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A STOICHIOMETRICALLY DERIVED ALGAL GROWTH MODEL AND ITS GLOBAL ANALYSIS

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Abstract. Organisms are composed of multiple chemical elements such as carbon, nitrogen, and phosphorus. The scarcity of any of these elements can severely restrict organismal and population growth. However, many trophic interaction models only consider carbon limitation via energy flow. In this paper, we construct an algal growth model with the explicit incorporation of light and nutrient availability to characterize both carbon and phosphorus limitations. We provide a global analysis of this model to illustrate how light and nutrient availability regulate algal dynamics.

1. **Introduction.** For growth and maintenance of organismal cells, carbon (C), nitrogen (N) and phosphorus (P) are vital chemical elements: C supplies energy, N is an essential component of proteins, and P is an essential component of nucleic acids. The scarcity of any of these elements can severely restrict organismal and population growth. This concept forms the framework of the newly emerging research area "ecological stoichiometry" that deals with the balance of energy and nutrient elements in ecology [17]. In many circumstances, natural stoichiometric constraints can be essential for modeling ecological interactions [7, 12, 16].

Suspended algae, called phytoplankton, live in almost all kinds of aquatic environments. Algae grow in open water by taking up energy from sunlight and nutrients such as N, P from the water. Light and nutrient availability are two most fundamental characteristics of an aquatic ecosystem for living organisms. Light intensity varies greatly along the depth of water column or seasonally or day-and-night. Nutrient availability is controlled by many environmental inputs such as surrounding farms, rivers, brooks, and atmosphere.

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Algae are the primary producer in aquatic ecosystems and the main food for herbivores and some small fishes. Furthermore, algae produce energy through photosynthesis to support the whole community of living organisms including fish and heterotrophic bacteria. Therefore, it is pivotal to better understand the dynamics of algal density and nutritional status.

Algal dynamics have been modeled and/or discussed by many scientists: Huisman and Weissing (1994,1995) [9, 10], Klausmeier and Litchman (2001) [11], Diehl (2002) [3], Diehl et al.(2005) [4], Berger et al. (2006) [2]. Many modeling efforts for stoichiometry of ecological interactions have been made by the following studies: Andersen (1997) [1], Hessen and Bjerkeng (1997) [8], Loladze et al. (2000) [16], Grover (2002) [7], Kuang et al. (2004) [13], Kuijper et al. (2004) [14], Logan et al. (2004) [15], Wang et al. (2007) [18], Wang et al. (2008) [19].

In this paper, we derive a new stoichiometric model for algal growth in a nutrient-closed system. Our model captures key biological features of light- and nutrient-dependent algal growth, especially, the algal cell quota is always above the minimum cell quota. We present rigorous mathematical analysis for the model. The main difficulty is that the system is undefined at the origin, which is a transformation generated steady state. To show the global stability of the origin, we devise a transformation to generate a new system that is defined at this steady state. The transformation converts variables algal C and algal P to variables algal C:P ratio and algal P. From our mathematical results, we obtain the following observations: 1) Algae go extinct if the nutrient is severely limiting; 2) Algae always survive with sufficient nutrient and any nonzero light intensity; 3) Whenever algae can survive, the unique internal steady state is globally attracting under strong light, whereas the boundary steady state with algal C at its carrying capacity is globally attracting under weak light. The simulation with realistic parameter values illustrates that the origin is always unstable and algae always survive with two possible globally attracting states: the internal equilibrium or the boundary equilibrium with algal C at its carrying capacity. We also find that algal quality is worse when light is stronger and algal quality is better when the nutrient availability is higher.

2. Derivation of algal growth model.

We consider a carbon-open but nutrient-closed ecosystem for algae. We define algal carbon biomass (measure in density) as x, algal phosphorus biomass (measure in density) as p, and thus $Q = p/x$ is algal cell quota (intracellular P:C ratio). Based on two recently published papers [13, 19], we introduce differential equations for algal P and cell quota, which are applied to derive the algal growth equation.

