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AN ALLELOPATHIC COMPETITION MODEL WITH QUORUM SENSING AND DELAYED TOXICANT PRODUCTION

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Abstract. The dynamics of a differential functional equation system representing an allelopathic competition is analyzed. The delayed allelochemical production process is represented by means of a distributed delay term in a linear quorum-sensing model. Sufficient conditions for local asymptotic stability properties of biologically meaningful steady-state solutions are given in terms of the parameters of the system. A global asymptotic stability result is also proved by constructing a suitable Lyapunov functional. Some simulations confirm the analytical results.

1. **Introduction.** A competition between two populations is called allelopathic when one (or both) species is able to produce allelochemicals which inhibit the growth of the other one. Allelopathic competitions occur between algal species [4], algae and bacteria [1], bacteria and bacteria [3], algae and aquatic plants [2], and plants and plants [7]. They may have a relevant role in applications; for instance, in materials biotechnology and bioremediation processes. On the basis of several experimental results in [5], a general mathematical model was proposed for the so-called quorum-sensing mechanism, consisting in the dependence of the allelochemical production on the concentrations of populations. In [8], the dynamics of allelopathic competitions were also studied by using linear quorum-sensing models, two different kinds of uptake models (Michelis-Menten and Andrews), and different types of toxic effects (inhibitory or lethal). In the quoted papers, all the biological processes involved have been considered instantaneous. In the present paper, by observing that the production of allelochemicals actually can be delayed, we introduce a linear delayed model of quorum sensing based on a distributed delay term which takes into account the past history of the interacting populations. Furthermore, the effects of allelochemicals are considered to be lethal and are represented through a mass-action term. As in [8], we also assume that the allelopathic competition occurs in a chemostat-like environment.

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The plan of this paper is as follows. In Section 1, basic notations and the mathematical model, consisting in a nonlinear functional differential system of four equations, are introduced. The analysis of steady-state solutions and their stability properties is performed in Sections 2 and 3. The global asymptotic stability of a boundary equilibrium is proved in Section 4 by constructing a suitable Lyapunov functional. All analytical results are expressed in terms of the parameters of the system. Finally, in Section 5, numerical simulations are presented, concerning the special case of an exponential delay kernel.

2. **Models and Notations.** The proposed mathematical model is the following:

$$\begin{cases} \dot{S} = (S^0 - S)D - f_1(S)N_1 - f_2(S)N_2 \\ \dot{N}_1 = N_1\left[f_1(S) - D - \gamma p\right] \\ \dot{N}_2 = N_2\left[\left(1 - \int_{-\tau}^{0} k\omega_1(\theta)N_1(t+\theta)d\theta\right) f_2(S) - D\right] \\ \dot{p} = N_2 f_2(S)\int_{-\tau}^{0} k\omega_1(\theta)N_1(t+\theta)d\theta - Dp, \end{cases} \tag{1}$$

where

$S(t)$	is the nutrient concentration at time t;
$N_1(t)$	is the density of the sensitive microorganism at time t;
$N_2(t)$	is the density of the toxin producing organism at time t;
p	is the concentration of toxicant in the environment at time t;
S^0	is the constant input rate of the limiting nutrient concentration ($S^0 > 0$);
D	is the constant washout rate ($D > 0$);
m_1	(> 0) is the maximal specific growth rate of population N_1;
m_2	(> 0) is the maximal specific growth rate of population N_2;
γ	(> 0) is the death rate of population N_1 due to the toxin;
$\omega_1(\theta)$	is the kernel function which weights the past values of the toxin production $\left(0 \le \int_{-\tau}^{0} kN_1\omega_1(\theta)d\theta \le 1\right)$ and represents the fraction of potential growth devoted to produce allelochemicals.

Moreover,

$$f_i(S) = \frac{m_i S}{a_i + S} \quad i = 1, 2 \tag{2}$$

is the functional response (Michaelis-Menten) of the two populations, and a_i, $i = 1, 2$ (> 0) is the half-saturation constant.

We now discuss the main properties of equations (1). Let us define

$$x(t) := (S(t), N_1(t), N_2(t), p(t)) \in \Re^4$$

and $x_t(\theta) = x(t+\theta)$, $\theta \in [-\tau, 0]$, for all $t \ge 0$. Then (1) can be rewritten as

$$\dot{x}(t) = F(x_t), \tag{3}$$

with initial conditions at $t = 0$ given by

$$\phi \in C([-\tau, 0], \Re^4),$$

where $C([-\tau, 0], \Re^4)$ is the Banach space of continuous functions mapping the interval $[-\tau, 0]$ into $\Re^4$ with the norm

$$\|\phi\| = \sup_{\theta \in [-\tau, 0]} |\phi(\theta)|,$$

where $|\cdot|$ is any norm in $\Re^4$. Moreover, a solution of (3) will be denoted as follows

$$x(t) = x(\phi, t) \qquad \theta \in [-\tau, 0]. \tag{4}$$

For biological relevance, we define nonnegative initial conditions $\phi(\theta) \geq 0$, $\theta \in [-\tau, 0]$, with $\phi(0) \geq 0$, to equations (3) ($\phi_i(\theta) \geq 0, \theta \in [-\tau, 0]$ and $\phi_i(0) \geq 0$, $i = 1, 2, 3, 4$). For this system, several qualitative properties of the solutions can be proved, such as positiveness, boundedness, global existence in the future, and uniqueness.

