_1, I; $\Delta_{N_1}^2(Q_2, I)$, $\Delta_{N_2}^2(Q_2, I)$, $\Delta_{Q_2}^2(Q_2, I)$ are functions of Q_2, I:

$$\Delta_{N_1}^1(x, y) = \frac{\partial}{\partial N_1}\min\{\mu_1(Q_1), \eta_1(I)\}\Big|_{(Q_1,I)=(x,y)} = \begin{cases} 0 & \text{if } \mu_1(x) < \eta_1(y), \\ -k_1 y \eta_1'(y) & \text{if } \mu_1(x) > \eta_1(y). \end{cases}$$

$$\Delta_{N_2}^1(x, y) = \frac{\partial}{\partial N_2}\min\{\mu_1(Q_1), \eta_1(I)\}\Big|_{(Q_1,I)=(x,y)} = \begin{cases} 0 & \text{if } \mu_1(x) < \eta_1(y)), \\ -k_2 y \eta_1'(y) & \text{if } \mu_1(x) > \eta_1(y)). \end{cases}$$

$$\Delta_{Q_1}^1(x, y) = \frac{\partial}{\partial Q_1}\min\{\mu_1(Q), \eta_1(I)\}\Big|_{(Q_1,I)=(x,y)} = \begin{cases} \mu_1'(x) & \text{if } \mu_1(x) < \eta_1(y)), \\ 0 & \text{if } \mu_1(x) > \eta_1(y). \end{cases}$$

$$\Delta^2_{N_1}(x,y)=\frac{\partial}{\partial N_1}\min\{\mu_2(Q_2),\eta_2(I)\}\Big|_{(Q_2,I)=(x,y)}=\begin{cases}0 & \text{if } \mu_2(x)<\eta_2(y),\\ -k_1y\eta_2'(y) & \text{if } \mu_2(x)>\eta_2(y).\end{cases}$$

$$\Delta^2_{N_2}(x,y)=\frac{\partial}{\partial N_2}\min\{\mu_2(Q_2),\eta_2(I)\}\Big|_{(Q_2,I)=(x,y)}=\begin{cases}0 & \text{if } \mu_2(x)<\eta_2(y),\\ -k_2y\eta_2'(y) & \text{if } \mu_2(x)>\eta_2(y).\end{cases}$$

$$\Delta^2_{Q_2}(x,y)=\frac{\partial}{\partial Q_2}\min\{\mu_2(Q),\eta_2(I)\}\Big|_{(Q_2,I)=(x,y)}=\begin{cases}\mu_2'(x) & \text{if } \mu_2(x)<\eta_2(y),\\ 0 & \text{if } \mu_2(x)>\eta_2(y).\end{cases}$$

The eigenvalues of $J(E_0)$ are

$$m_{11},\ m_{22}<0,\ m_{33}<0,\ m_{44}<0,$$

hence E_{R1} is locally stable if $m_{11}<0$.

For equilibrium $E_{R1}=(N_1^{R1},Q_1^{R1},0,Q_2^{R1})$,

$$J(E_{R1})=\begin{bmatrix}0 & m_{12} & 0 & 0\\ m_{21} & m_{22} & m_{23} & 0\\ 0 & 0 & m_{33} & 0\\ m_{41} & m_{42} & m_{43} & m_{44}\end{bmatrix},$$

where

$$\begin{aligned}
m_{12}&=\mu_1'(\sigma_1)N_1^{R1}>0,\ m_{21}=-\frac{\partial\nu_1}{\partial R}(\lambda_1,\sigma_1)\sigma_1<0,\\
m_{22}&=-\frac{\partial\nu_1}{\partial R}(\lambda_1,\sigma_1)N_1^{R1}+\frac{\partial\nu_1}{\partial Q_1}(\lambda_1,\sigma_1)-D-\mu_1'(\sigma_1)\sigma_1<0,\\
m_{23}&=-\frac{\partial\nu_1}{\partial R}(\lambda_1,\sigma_1)Q_2^{R1},\ m_{33}=\min\{\mu_2(Q_2^{R1}),\eta_2(I^{R1})\}-D,\\
m_{41}&=-\frac{\partial\nu_2}{\partial R}(\lambda_1,Q_2^{R1})\sigma_1-\Delta^2_{N_1}(Q_2^{R1},I^{R1})Q_2^{R1},\ m_{42}=-\frac{\partial\nu_2}{\partial Q_1}(\lambda_1,Q_2^{R1})N_1^{R1},\\
m_{43}&=-\frac{\partial\nu_2}{\partial R}(\lambda_1,Q_2^{R1})Q_2^{R1}-\Delta^2_{N_2}(Q_2^{R1},I^{R1})Q_2^{R1},\\
m_{44}&=\frac{\partial\nu_2}{\partial Q_2}(\lambda_1,Q_2^{R1})-\min\{\mu_2(Q_2^{R1}),\eta_2(I^{R1})\}-\Delta^2_{Q_2}(Q_2^{R1},I^{R1})Q_2^{R1}<0.
\end{aligned}$$