According to Wang et al. (2008) [19], we have the following equation for algal P:

$$\frac{dp}{dt} = g(T-p)x - dp,$$

where T is the total P, $g(T-p)$ is the P-uptake function, and d is the P loss/recycling rate of algae.

According to Kuang et al. (2004) [13], we have the following equation for algal cell quota:

$$\frac{dQ}{dt} = g(T-p) - \mu(Q-q),$$

where q is the minimum cell quota of algae, and μ is the algal maximal growth rate.

We apply the equations for p and Q to derive the equation for nutrient-dependent algal growth (measured by carbon content):

$$\begin{aligned}\frac{dx}{dt} &= \frac{d}{dt}\left(\frac{p}{Q}\right)\\ &= \left(\frac{dp}{dt}Q - p\frac{dQ}{dt}\right)\Big/Q^2\\ &= [g(T-p)xQ - dpQ - g(T-p)p + \mu(Q-q)p]/Q^2\\ &= [(\mu-d)pQ - \mu qp]/Q^2\\ &= (\mu-d)x - \mu q x^2/p\\ &= (\mu-d)x\left[1 - \frac{\mu}{\mu-d}\frac{x}{p/q}\right].\end{aligned}$$

This new equation obeys the framework of Droop's cell quota model [5, 6].

Together with the logistic equation for light-dependent algal growth, we obtain the full version of algal growth equation:

$$\frac{dx}{dt} = (\mu-d)x\left(1 - \max\left\{\frac{x}{K}, \frac{\mu}{\mu-d}\frac{x}{p/q}\right\}\right).$$

Let $\mu - d = r$ and $\bar{q} = \frac{\mu}{\mu-d}q > q$, then the model for nutrient- and light-dependent algal growth is simplified to be

$$\frac{dx}{dt} = rx\Big(1 - \frac{x}{\min\{K, p/\bar{q}\}}\Big), \tag{1}$$

$$\frac{dp}{dt} = g(T-p)x - dp. \tag{2}$$

3. **Mathematical analysis.** Let $k = \min\{K, T/\bar{q}\}$ and $\Omega = \{(x,p) \in \mathbb{R}^2_+ : 0 < x < k, qx < p < T\}$. Biologically any solution starting from a point in the region Ω should stay in Ω for ever (i.e., Ω is positively invariant), because algal C biomass should be less than the limiting carrying capacity K (if light is limiting) or $T/\bar{q}$ (if the nutrient is limiting), algal P biomass should be less than T (the total nutrient availability), and the algal cell quota p/x should be greater than the minimum structural cell quota q. Mathematically we can also show that Ω is a positively invariant region for the system (1)-(2) (see Theorem 1), thus our new model is biologically reasonable.

Theorem 1. *The open trapezoid domain Ω is positively invariant for the flow generated by the system (1)-(2).*

Proof. To prove the positive invariance of Ω, we only need to examine direction fields on the boundary of Ω. On the upper boundary of Ω, $p = T$, $x \in [0, k]$, $\frac{dp}{dt} = -dT < 0$. On the left boundary of Ω, $x = 0$, $p \in (0, T)$, $\frac{dx}{dt} = 0$. On the right boundary of Ω, $x = k$, $p \in (0, T)$, $\frac{dx}{dt} = rk\left(1 - \frac{k}{\min\{K, p/\bar{q}\}}\right) \leq 0$. Therefore, all orbits starting from Ω cannot escape Ω from these three boundaries.

It remains to show that all orbits starting from Ω cannot leave Ω from the bottom boundary $\{(x,p) : 0 < x < k, p = qx\}$ of Ω. Observe that if the light is more limiting at time t, then $K < \frac{\mu-d}{\mu q} p(t)$, i.e.,

$$\frac{(\mu-d)x}{\mu K} > \frac{q}{Q}. \tag{3}$$

In the following, we show that if $p(0)/x(0) > q$, then $p(t)/x(t) > q$ for all $t > 0$. If this is not true, there is a $t_1 > 0$ such that $Q(t_1) = p(t_1)/x(t_1) = q$ and $Q(t) = p(t)/x(t) > q$ for $t \in [0, t_1)$. These clearly imply that $\frac{dQ}{dt}(t_1) \leq 0$. We consider below the case that the light is limiting at time t_1 (the other case is obvious from the derivation of the x equation)