3. **Steady-State Solutions.** We turn now to the analysis of the equilibria of system (1). We look for nonnegative constant solutions of type $\bar{E} = (\bar{S}, \bar{N}_1, \bar{N}_2, \bar{p})$ of the following algebraic system:

$$\begin{cases} (S^0 - S)D - f_1(S)N_1 - f_2(S)N_2 = 0 \\ N_1\left[f_1(S) - D - \gamma p\right] = 0 \\ N_2\left[(1 - kN_1\Delta(\tau))\, f_2(S) - D\right] = 0 \\ f_2(S)kN_1N_2\Delta(\tau) - Dp = 0, \end{cases} \tag{5}$$

where

$$\Delta(\tau) = \int_{-\tau}^{0} \omega_1(\theta) d\theta.$$

We consider the model under the assumption that

$$\min\{m_1, m_2\} > D, \tag{6}$$

we can define the quantities λ_i, (> 0) such that

$$f_i(\lambda_i) = D \quad i = 1, 2.$$

Hence, it is immediately seen that $E_0 = E_{+000} = (S^0, 0, 0, 0)$ is an equilibrium of system (3) whatever the value of S^0 is. Moreover the following theorem holds:

THEOREM 3.1. *By assuming that (6) holds true, it is possible to prove that*

i. *a steady-state solution* $E_1 = E_{++00} = (\lambda_1, S^0 - \lambda_1, 0, 0)$ *exists if* $\lambda_1 < S^0$*;*
ii. *a steady-state solution* $E_2 = E_{+0+0} = (\lambda_2, 0, S^0 - \lambda_2, 0)$ *exists if* $\lambda_2 < S^0$*.*

Let us now look for a positive equilibrium $E_3 = (S^*, N_1^*, N_2^*, p^*)$, $S^* > 0$, $N_1^* > 0$, $N_2^* > 0$, $p^* > 0$. From system (5) we have

$$\begin{cases} (S^0 - S^*)D - f_1(S^*)N_1^* - f_2(S^*)N_2^* = 0 \\ p^* = \dfrac{f_1(S^*) - D}{\gamma} \\ N_1^* = \dfrac{f_2(S^*) - D}{k\Delta(\tau)f_2(S^*)} \\ N_2^* = \dfrac{D(f_1(S^*) - D)}{\gamma(f_2(S^*) - D)}. \end{cases} \tag{7}$$

We can prove the following:

LEMMA 3.1. *There are at most two positive values of the* S^* *solution of* $(7)_1$*.*

Proof. By substitution of N_1^*, N_2^* in $(7)_1$, we get $(S \neq \lambda_2)$:

$$(S^0 - S^*)D - f_1(S^*)\frac{f_2(S^*) - D}{k\Delta(\tau)f_2(S^*)} - f_2(S^*)\frac{D(f_1(S^*) - D)}{\gamma(f_2(S^*) - D)} = 0. \tag{8}$$

Substituting $f_i(S^*) = \dfrac{m_i S^*}{a_i + S^*}$ $i = 1, 2$ we obtain that S^* are positive zeros of the cubic equation

$$\alpha_0 S^3 + \alpha_1 S^2 + \alpha_2 S + \alpha_3 = 0, \tag{9}$$

where the coefficients are real and

$$\begin{aligned} \alpha_0 &= Dk\Delta(\tau)m_2(m_2 - D) > 0, \\ \alpha_3 &= D^2\gamma a_2^2 m_1 + D^2 K S^0 \gamma \Delta(\tau) a_1 a_2 m_2 > 0. \end{aligned}$$

Then (9) has one negative root, and therefore there are at most two positive values of S, solutions of (9). □

THEOREM 3.2. *Assume that*

$$\lambda_1 > \lambda_2; \tag{10}$$

then there exists a unique positive equilibrium of (5):

$$E_3 = E_{++++} = (S^*, N_1^*, N_2^*, p^*) \tag{11}$$

if and only if

$$\Delta(\tau) > \Delta^* \qquad \textit{with} \qquad \Delta^* := \frac{f_2(\lambda_1) - D}{f_2(\lambda_1)(S^0 - \lambda_1)k}. \tag{12}$$

Proof. The components of E_3 are solutions of (7). We devote our attention to the equation $(7)_1$ because all the other components are expressed in terms of S^*.

We can observe that all the other components are positive if and only if

$$S^* > \lambda = \max\{\lambda_1, \lambda_2\},$$

where S^* is a zero of the function

$$F(S) = (S^0 - S)D - f_1(S)\frac{f_2(S) - D}{k\Delta(\tau)f_2(S)} - f_2(S)\frac{D(f_1(S) - D)}{\gamma(f_2(S) - D)} \tag{13}$$

which is the left-hand side of (8).

Of course, $F(S)$ is negative if $S > S^0$, and therefore at positive equilibrium S^* must be such that $\lambda < S^* < S^0$; that is, S^* is a zero of function (13) in the interval (λ, S^0). By assumption (10), $\lambda = \lambda_1$, we consider the function (13) in the interval $[\lambda_1, S^0]$. Note that in $[\lambda_1, S^0]$, the function $F(S)$ is continuous: in fact functions $f_i(S)$, $i = 1, 2$ are continuous and positive if $S > 0$. Moreover, since $S \geq \lambda_1$ implies $S > \lambda_2$, it follows that $f_2(S) \geq f_2(\lambda_2) = D$; that is, in $[\lambda_1, S^0]$ $f_2(S) - D > 0$.