The eigenvalues of $J(E_{R1})$ are $m_{33},\ m_{44}<0$ and the eigenvalues of $\begin{bmatrix}0 & m_{12}\\ m_{21} & m_{22}\end{bmatrix}$. Since $m_{22}<0,\ m_{12}m_{21}<0$, there are three eigenvalues of $J(E_{R1})$ with negative real part, and E_{R1} is locally stable if $m_{33}<0$, that is $\min\{\mu_2(Q_2^{R1}),\eta_2(I^{R1})\}-D<0$.

Similarly, for equilibrium $E_{R2}=(0,Q_1^{R2},N_2^{R2},Q_2^{R2})$, there are three eigenvalues of $J(E_{R2})$ with negative real part and it is locally stable if $\min\{\mu_1(Q_1^{R2}),\eta_1(I^{R2})\}-D<0$.

For equilibrium $E_{I1}=(N_1^{I1},Q_1^{I1},0,Q_2^{I1})$,

$$J(E_{I1})=\begin{bmatrix}m_{11} & 0 & m_{13} & 0\\ m_{21} & m_{22} & m_{23} & 0\\ 0 & 0 & m_{33} & 0\\ m_{41} & m_{42} & m_{43} & m_{44}\end{bmatrix},$$

$m_{11} = -k_1\eta_1'(\xi_1)\xi_1 N_1^{I1},\ m_{13} = -k_2\eta_1'(\xi_1)\xi_1 N_1^{I1},$

$m_{21} = -\dfrac{\partial\nu_1}{\partial R}(R^{I1}, Q_1^{I1})Q_1^{I1} + k_1\eta_1'(\xi_1)\xi_1 Q_1^{I1},$

$m_{22} = -\dfrac{\partial\nu_1}{\partial R}(R^{I1}, Q_1^{I1})N_1^{I1} + \dfrac{\partial\nu_1}{\partial Q_1}(R^{I1}, Q_1^{I1}) - D,$

$m_{23} = -\dfrac{\partial\nu_1}{\partial R}(R^{I1}, Q_1^{I1})Q_2^{I1} + k_2\eta_1'(\xi_1)\xi_1 Q_1^{I1},$

$m_{33} = \min\{\mu_2(Q_2^{I1}), \eta_2(\xi_1)\} - D,\ m_{41} = -\dfrac{\partial\nu_2}{\partial R}(R^{I1}, Q_2^{I1})Q_1^{I1} - \Delta_{N_1}^2(Q_2^{I1}, \xi_1)Q_2^{I1},$

$m_{42} = -\dfrac{\partial\nu_2}{\partial Q_1}(R^{I1}, Q_2^{I1})N_1^{I1},\ m_{43} = -\dfrac{\partial\nu_2}{\partial R}(R^{I1}, Q_2^{I1})Q_2^{I1} - \Delta_{N_2}^2(Q_2^{I1}, \xi_1)Q_2^{I1},$

$m_{44} = \dfrac{\partial\nu_2}{\partial Q_2}(R^{I1}, Q_2^{I1}) - \min\{\mu_2(Q_2^{I1}), \eta_2(\xi_1)\} - \Delta_{Q_2}^2(Q_2^{I1}, \xi_1)Q_2^{I1}.$

There are three eigenvalues of $J(E_{I1})$ with negative real part, and it is locally stable if $\min\{\mu_2(Q_2^{I1}), \eta_2(\xi_1)\} < D$

Similarly, for equilibrium $E_{I2} = (0, Q_1^{I2}, N_2^{I2}, Q_2^{I2})$, there are three eigenvalues of $J(E_{I2})$ with negative real part and it is locally stable if $\min\{\mu_1(Q_1^{I2}), \eta_1(\xi_2)\} < D$.