$$\begin{aligned} \frac{dQ(t)}{dt} &= \frac{d}{dt}\left(\frac{p(t)}{x(t)}\right) = \frac{dp(t)}{dt}\frac{1}{x(t)} - \frac{Q}{x(t)}\frac{dx(t)}{dt} \\ &= g(T-p) - dQ - Q(\mu-d)\left(1 - \frac{x}{K}\right) \\ &= g(T-p) - \mu Q\left(1 - \frac{\mu-d}{\mu K}x\right). \end{aligned}$$

This together with (3) implies

$$\frac{dQ}{dt}(t_1) > g(T - p(t_1)) > 0$$

which contradicts $\frac{dQ}{dt}(t_1) \leq 0$. This concludes the proof. □

To analyze the stability of equilibria, we first compute the nullclines. Define that

$$\begin{aligned} F(x,p) &= rx\left(1 - \frac{x}{\min\{K, p/\bar{q}\}}\right) = \begin{cases} rx(1-\frac{x}{K}), & p \geq \bar{q}K; \\ rx(1-\frac{\bar{q}x}{p}), & p < \bar{q}K. \end{cases} \\ G(x,p) &= g(T-p)x - dp. \end{aligned}$$

Algal C-nullcline: $x = 0$, and $x = K$ (if $p \geq \bar{q}K$) or $p = \bar{q}x$ (if $p < \bar{q}K$). Denote $l_1 : p = \bar{q}x \triangleq p_1(x)$.

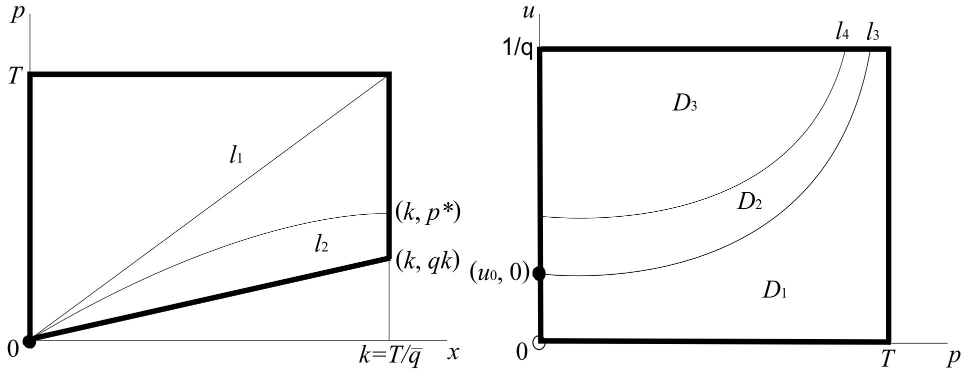
Algal P-nullcline: $g(T-p)x = dp$. Since $G(0,0) = 0$, $\frac{\partial G}{\partial p} = -g'(T-p)x - d < 0$, we can deduce the existence of the smooth curve $l_2 : p = p_2(x)$ satisfying

i): $G(x, p_2(x)) \equiv 0, \forall x \in (0, k]$;
ii): $p_2(0) = 0, p_2(k) = p^* \in (0, T)$;
iii): $\frac{dp_2(x)}{dx} = -\frac{G_x(x, p_2(x))}{G_p(x, p_2(x))} > 0$;
iv): $\frac{d^2 p_2(x)}{dx^2} < 0$.

We now discuss steady states and their stabilities for all possible cases. There are five possible cases according to light intensity (K) and nutrient availability (T).

★ Case 1. $K \geq T/\bar{q}$, $g(T) \leq d\bar{q}$.