Now note that, owing to (13),

$$F(S^0) < 0,$$

and by assumption (12),

$$F(\lambda_1) = D(S^0 - \lambda_1) - \frac{D(f_2(\lambda_1) - D)}{f_2(\lambda_1)k\Delta(\tau)} > 0.$$

Hence $F(S)$ has at least one zero $S^* \in (\lambda_1, S^0)$. We prove that the zero in (λ_1, S^0) is unique. Consider the interval $(0, \lambda_2)$, where $f_i(S) - D < 0$, $i = 1, 2$. Observe that

$$\lim_{S \to 0^+} F(S) = DS^0 + \frac{m_1 a_2 D}{m_2 a_1 k \Delta(\tau)} > 0$$

and that

$$\lim_{S \to \lambda_2^-} F(S) = -\infty.$$

Since $F(S)$ is continuous in $(0, \lambda_2)$, there exists another zero of the function (13) in $(0, \lambda_2)$. Owing to Lemma 3.1, there are at most two positive values for the S^* solution of $(7)_1$. Hence, there is exactly one zero of $F(S)$ in (λ_1, S^0) and therefore exactly one positive equilibrium solution of (7).

Assume now that (10) holds but (12) is violated; that is, $\Delta(\tau) \leq \Delta^*$.

If $\Delta(\tau) = \Delta^*$, then $F(\lambda_1) = 0$, and we have two zeros of $F(S)$ in $(0, \lambda_1]$, one in $(0, \lambda_2)$ and the other one in $S^* = \lambda_1$, but no zero in (λ_1, S^0). Hence, we do not have positive equilibria.

Finally, if $\Delta(\tau) < \Delta^*$, then $F(\lambda_1) < 0$. Since $\lim_{S \to \lambda_2^+} F(S) = +\infty$, there is at least one zero in (λ_2, λ_1). Since another zero of $F(S)$ is in $(0, \lambda_2)$, we have two zeros of $F(S)$ in $(0, \lambda_1)$, so we cannot have zeros of $F(S)$ in (λ_1, S^0). Hence, again, positive equilibria do not exist.

In conclusion, if $\lambda_1 > \lambda_2$ we have one positive equilibrium if $\Delta(\tau) > \Delta^*$. □

Remark 1. *When $\Delta(\tau) = \Delta^*$, the positive equilibrium E_3 coincides with the boundary equilibrium E_1.*

Theorem 3.3. *Assume that*

$$\lambda_2 > \lambda_1 \tag{14}$$

and

$$\gamma < \inf_{(\lambda_2, S^0)} \frac{f_2(S)(f_1(S) - D)}{(f_2(S) - D)(S^0 - S)}. \tag{15}$$

Then, there are no positive equilibria of (5).

Proof. The existence of positive equilibria requires that the function

$$F(S) = (S^0 - S)D - f_1(S)\frac{f_2(S) - D}{k\Delta(\tau)f_2(S)} - f_2(S)\frac{D(f_1(S) - D)}{\gamma(f_2(S) - D)}$$

has zeros in the interval (λ, S^0), that is, in (λ_2, S^0). If we prove that $F(S) < 0$ for all $S \in (\lambda_2, S^0)$, the theorem holds true. By the assumptions (14) and (15), we obtain

$$(S^0 - S)D - f_1(S)\frac{f_2(S) - D}{k\Delta(\tau)f_2(S)} - f_2(S)\frac{D(f_1(S) - D)}{\gamma(f_2(S) - D)} <$$

$$(S^0 - S)D - f_2(S)\frac{D(f_1(S) - D)}{\gamma(f_2(S) - D)} < 0;$$

that is, $F(S) < 0$ for all $S \in (\lambda_2, S^0)$, and the proof is complete. □

Remark 2. *When $\tau = 0$, the positive equilibrium E_3 does not exist. However if $\tau = 0$ and $\lambda_1 = \lambda_2$, there is a continuous infinity of boundary equilibria $\bar{E} \equiv (\bar{S}, \bar{N}_1, \bar{N}_2, 0)$.*

4. **Local Stability Properties.** By means of a change of variables involving the generic equilibrium $\bar{E} = (\bar{S}, \bar{N}_1, \bar{N}_2, \bar{p})$, system (1) is transformed into the system

$$\begin{cases} \dot{x}_1 = (S^0 - \bar{S} - x_1)D - \sum_{i=1}^{2} f_i(x_1 + \bar{S})(N_i^* + x_{i+1}) \\ \dot{x}_2 = (x_2 + \bar{N}_1)\left[f_1(x_1 + \bar{S}) - D - \gamma(\bar{p} + x_4)\right] \\ \dot{x}_3 = (x_3 + \bar{N}_2)\left[F_2(x_1 + \bar{S}) - \int_{-\tau}^{0} k\omega_1(\theta)x_2(t+\theta)d\theta f_2(x_1 + \bar{S}) - D\right] \\ \dot{x}_4 = (x_3 + \bar{N}_2)f_2(x_1 + \bar{S})\int_{-\tau}^{0} k\omega_1(\theta)(x_2(t+\theta) + \bar{N}_1)d\theta - D(x_4 + \bar{p}), \end{cases} \tag{16}$$

where $F_2(x) = (1 - k\bar{N}_1\Delta(\tau))f_2(x)$. The stability analysis of the generic equilibrium $\bar{E}$ can be performed by means of the characteristic equation associated to the linearized system of (16) in $\bar{E}$:

$$\begin{cases} \dot{x}_1 &= (-D - \sum_{i=1}^{2} f_i'(\bar{S})N_i^*)x_1 - f_1(\bar{S})x_2 - f_2(\bar{S})x_3 \\ \dot{x}_2 &= f_1'(\bar{S})\bar{N}_1 x_1 + [f_1(\bar{S}) - D - \gamma\bar{p}]x_2 - \gamma\bar{N}_1 x_4 \\ \dot{x}_3 &= f_2'(\bar{S})\bar{N}_2\left(1 - k\bar{N}_1\Delta(\tau)\right)x_1 + [F_2(\bar{S}) - D]x_3 + \\ &\quad -\bar{N}_2 f_2(\bar{S})\int_{-\tau}^{0} k\omega_1(\theta)x_2(t+\theta)d\theta \\ \dot{x}_4 &= f_2'(\bar{S})\bar{N}_1\bar{N}_2 k\Delta(\tau)x_1 + f_2(\bar{S})\bar{N}_1 k\Delta(\tau)x_3 - Dx_4 + \\ &\quad +\bar{N}_2 f_2(\bar{S})\int_{-\tau}^{0} k\omega_1(\theta)x_2(t+\theta)d\theta. \end{cases} \tag{17}$$