For equilibrium $E_c^{RI} = (N_1^{RI}, Q_1^{RI}, N_2^{RI}, Q_2^{RI})$ is

$$J(E_c^{RI}) = \begin{bmatrix} 0 & m_{12} & 0 & 0 \\ m_{21} & m_{22} & m_{23} & m_{24} \\ m_{31} & 0 & m_{33} & 0 \\ m_{41} & m_{42} & m_{43} & m_{44} \end{bmatrix},$$

$m_{12} = \mu_1'(\sigma_1)N_1^{RI},\ m_{21} = -\dfrac{\partial\nu_1}{\partial R}(\lambda_1, \sigma_1)\sigma_1,$

$m_{22} = -\dfrac{\partial\nu_1}{\partial R}(\lambda_1, \sigma_1)N_1^{RI} + \dfrac{\partial\nu_1}{\partial Q_1}(\lambda_1, \sigma_1) - D - \mu_1'(\sigma_1)\sigma_1,\ m_{23} = -\dfrac{\partial\nu_1}{\partial R}(\lambda_1, \sigma_1)Q_2^{RI},$

$m_{24} = -\dfrac{\partial\nu_1}{\partial R}(\lambda_1, \sigma_1)N_2^{RI},\ m_{31} = -k_1\eta_2'(\xi_2)\xi_2 N_2^{RI},\ m_{33} = -k_2\eta_2'(\xi_2)\xi_2 N_2^{RI},$

$m_{41} = -\dfrac{\partial\nu_2}{\partial R}(\lambda_1, Q_2^{RI})\sigma_1 + k_1\eta_2'(\xi_2)\xi_2 Q_2^{RI},$

$m_{42} = -\dfrac{\partial\nu_2}{\partial R}(\lambda_1, Q_2^{RI})N_1^{RI},\ m_{43} = -\dfrac{\partial\nu_2}{\partial R}(\lambda_1, Q_2^{RI})Q_2^{RI} + k_2\eta_2'(\xi_2)\xi_2 Q_2^{RI},$

$m_{44} = -\dfrac{\partial\nu_2}{\partial R}(\lambda_1, Q_2^{RI})N_2^{RI} + \dfrac{\partial\nu_2}{\partial Q_2}(\lambda_1, Q_2^{RI}) - D.$

B. Geometric properties of $T^* = C_{I2},\ T^* = C_{R1},\ T^* = C_{S2}$. First of all, we consider the geometric properties of the curve of $T^* = C_{I2}$. The equation $T^* = C_{I2}$ implies

$$\frac{\ln I_0 - \ln \xi_2}{R_{\rm in} - \lambda_1} = \frac{k_2}{Q_2^{I2}},$$

and

$$(\ln I_0 - \ln \xi_2)Q_2^{I2} = k_2(R_{\rm in} - \lambda_1).$$

We denote the function $G(R_{\rm in}, \ln I_0)$ as following

$$G(R_{\rm in}, \ln I_0) = (\ln I_0 - \ln \xi_2)Q_2^{I2} - k_2(R_{\rm in} - \lambda_1),$$

where $Q_2^{I2} = Q_2^{I2}(R_{\rm in}, \ln I_0)$. Note that $G(\lambda_1, \ln \xi_2) = 0$.

Computation of the first order partial derivative of G is

$$\frac{\partial}{\partial R_{\text{in}}}G(R_{\text{in}},\ln I_0)=\frac{-k_2\Big(-\frac{\partial\nu_2}{\partial Q}(R^{I2},Q_2^{I2})+D\Big)}{\frac{\partial\nu_2}{\partial R}(R^{I2},Q_2^{I2})N_2^{I2}-\frac{\partial\nu_2}{\partial Q}(R^{I2},Q_2^{I2})+D}<0,$$

where $R^{I2}=R_{\text{in}}-N_2^{I2}Q_2^{I2}$, and

$$\frac{\partial}{\partial \ln I_0}G(R_{\text{in}},\ln I_0)=\frac{Q_2^{I2}\Big(-\frac{\partial\nu_2}{\partial Q}(R^{I2},Q_2^{I2})+D\Big)}{\frac{\partial\nu_2}{\partial R}(R^{I2},Q_2^{I2})N_2^{I2}-\frac{\partial\nu_2}{\partial Q}(R^{I2},Q_2^{I2})+D}>0.$$