In this case, $k = \min\{K, T/\bar{q}\} = T/\bar{q}$, $F(x,p) = rx(1 - \bar{q}x/p)$, $G(x,p) = g(T-p)x - dp$. The condition $g(T) \leq d\bar{q}$ implies the slope of l_1 is larger than that of l_2 at the origin. Note that $p_2''(x) < 0$, then l_2 is below l_1 (see Figure 1(a)). Thus, no



(a) The nullclines of the original system (1)-(2) in case 1

(b) The nullclines of the transformed system (5)-(6) in case 1

FIGURE 1. The nullclines and notations for case 1.

equilibria exist in this case. A natural question arises: where will orbits go? We will prove that all orbits tend to the origin $E_0 = (0, 0)$, i.e., algae go extinct. Actually, the origin is not a steady state but plays a similar role as a steady state.

Theorem 2. *All solutions in Ω tend to the origin E_0, i.e., E_0 is G.A.S. (globally asymptotically stable).*

Proof. we introduce the transformation

$$\Phi : \Omega \to \Phi(\Omega), (x, p) \mapsto (u = x/p, p), \tag{4}$$

which converts the system (1)-(2) in Ω into the new system

$$\frac{du}{dt} = u[d + r - (\bar{q}r + g(T - p))u], \tag{5}$$

$$\frac{dp}{dt} = p[g(T - p)u - d]. \tag{6}$$

Here

$$\Phi(\Omega) = \{(u, p) \in \mathbb{R}^2_+ : 0 < u < 1/q, 0 < p < T\}.$$

This system has two equilibria $(0, 0)$ and $(u_0, 0)$ with $u_0 = \dfrac{d + r}{\bar{q}r + g(T)}$ (see Figure 1(b)). Note that $g(T) \le d\bar{q}$, then $u_0 < 1/\bar{q} < 1/q$, and the equilibrium $(u_0, 0)$ lies on the left boundary of $\Phi(\Omega)$.

The u-nullcline is $l_3 : u = 0$ and $u = u_1(p) = \frac{d+r}{\bar{q}r+g(T-p)}$, $0 \le p < T$. The p-nullcline is $l_4 : p = 0$ and $u = u_2(p) = \frac{d}{g(T-p)}$, $0 \le p < T$. Since $1/q > \dfrac{d}{g(T - p)} \ge \dfrac{dr}{\bar{q}r + g(T)}$ by $d\bar{q} \ge g(T)$, l_4 is above l_3 (see Figure 1(b)).

Define the regions

$$\begin{aligned} D_1 &= \{(u, p) : 0 < p < T, 0 < u < u_1(p)\}, \\ D_2 &= \{(u, p) : 0 < p < T, u_1(p) < u < u_2(p)\}, \\ D_3 &= \{(u, p) : 0 < p < T, u_2(p) < u < 1/q\}. \end{aligned}$$

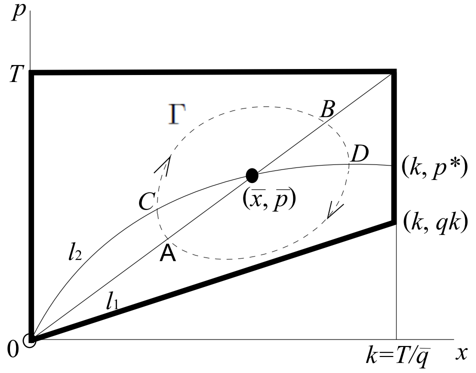


FIGURE 2. The nullclines and notations for case 2.

In D_1, $\dfrac{du}{dt} > 0$, $\dfrac{dp}{dt} < 0$. In D_2: $\dfrac{du}{dt} < 0$, $\dfrac{dp}{dt} < 0$. In D_3: $\dfrac{du}{dt} < 0$, $\dfrac{dp}{dt} > 0$. Thus, any solution starting from the region D_1 tends to the equilibrium $(u_0, 0)$. Any solution starting from the region D_3 first enters the region D_2, and then either directly tends to the equilibrium $(u_0, 0)$ or passes through the region D_1 and then tends to the equilibrium $(u_0, 0)$. Thus, any solution $(u(t), p(t))$ of the system (5)-(6) tends to the equilibrium $(u_0, 0)$, i.e.,

$$\lim_{t\to\infty} u(t) = u_0 = \frac{d+r}{\bar{q}r + g(T)}, \quad \lim_{t\to\infty} p(t) = 0,$$

which implies that

$$\lim_{t\to\infty} x(t) = \lim_{t\to\infty} u(t)p(t) = 0, \quad \lim_{t\to\infty} p(t) = 0.$$

Therefore, the origin of the system (1)-(2) is G.A.S. □

In the proof of Theorem 2, we introduce the transformation Φ in (4) to prevent orbits entering into the origin where the system is undefined. This transformation converts variables algae C and algal P to variables algal C:P ratio (reciprocal of cell quota) and algal P. In many of the following theorems, this transformation will be used again.