REMARK 3. *We can represent the right-hand side of system (17) as a sum of two terms as follows:*

$$\dot{x} = Lx + \int_{-\tau}^{0} K(\theta)x(t+\theta)d\theta,$$

where

$$L = \begin{bmatrix} -D - f_1'(\bar{S})\bar{N}_1 - f_2'(\bar{S})\bar{N}_2 & -f_1(\bar{S}) & -f_2(\bar{S}) & 0 \\ f_1'(\bar{S})\bar{N}_1 & f_1(\bar{S}) - D - \gamma\bar{p} & 0 & -\gamma\bar{N}_1 \\ f_2'(\bar{S})\bar{N}_2\left(1 - k\bar{N}_1\Delta(\tau)\right) & 0 & F_2(\bar{S}) - D & 0 \\ f_2'(\bar{S})\bar{N}_1\bar{N}_2 k\Delta(\tau) & 0 & f_2(\bar{S})\bar{N}_1 k\Delta(\tau) & -D \end{bmatrix} \tag{18}$$

and

$$K(\theta) = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & -\bar{N}_2 f_2(\bar{S})k\omega_1(\theta) & 0 & 0 \\ 0 & \bar{N}_2 f_2(\bar{S})k\omega_1(\theta) & 0 & 0 \end{bmatrix}. \tag{19}$$

The characteristic equation, given by

$$\det\left|\rho I - L - \int_{-\tau}^{0} K(\theta)e^{\rho\theta}d\theta\right| = 0, \tag{20}$$

where $I \in \Re^4$ is the identity matrix, can be written as follows:

$$\begin{Vmatrix} \rho + D + f_1'(\bar{S})\bar{N}_1 + f_2'(\bar{S})\bar{N}_2 & f_1(\bar{S}) & f_2(\bar{S}) & 0 \\ -f_1'(\bar{S})\bar{N}_1 & \rho - (f_1(\bar{S}) - D - \gamma\bar{p}) & 0 & \gamma\bar{N}_1 \\ -f_2'(\bar{S})\bar{N}_2\left(1 - k\bar{N}_1\Delta(\tau)\right) & \Phi(\rho) & \rho - [(F_2(\bar{S}) - D] & 0 \\ -f_2'(\bar{S})\bar{N}_1\bar{N}_2 k\Delta(\tau) & -\Phi(\rho) & -f_2(\bar{S})\bar{N}_1 k\Delta(\tau) & \rho + D \end{Vmatrix} = 0 \tag{21}$$

where

$$\Phi(\rho) = \int_{-\tau}^{0} \bar{N}_2 f_2(\bar{S}) k\omega_1(\theta) e^{\rho\theta} d\theta.$$

Local stability properties of boundary equilibria are proved as follows:

THEOREM 4.1. *The following statements hold true:*

i. *If $S^0 < \lambda_1$ and $S^0 < \lambda_2$, then the equilibrium E_0 is locally asymptotically stable.*
ii. *If E_1 exists and $\Delta(\tau) > \Delta^*$, then E_1 is locally asymptotically stable.*
iii. *If E_2 exists and $\lambda_2 < \lambda_1$, then E_2 is locally asymptotically stable.*

Proof. (i) It is easy to show that the characteristic equation obtained by computing (21) in $E_0 = (S^0, 0, 0, 0)$ admits the following roots:

$$\rho_1 = -D, \qquad \rho_2 = f_1(S^0) - D, \qquad \rho_3 = f_2(S^0) - D, \qquad \rho_4 = -D.$$

The steady-state E_0 is asymptotically stable if

$$\begin{gathered} \rho_2 < 0 \Longrightarrow f_1(S^0) < D \Longrightarrow S^0 < \lambda_1, \\ \rho_3 < 0 \Longrightarrow f_2(S^0) < D \Longrightarrow S^0 < \lambda_2. \end{gathered}$$

(ii) The characteristic equation obtained by computing (21) in $E_1 = (\lambda_1, S^0 - \lambda_1, 0, 0)$ can be written as follows:

$$[\rho + D][\rho - (1 - k\bar{N}_1\Delta(\tau))f_2(\lambda_1) - D)][\rho^2 + (D + \bar{N}_1 f_1'(\lambda_1))\rho + D\bar{N}_1 f_1'(\lambda_1)] = 0. \tag{22}$$

By computing the roots of (22), we obtain

$$\rho_1 = -D, \qquad \rho_2 = (1 - k\bar{N}_1\Delta(\tau))f_2(\lambda_1) - D, \qquad \rho_3 = -D, \qquad \rho_4 = -\bar{N}_1 f_1'(\lambda_1).$$

If E_1 exists, it is locally asymptotically stable if $(1 - k\bar{N}_1\Delta(\tau))f_2(\lambda_1) - D < 0$; that is,

$$\Delta(\tau) > \frac{f_2(\lambda_1) - D}{k(S^0 - \lambda_1)f_2(\lambda_1)} (:= \Delta^*).$$