When $(R_{\text{in}},\ln I_0)=(\lambda_1,\ln\xi_2)$, then $N_2^{I2}(\ln\xi_2)=0$ and Q_2^{I2} satisfies $\nu_2(R^{I2},Q_2^{I2})=DQ_2^{I2}$ and $R^{I2}=R_{\text{in}}=\lambda_1$. Hence $\frac{\partial}{\partial R_{\text{in}}}G(\lambda_1,\ln\xi_2)=-k_2<0$ and $\frac{\partial}{\partial\ln I_0}G(\lambda_1,\ln\xi_2)$ $=Q_2^{I2}(\lambda_1,\ln\xi_2)>0$. By implicit function theorem, there exists a differentiable function h satisfies $\ln I_0=h(R_{\text{in}})$, $\ln\xi_2=h(\lambda_1)$, and $G(R_{\text{in}},h(R_{\text{in}}))=0$. Hence

$$h'(R_{\text{in}})=-\frac{\frac{\partial}{\partial R_{\text{in}}}G(R_{\text{in}},\ln I_0)}{\frac{\partial}{\partial\ln I_0}G(R_{\text{in}},\ln I_0)}=\frac{k_2}{Q_2^{I2}}=\frac{h(R_{\text{in}})-\ln\xi_2}{R_{\text{in}}-\lambda_1}>0. \tag{27}$$

From (27),

$$h''(R_{\text{in}})=\frac{1}{(R_{\text{in}}-\lambda_1)^2}\Big[h'(R_{\text{in}})(R_{\text{in}}-\lambda_1)-(h(R_{\text{in}})-\ln\xi_2)\Big]=0.$$

Hence

$$h(R_{\text{in}})=\frac{k_2}{Q_2^{I2}(\lambda_1,\ln\xi_2)}(R_{\text{in}}-\lambda_1)+\ln\xi_2,$$

it is a straight line.

In the following, we consider the geometric properties of curves of $T^*=C_{R1}$ and $T^*=C_{S2}$. Let

$$\begin{aligned}G_1(R^0,S^0)&=(S^0-\lambda_{S2})\sigma_{R1}-Q_{S1}^{R1}(R^0-\lambda_{R1}),\\ G_2(R^0,S^0)&=(S^0-\lambda_{S2})Q_{R2}^{S2}-(R^0-\lambda_{R1})\sigma_{S2},\end{aligned}$$

then $T^*=C_{R1}$ means $G_1(R^0,S^0)=0$, and $T^*=C_{S2}$ means $G_2(R^0,S^0)=0$.

From (5.3) and (5.5) in [10], we know that Q_{S1}^{R1} and Q_{R2}^{S2} satisfy

$$\begin{aligned}\rho_{S1}(S^0-x_1^{R1}Q_{S1}^{R1},Q_{S1}^{R1})-DQ_{S1}^{R1}&=0,\\ \rho_{R2}(R^0-x_2^{S2}Q_{R2}^{S2},Q_{R2}^{S2})-DQ_{R2}^{S2}&=0,\end{aligned}$$

where $x_1^{R1}=x_1^{R1}(R^0)=\frac{R^0-\lambda_{R1}}{\sigma_{R1}}$, and $x_2^{S2}=x_2^{S2}(S^0)=\frac{S^0-\lambda_{S2}}{\sigma_{S2}}$, therefore $Q_{S1}^{R1}=Q_{S1}^{R1}(R^0,S^0)$ and $Q_{R2}^{S2}=Q_{R2}^{S2}(R^0,S^0)$ are functions of R^0 and S^0. Then