★ Case 2. $K \geq T/\bar{q}$, $g(T) > d\bar{q}$.

In this case, $k = \min\{K, T/\bar{q}\} = T/\bar{q}$, $F(x,p) = rx(1 - \bar{q}x/p)$, $G(x,p) = g(T - p)x - dp$.

The condition $g(T) > d\bar{q}$ means that the slope of l_2 at the origin is larger than that of l_1 at the origin (see Figure 2). Thus, l_1 and l_2 have a unique intersection $E_1 = (\bar{x}, \bar{p})$, which is the unique equilibrium of the system (1)-(2) with $\bar{p} = \bar{q}\bar{x}$, and $\bar{p}$ satisfies

$$g(T - \bar{p}) = d\bar{q}. \tag{7}$$

Theorem 3. *The internal equilibrium E_1 is G.A.S.*

Proof. We first show that E_1 is L.A.S. (locally asymptotically stable). At the equilibrium E_1,

$$F_x = r(1 - 2\bar{q}\bar{x}/\bar{p}) = -r, \qquad F_p = r\bar{q}\bar{x}^2/\bar{p}^2 = r/\bar{q},$$

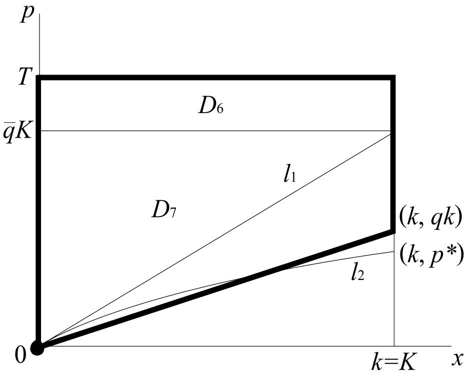


FIGURE 3. The nullclines and notations for case 3.

$$G_x = g(T - \bar{p}), \qquad G_p = -g'(T - \bar{p})\bar{x} - d.$$

The determinant of Jacobian Matrix at E_1 is

$$F_x G_p - G_x F_p = rg'(T - \bar{p})\bar{x} + rd - (r/q)g(T - \bar{p}) = rg'(T - \bar{p})\bar{x} > 0.$$

The trace of Jacobian Matrix at E_1 is

$$F_x + G_p = -r - g'(T - \bar{p})\bar{x} - d < 0.$$

Therefore, E_1 is L.A.S.

Next, we show that all solutions $(x(t), p(t))$ of the system (1)-(2) satisfy the condition $\lim_{t\to+\infty} p(t) \neq 0$, i.e., solutions of (1)-(2) never tend to the origin. Note that Theorem 1 has shown that all solutions of (1)-(2) do not touch the origin at a finite time. Following the same logic, we introduce the transformation Φ defined in (4) and the transformed system (5)-(6). This system has two equilibria $(u_0, 0)$ and $(1/\bar{q}, \bar{p})$. Therefore, in order to show that any solution of the original system (1)-(2) does not tend to the origin as time goes to infinity, we only need to prove that any solution of the transformed system (5)-(6) does not tend to the equilibrium $(u_0, 0)$. This result is obvious because the equilibrium $(u_0, 0)$ is a saddle whose stable manifold is the u-axis.

Finally, in order to show that E_1 is G.A.S., we only need to show that the system (1)-(2) in Ω has no periodic orbits. Suppose that the system (1)-(2) has a periodic solution $\Gamma : (x(t), p(t))$ in Ω. Since E_1 is the unique equilibrium of (1)-(2), then it has to be inside closed orbit Γ. Therefore, Γ must intersect with l_1, l_2. Denote the intersections of Γ and l_1 as A (left) and B (right); denote the intersections of Γ and l_2 as C (left) and D (right) (see Figure 2).