(iii) The characteristic equation obtained by computing (21) in $E_2 = (\lambda_2, 0, S^0 - \lambda_2, 0)$ can be written as follows:

$$(\rho + D)(f_1(\lambda_2) - D - \rho)[\rho^2 + (D + \bar{N}_2 f_2'(\lambda_2))\rho + D\bar{N}_2 f_2'(\lambda_2)] = 0. \tag{23}$$

By computing its roots, we obtain

$$\rho_1 = -D, \qquad \rho_2 = f_1(\lambda_2) - D, \qquad \rho_3 = -D, \qquad \rho_4 = -\bar{N}_2 f_2'(\lambda_2).$$

If E_2 exists, it is locally asymptotically stable if

$$\rho_2 < 0 \Longrightarrow f_1(\lambda_2) - D < 0 \Longrightarrow \lambda_2 < \lambda_1.$$

□

Regarding the positive equilibrium $E_3 = (S^*, N_1^*, N_2^*, p^*)$, we observe that the characteristic equation (21) becomes

$$\det \begin{bmatrix} \rho + a_{11} & a_{12} & a_{13} & 0 \\ -a_{21} & \rho & 0 & a_{24} \\ -a_{31} & \Phi(\rho) & \rho & 0 \\ -a_{41} & -\Phi(\rho) & -a_{43} & \rho + a_{44} \end{bmatrix} = 0; \quad (24)$$

that is,

$$\rho^4 + (a_{11} + a_{44})\rho^3 + (a_{11}a_{44} + a_{13}a_{31} + a_{12}a_{21})\rho^2 + (a_{13}a_{31}a_{44} + a_{12}\cdot a_{21}a_{44} - a_{12}a_{41}a_{24})\rho - a_{12}a_{24}a_{31}a_{43} + [a_{24}\rho^2 - (a_{13}a_{21} + a_{24}a_{43} - a_{11}\cdot a_{24})\rho - (a_{21}a_{13}a_{44} + a_{24}a_{43}a_{11} - a_{13}a_{31}a_{24} - a_{13}a_{41}a_{24})]\Phi(\rho) = 0, \quad (25)$$

where

$$\begin{array}{lll} a_{11} = D + f_1'(S^*)N_1^* + f_2'(S^*)N_2^* & a_{12} = f_1(S^*) & a_{13} = f_2(S^*) \\ a_{31} = f_2'(S^*)N_2^*\,(1 - kN_1^*\Delta(\tau)) & a_{24} = \gamma N_1^* & a_{21} = f_1'(S^*)N_1^* \\ a_{41} = f_2'(S^*)N_1^*N_2^*k\Delta(\tau) & a_{43} = f_2(S^*)N_1^*k\Delta(\tau) & a_{44} = D \end{array}$$

and the information of the delay τ is carried by $\Phi(\rho)$. Therefore, the analysis of the asymptotic stability of E_3 can not be performed without specifying the choice of the delay kernel $\omega_1(\theta)$.

5. **Global Stability of Equilibria.** Return to system (1) rewritten as (3), centered about one equilibrium. To prove the global stability we will use the following results:

THEOREM 5.1. *Assume that $a(\cdot), b(\cdot)$ are nonnegative continuous functions, $a(0) = b(0) = 0$, $\lim_{s\to+\infty} a(s) = +\infty$, and that $V : C \to \Re$ ($C = C([-\tau, 0], \Re^n)$) is continuous and satisfies*

$$V(\phi) \geq a(|\phi(0)|),\ \dot{V}_{(3)}(\phi) \leq -b(|\phi(0)|).$$

Then the solution $x = 0$ of (3) is uniformly stable, and every solution is bounded. If in addition, $b(s) > 0$ for $s > 0$, then $x = 0$ is globally asymptotically stable; that is, every solution of (3) approaches $x = 0$ as $t \to +\infty$.

If we set

$$g(S) = \frac{f_2(S)(f_1(S) - D)}{(S^0 - S)(f_2(S) - D)}, \quad (26)$$

then we can prove the following:

LEMMA 5.1. *Assume that*

$$\lambda_2 > \lambda_1. \quad (27)$$

Then there exists a positive number c_1 such that

$$\sup_{0<S<\lambda_2} g(S) < c_1 < \inf_{\lambda_2 \leq S \leq S^0} g(S). \quad (28)$$

Proof. We first examine the numerator of $g(S)$. Let $\psi(S) = f_2(S)(f_1(S) - D)$. This quantity is positive in $S = \lambda_2$; in fact, since (27) holds, then $f_1(\lambda_2) > f_1(\lambda_1) = D$. Therefore, $\psi(\lambda_2) = D(f_1(\lambda_2) - D) > 0$.

Furthermore, $\psi(S)$ is negative in $(0, \lambda_1)$; in fact, if $S < \lambda_1$, then $f_1(S) < f_1(\lambda_1) = D$ and $\psi(S) < 0$. $\psi(S)$ has a zero in λ_1 and, if $S > \lambda_1$, by considering the derivative of $\psi(S)$, we obtain

$$\psi'(S) = f_2'(S)(f_1(S) - D) + f_1'(S)f_2(S) > 0, \qquad S \in (\lambda_1, S^0).$$

Therefore, $\psi(S) > 0$ in (λ_1, S^0).

Since $\psi(S)$ has a unique zero in λ_1 and since $g(S) < 0$ in (λ_1, λ_2), then instead of (28) we need only show that

$$\sup_{0<S<\lambda_1} g(S) < \inf_{\lambda_2<S<S^0} g(S). \tag{29}$$

To prove (29) consider the function

$$w(S) = g(S)\frac{S-\lambda_2}{S-\lambda_1}.$$

$(S-\lambda_2)$ in the numerator removes the pole in $g(S)$, and $(S-\lambda_1)$ in the denominator removes the zero.