$$\begin{aligned}\frac{\partial Q_{S1}^{R1}}{\partial R^0}&=\frac{-\frac{Q_{S1}^{R1}}{\sigma_{R1}}\frac{\partial\rho_{S1}}{\partial R}}{x_1^{R1}\frac{\partial\rho_{S1}}{\partial R}-\frac{\partial\rho_{S1}}{\partial Q_{S1}}+D}=-\frac{Q_{S1}^{R1}}{\sigma_{R1}}\frac{\partial Q_{S1}^{R1}}{\partial S^0}<0\\ \frac{\partial Q_{R2}^{S2}}{\partial R^0}&=\frac{\frac{\partial\rho_{R2}}{\partial R}}{x_2^{S2}\frac{\partial\rho_{R2}}{\partial R}-\frac{\partial\rho_{R2}}{\partial Q_{R2}}+D}=-\frac{\sigma_{S2}}{Q_{R2}^{S2}}\frac{\partial Q_{R2}^{S2}}{\partial S^0}>0.\end{aligned}$$

Hence

$$\frac{\partial G_1}{\partial R^0} = \frac{-Q_{S1}^{R1}(-\frac{\partial \rho_{S1}}{\partial Q_{S1}} + D)}{x_1^{R1}\frac{\partial \rho_{S1}}{\partial R} - \frac{\partial \rho_{S1}}{\partial Q_{S1}} + D} = -\frac{Q_{S1}^{R1}}{\sigma_{R1}}\frac{\partial G_1}{\partial S^0}$$

$$\frac{\partial G_2}{\partial R^0} = \frac{-\sigma_{S2}(-\frac{\partial \rho_{R2}}{\partial Q_{R2}} + D)}{x_2^{S2}\frac{\partial \rho_{R2}}{\partial R} - \frac{\partial \rho_{R2}}{\partial Q_{R2}} + D} = -\frac{\sigma_{S2}}{Q_{R2}^{S2}}\frac{\partial G_2}{\partial S^0}.$$

We know that $G_1(\lambda_{R1}, \lambda_{S2}) = G_2(\lambda_{R1}, \lambda_{S2}) = 0$, and when $(R^0, S^0) = (\lambda_{R1}, \lambda_{S2})$, $x_1^{R1}(\lambda_{R1}) = 0 = x_2^{S2}(\lambda_{S2})$, and $Q_{S1}^{R1}(\lambda_{R1}, \lambda_{S2})$ satisfies $\rho_{S1}(\lambda_{S2}, Q_{S1}^{R1}) - DQ_{S1}^{R1} = 0$, $Q_{R2}^{S2}(\lambda_{R1}, \lambda_{S2})$ satisfies $\rho_{R2}(\lambda_{R1}, Q_{R2}^{S2}) - DQ_{R2}^{S2} = 0$. It follows that

$$\frac{\partial G_1(\lambda_{R1}, \lambda_{S2})}{\partial R^0} = -\frac{Q_{S1}^{R1}(\lambda_{R1}, \lambda_{S2})}{\sigma_{R1}}\frac{\partial G_1(\lambda_{R1}, \lambda_{S2})}{\partial S^0} < 0,$$

$$\frac{\partial G_2(\lambda_{R1}, \lambda_{S2})}{\partial R^0} = -\frac{\sigma_{S2}}{Q_{R2}^{S2}(\lambda_{R1}, \lambda_{S2})}\frac{\partial G_2(\lambda_{R1}, \lambda_{S2})}{\partial S^0} < 0.$$

Therefore, by implicit function theorem, there exists differentiable functions h_1, h_2 satisfies $S^0 = h_1(R^0)$, $S^0 = h_2(R^0)$, $\lambda_{S2} = h_1(\lambda_{R1}) = h_2(\lambda_{R1})$, and $G_1(R^0, h_1(R^0)) = 0 = G_2(R^0, h_2(R^0))$. Hence

$$h_1'(R^0) = -\frac{\frac{\partial}{\partial R^0}G_1(R^0, S^0)}{\frac{\partial}{\partial S^0}G_1(R^0, S^0)} = \frac{Q_{S1}^{R1}}{\sigma_{R1}} = \frac{h_1(R^0) - \lambda_{S2}}{R^0 - \lambda_{R1}} > 0, \tag{28}$$

$$h_2'(R^0) = -\frac{\frac{\partial}{\partial R^0}G_2(R^0, S^0)}{\frac{\partial}{\partial S^0}G_2(R^0, S^0)} = \frac{\sigma_{S2}}{Q_{R2}^{S2}} = \frac{h_2(R^0) - \lambda_{S2}}{R^0 - \lambda_{R1}} > 0 \tag{29}$$