First of all we can show that $w(S)$ is monotone increasing; in fact, by remembering that $f_1(\lambda_1) = f_2(\lambda_2) = D$, we can write

$$\begin{aligned} w(S) &= g(S)\frac{S-\lambda_2}{S-\lambda_1} = \frac{f_2(S)(f_1(S)-f_1(\lambda_1)}{(S^0-S)(S-\lambda_1)}\,\frac{S-\lambda_2}{f_2(S)-f_2(\lambda_2)} \\ &= \frac{m_2 S}{a_2+S}\,\frac{1}{(S^0-S)}\,\frac{a_1 m_1}{(a_1+S)(a_1+\lambda_1)}\,\frac{(a_2+S)(a_2+\lambda_2)}{a_2 m_2} \\ &= \frac{S}{(S^0-S)(a_1+S)}\left[\frac{a_1 m_1(a_2+\lambda_2)}{a_2(a_1+\lambda_1)}\right]. \end{aligned}$$

Thus,

$$w(S) = \frac{AS}{(S^0-S)(a_1+S)},$$

where

$$A = \left[\frac{a_1 m_1(a_2+\lambda_2)}{a_2(a_1+\lambda_1)}\right] > 0.$$

If we compute $w'(S)$ we obtain

$$w'(S) = \frac{Aa_1S^0 + AS^2}{(S^0-S)^2(a_1+S)^2} > 0.$$

Then $w(S)$ is monotone increasing. Moreover, consider the function $\dfrac{S-\lambda_1}{S-\lambda_2}$. It is easy to check, by computing its derivative, that it is monotone decreasing. Furthermore, from (27) we obtain

$$\lambda_1(S^0-\lambda_2) < \lambda_2(S^0-\lambda_1),$$

that is,

$$\frac{\lambda_1}{\lambda_2} < \frac{S^0-\lambda_1}{S^0-\lambda_2}.$$

Hence,

$$\sup_{0<S<\lambda_1}\frac{S-\lambda_1}{S-\lambda_2} < \inf_{\lambda_2<S<S^0}\frac{S-\lambda_1}{S-\lambda_2}.$$

Finally, since we can write

$$g(S) = w(S)\frac{S-\lambda_1}{S-\lambda_2},$$

we obtain, by the monotone growth of $w(S)$ and the properties of $\dfrac{S-\lambda_1}{S-\lambda_2}$, that

$$\sup_{0<S<\lambda_1} g(S) < \inf_{\lambda_2<S<S^0} g(S),$$

and the proof is complete. □

THEOREM 5.2. *Assume that* $\lambda_2 > \lambda_1$ *and* $\gamma < \inf_{\lambda_2 \le S \le S^0} g(S)$. *Then the equilibrium* $E_1 = (\lambda_1, S^0 - \lambda_1, 0, 0)$ *is globally asymptotically stable in* $\Re^4_{B_1}$ $(\Re^4_{B_1} = \{x \in \Re^4 | x_3, x_4 \ge 0 \text{ and } x_i > 0,\ i = 1, 2\})$.

Proof. Consider the function

$$V = \int_{\lambda_1}^{S} \frac{N_1^*(f_1(\xi) - D)}{S^0 - \xi} d\xi + D \int_{N_1^*}^{N_1} \frac{\xi - N_1^*}{\xi} d\xi + \alpha D N_2 + \alpha D p, \tag{30}$$

where $\alpha > 0$ is to be chosen and we have written N_1^* for $S^0 - \lambda_1$. It follows that

$$\begin{aligned}
\dot{V}_{(1)} &= \frac{N_1^*(f_1(S) - D)}{(S^0 - S)} \dot{S} + D \frac{N_1 - N_1^*}{N_1} \dot{N}_1 + \alpha D \dot{N}_2 + \alpha D \dot{p} \\
&= \frac{N_1^*(f_1(S) - D)}{(S^0 - S)} \left[(S^0 - S)D - f_1(S)N_1 - f_2(S)N_2\right] + D \frac{N_1 - N_1^*}{N_1} N_1 \\
&\quad [f_1(S) + -D - \gamma p] + \alpha D N_2 \left[\left(1 - \int_{-\tau}^{0} k\omega_1(\theta) N_1(t+\theta) d\theta\right) f_2(S) - D\right] + \\
&\quad + \alpha D \left[N_2 f_2(S) \int_{-\tau}^{0} k\omega_1(\theta) N_1(t+\theta) d\theta - Dp\right] \\
&= D N_1^*(f_1(S) - D) - \frac{f_1(S)(f_1(S) - D)N_1^*}{(S^0 - S)} N_1 - \frac{f_2(S)(f_1(S) - D)N_1^*}{(S^0 - S)} N_2 \\
&\quad + D N_1 (f_1(S) - D) - D N_1^*(f_1(S) - D) - D(N_1 - N_1^*)\gamma p + \alpha D N_2 f_2(S) + \\
&\quad - \alpha D^2 N_2 - \alpha D^2 p \\
&= \left[\alpha D(f_2(S) - D) - \frac{f_2(S)(f_1(S) - D)N_1^*}{(S^0 - S)}\right] N_2 + \\
&\quad (f_1(S) - D)\left[D - \frac{f_1(S)N_1^*}{(S^0 - S)}\right] N_1 - D N_1 \gamma p - D p(\alpha D - N_1^* \gamma).
\end{aligned}$$

We can write

$$\dot{V} = T_1 + T_2 + T_3 + T_4,$$

where the meaning of the letters T_1, T_2, T_3, T_4 is obvious. Clearly, $T_3 \le 0$ since $N_1 \ge 0$ and $p \ge 0$. If $f_1(S) < D$, then $S < \lambda_1$, so

$$\frac{f_1(S)N_1^*}{(S^0 - S)} < \frac{f_1(\lambda_1)N_1^*}{(S^0 - \lambda_1)} = D.$$

So, the first factor of T_1 is negative, and the second is positive. If $f_1(S) > D$, then $S > \lambda_1$, so

$$\frac{f_1(S)N_1^*}{(S^0 - S)} > \frac{f_1(\lambda_1)N_1^*}{(S^0 - \lambda_1)} = D.$$

So, the first factor of T_1 is positive, and the second is negative. Therefore, $T_1 \le 0$. About T_4, we can see that it is negative if we choose α as follows:

$$\alpha > \frac{N_1^* \gamma}{D}. \tag{31}$$

Now we want to show that $T_2 \le 0$. We can write $T_2 = N_2 \Phi(S)$; it is immediately seen that $\Phi(\lambda_2) < 0$. Consider now $S \ne \lambda_2$; then

$$\begin{aligned}
\Phi(S) &= \alpha D(f_2(S) - D) - \frac{f_2(S)(f_1(S) - D)N_1^*}{(S^0 - S)} \\
&= N_1^*(f_2(S) - D)\left[c_1 - \frac{f_2(S)(f_1(S) - D)}{(S^0 - S)(f_2(S) - D)}\right],
\end{aligned}$$

where $c_1 = \dfrac{\alpha D}{N_1^*}$. Therefore, if α is positive, then c_1 is positive. The aim is to choose c_1 so that if $f_2(S) > D$, that is, $S > \lambda_2$, then the term in square brackets is negative, and if $f_2(S) < D$, i.e. $S < \lambda_2$, then it is positive. To study the term in square brackets, let us set

$$g(S) = \frac{f_2(S)(f_1(S) - D)}{(S^0 - S)(f_2(S) - D)}.$$

It holds that

$$\lim_{S \to \lambda_2^-} g(S) = -\infty \qquad \lim_{S \to \lambda_2^+} g(S) = +\infty.$$

Moreover,

$$\lim_{S \to S^0} g(S) = +\infty \quad \text{and} \quad g(0) = g(\lambda_1) = 0.$$

Therefore, by using Lemma 5.1 we can choose c_1 so that

$$\sup_{0<S<\lambda_2} g(S) \leq c_1 \leq \inf_{\lambda_2 \leq S \leq S^0} g(S),$$

obtaining that $T_2 < 0$ (see Figure 1).

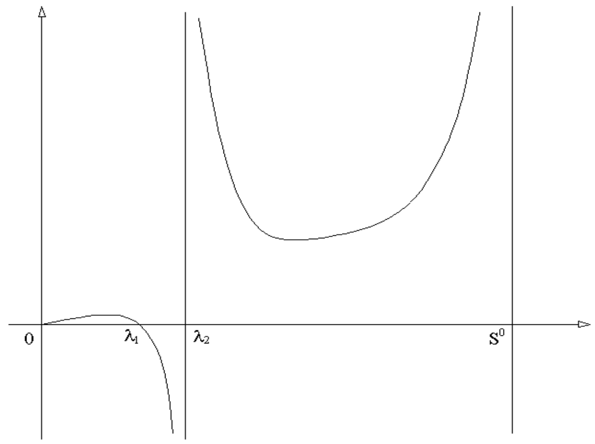

FIGURE 1. Graph of $g(S)$.

So, by considering condition (31), if we choose

$$\max\{\gamma, \sup_{0<S<\lambda_2} g(S)\} < c_1 \leq \inf_{\lambda_2 \leq S \leq S^0} g(S),$$

then all the assumptions of Theorem 5.1 hold true for the Liapunov functional (30) if we consider that $V(\phi) = V(\phi(0)) := a(|\phi(0)|)$, which is positive definite, and $\dot{V}(\phi)|_{(1)} = -b(|\phi(0)|)$ where $b(|\phi(0)|)$ is positive definite. This completes the proof for the global asymptotic stability of the equilibrium E_1. □

6. **Numerical Simulations: Solver Details.** First we observe that the complexity of the system has not allowed us to compute stability switches of equilibria through the Beretta-Kuang procedure [6]. Therefore, we will limit ourselves to presenting some numerical simulations obtained by specifying the nature of the kernel to illustrate the analytical results.
The simulations were obtained by using Matlab's ODE15s solver and by changing (1) in a finite-delay differential system.

Exponential delay kernel:

Consider the exponential delay kernel

$$\omega_1(\theta) = \begin{cases} \beta e^{\alpha\theta} & \alpha,\, \beta \in \Re_+,\ \theta \in [-\tau, 0] \\ 0 & \theta \in \Re - [-\tau, 0] \end{cases}.$$

We transform system (1) into an equivalent system of delay differential equations (35) with a fixed delay τ. "Equivalent" means that such a new system has the same equilibria and the same characteristic equation (regarding the original variables) as the original system (1). Define

$$u(t) = \int_{-\tau}^{0} \omega_1(\theta) N_1(t+\theta) d\theta. \tag{32}$$

By the transformation $s = t + \theta$ in (32), we obtain

$$u(t) = \int_{t-\tau}^{t} \omega_1(s-t) N_1(s) ds. \tag{33}$$

Therefore,

$$\begin{aligned} \frac{du}{dt} &= \omega_1(0)N_1(t) - \omega_1(-\tau)N_1(t-\tau) + \textstyle\int_{t-\tau}^{t} \frac{\partial \omega_1(s-t)}{\partial t} N_1(s)ds = \\ &= \beta N_1(t) - \beta e^{-\alpha\tau} N_1(t-\tau) + \textstyle\int_{t-\tau}^{t} \frac{\partial}{\partial t}(\beta e^{\alpha(s-t)}) N_1(s) ds = \\ &= \beta N_1(t) - \beta e^{-\alpha\tau} N_1(t-\tau) - \alpha u(t). \end{aligned} \tag{34}$$