From (28) and (29),

$$h_1''(R^0) = \frac{1}{(R^0 - \lambda_{R1})^2}\Big[h_1'(R^0)(R^0 - \lambda_{R1}) - (h_1(R^0) - \lambda_{S2})\Big] = 0.$$

$$h_2''(R^0) = \frac{1}{(R^0 - \lambda_{R1})^2}\Big[h_2'(R^0)(R^0 - \lambda_{R1}) - (h_2(R^0) - \lambda_{S2})\Big] = 0.$$

Hence

$$h_1(R^0) = \frac{Q_{S1}^{R1}(\lambda_{R1}, \lambda_{S2})}{\sigma_{R1}}(R^0 - \lambda_{R1}) + \lambda_{S2},$$

$$h_2(R^0) = \frac{\sigma_{S2}}{Q_{R2}^{S2}(\lambda_{R1}, \lambda_{S2})}(R^0 - \lambda_{R1}) + \lambda_{S2},$$

they are straight lines.

REFERENCES

[1] M. Droop, Some thoughts on nutrient limitation in algae, *J. Phycol.*, **9** (1973), 264–272.

[2] J. P. Grover, Constant- and variable-yield models of population growth: Responses to environmental variability and implications for competition, *J. Theoret. Biol.*, **158** (1992), 409–428.

[3] S.-B. Hsu, K.-S. Cheng and S. P. Hubbell, Exploitative competition of microorganism for two complementary nutrients in continuous cultures, *SIAM J. Appl. Math.*, **41** (1981), 422–444.

[4] S.-B. Hsu and T.-H. Hsu, Competitive exclusion of microbial species for a single-nutrient with internal storage, *SIAM J. Appl. Math.*, **68** (2008), 1600–1617.

[5] S.-B. Hsu, S. P. Hubbell and P. Waltman, A mathematical theory for single-nutrient competition in continuous culture of micro-organisms, *SIAM J. Appl. Math.*, **32** (1977), 366–383.

[6] S.-B. Hsu, H. L. Smith and P. Waltman, Competitive exclusion and coexistence for competitive systems on ordered Banach spaces, *Trans. Amer. Math. Soc.*, **348** (1996), 4083–4094.

[7] J. Huisman and F. J. Weissing, Light limited growth and competition for light in well-mixed aquatic environments: An elementary, *Ecology*, **75** (1994), 507–520.

[8] J. Huisman and F. J. Weissing, Competition for nutrients and light in a mixed water column: A theoretical analysis, *Am. Nat.*, **146** (1995), 536–564.

[9] J. Jiang, X. Liang and X. Zhao, Saddle-point behavior for monotone semifolws and reaction-diffusion models, *J. Diff. Equations*, **203** (2004), 313–330.

[10] B. Li and H. L. Smith, Global dynamics of microbial competition for two resources with internal storage, *J. Math. Biol.*, **55** (2007), 481–515.

[11] J. Passarge, S. Hol, M. Escher and J. Huisman, Competition for nutrients and light: Stable coexistence, alternative stable states, or competitive exclusion?, *Ecological Monographs*, **76** (2006), 57–72.

[12] H. L. Smith and H. R. Thieme, Stable coexistence and bi-stablility for competitive systems on ordered Banach spaces, *J. Diff. Equations*, **176** (2001), 195–222.

[13] H. L. Smith and P. Waltman, *The Theory of the Chemostat*, Cambridge University Press, 1995.

[14] D. Tilman, *Resource Competition and Community Structure*, Princeton University Press, New Jersey, 1982.

[15] K. Yoshiyama, J. P. Mellard, E. Litchman and C. A. Klausmeier, Phytoplankton competition for nutrients and light in a statified water column, *Am. Nat.*, **174** (2009), 190–203.

[16] X.-Q. Zhao, *Dynamical Systems in Population Biology*, Springer-Verlag, New York, 2003.

Received March 2013; revised November 2013.

E-mail address: sbhsu@math.nthu.edu.tw
E-mail address: d9621806@oz.nthu.edu.tw