Hence, system (1) is transformed into

$$\begin{cases} \dot{S} = (S^0 - S)D - f_1(S)N_1 - f_2(S)N_2 \\ \dot{N}_1 = N_1\left[f_1(S) - D - \gamma p\right] \\ \dot{N}_2 = N_2\left[(1 - ku(t))\, f_2(S) - D\right] \\ \dot{p} = N_2 f_2(S) k u(t) - Dp \\ \dot{u} = \beta N_1 - \beta e^{-\alpha\tau} N_1(t-\tau) - \alpha u, \end{cases} \tag{35}$$

with the following initial conditions for the original state variables:

$$\begin{array}{ll} S(t) = S(0) & \text{for } t \in [-\tau, 0]; \\ N_1(s) = \phi(s) & \text{for } s \in [-\tau, 0]; \\ N_2(t) = N_2(0) & \text{for } t \in [-\tau, 0]; \\ p(t) = p(0) & \text{for } t \in [-\tau, 0]. \end{array} \tag{36}$$

Furthermore, we define at $t = 0$ the initial condition for u in (35) by

$$u(0) = \int_{-\tau}^{0} \omega_1(s)\phi(s) ds. \tag{37}$$

The equilibria of system (35) are the same as those of system (1); in fact, if we consider the last equation of the following system,

$$\begin{cases} (S^0 - S)D - f_1(S)N_1 - f_2(S)N_2 = 0 \\ N_1\left[f_1(S) - D - \gamma p\right] = 0 \\ N_2\left[(1 - kN_1\Delta(\tau))\, f_2(S) - D\right] = 0 \\ f_2(S) k N_1 N_2 \Delta(\tau) - Dp = 0 \\ \beta N_1 - \beta e^{-\alpha\tau} N_1(t-\tau) - \alpha u = 0, \end{cases} \tag{38}$$

we obtain

$$\beta N_1(1 - e^{-\alpha\tau}) = \alpha u;$$

that is,

$$u = N_1 \frac{\beta(1 - e^{-\alpha\tau})}{\alpha} = N_1 \Delta(\tau).$$

By substituting this expression of u in the remaining equations of (38), we get

$$\begin{cases} (S^0 - S)D - f_1(S)N_1 - f_2(S)N_2 = 0 \\ N_1 \left[f_1(S) - D - \gamma p\right] = 0 \\ N_2 \left[(1 - kN_1\Delta(\tau))\, f_2(S) - D\right] = 0 \\ f_2(S)kN_1N_2\Delta(\tau) - Dp = 0, \end{cases}$$

which is exactly the original set of algebraic equations for equilibria of (1).

Moreover, with few calculations, it is easy to show that the characteristic equations of (35), corresponding to the equilibria, are the same of those of system (1). In the four simulations performed, only the size of the delay has been changed, whereas the set of initial conditions and the numerical values of the parameters

$$S^0 = 1.86,\ D = 0.6,\ m_1 = 1.45,\ m_2 = 1.58,\ a_1 = 2.39,\ a_2 = 2.73,\ \gamma = 0.8,$$
$$\beta = 2\log 2,\ \alpha = \log 1.2,\ k = 0.4.$$

have been kept fixed.

In Figure 2**a** there are three boundary rest points; hypotheses of Theorem 4.1$-$*iii*. hold and E_2 is locally asymptotically stable. In Figure 2**b** an interior rest point appears, and both E_1 and E_2 are locally asymptotically stable (*bistable attractors*).

Finally, in Figures 2**c** and 2**d**, according to the increasing of the size of delay, we note that the same initial conditions are attracted by different boundary equilibria, which proves that the basins of attraction of the asymptotic stable equilibria are changing.

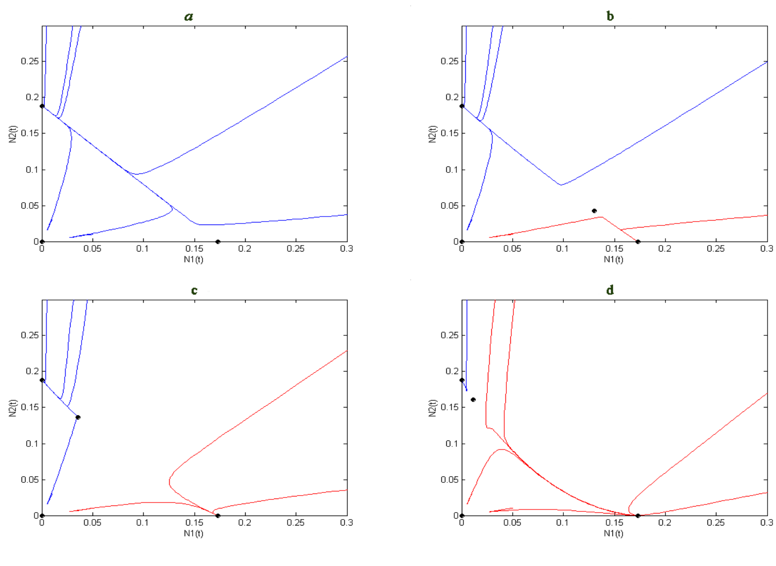

FIGURE 2. In graph (**a**), $\tau = 0.01$; in (**b**), $\tau = 0.08$; in (**c**), $\tau = 0.3$; and in (**d**), $\tau = 1$.

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