Note that in the region $D_4 = \{(x, p) : 0 < x < k, \bar{q}x < p < T\}$, $\dfrac{dx}{dt} > 0$, and in the region $D_5 = \{(x, p) : 0 < x < k, p_2(x) < p < T\}$, $\dfrac{dp}{dt} < 0$.

From the first fact, we deduce that the orbit Γ has the clockwise direction. On the other hand, integrating the equation (2) and from the second fact, we deduce that the p-coordinate of the point D is smaller than that of the point C, which contradicts to the fact that the curve l_2 is monotone increasing. This concludes the proof. □

★ Case 3. $p^*/\bar{q} < K \leq T/\bar{q}$, $g(T) \leq d\bar{q}$.

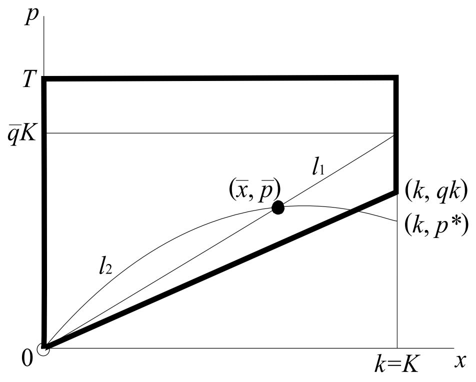


FIGURE 4. The nullclines and notations for case 4.

The number p^* satisfies $g(T - p^*)k = dp^*$. In this case, $k = \min\{K, T/\bar{q}\} = K$,
$$F(x,p) = \begin{cases} rx(1 - \bar{q}x/p), & 0 < p < \bar{q}K \\ rx(1 - x/K), & \bar{q}K \leq p < T \end{cases}, \; G(x,p) = g(T-p)x - dp.$$

In this case, the system has no equilibria, and the origin E_0 is G.A.S.

Theorem 4. *The origin E_0 is G.A.S.*

Proof. Denote $D_6 = \{(x,p) : 0 < x < K, \bar{q}K < p < T\}$, $D_7 = \{(x,p) : 0 < x < K, 0 < p < \bar{q}K\}$. Since $\dfrac{dp}{dt} < 0$ in D_6, any solution starting from D_6 will enter the region D_7 and stay in D_7 for all times. The remaining proof is the same as that in Theorem 1. ☐

★ Case 4. $p^*/\bar{q} < K \leq T/\bar{q}$, $g(T) > d\bar{q}$.

In this case, $k = \min\{K, T/\bar{q}\} = K$, $F(x,p) = \begin{cases} rx(1 - \bar{q}x/p), & 0 < p < \bar{q}K \\ rx(1 - x/K), & \bar{q}K \leq p < T \end{cases}$, $G(x,p) = g(T-p)x - dp$, $\bar{x} = \bar{p}/\bar{q}$, $g(T - \bar{p}) = \bar{q}d$.

Theorem 5. *The internal equilibrium $E_1 = (\bar{x}, \bar{p})$ is G.A.S.*

Proof. The proof is completely same as that of Theorem 3. ☐

★ Case 5. $K \leq p^*/\bar{q}$.

In this case, $k = \min\{K, T/\bar{q}\} = K$, $F(x,p) = \begin{cases} rx(1 - \bar{q}x/p), & 0 < p < \bar{q}K \\ rx(1 - x/K), & \bar{q}K \leq p < T \end{cases}$, $G(x,p) = g(T-p)x - dp$. The system (1)-(2) has a unique equilibrium $E_2 = (K, p^*)$ on the boundary of Ω.

Theorem 6. *The boundary equilibrium E_2 is G.A.S.*

Proof. E_2 is L.A.S because $F_x = -r$, $F_p = 0$, $G_x = g(T - p^*)$ and $G_p = -g'(T - p^*)K - d$. In order to prove that E_2 is G.A.S., we only need to prove that $\lim\limits_{t\to\infty} p(t) \neq 0$.

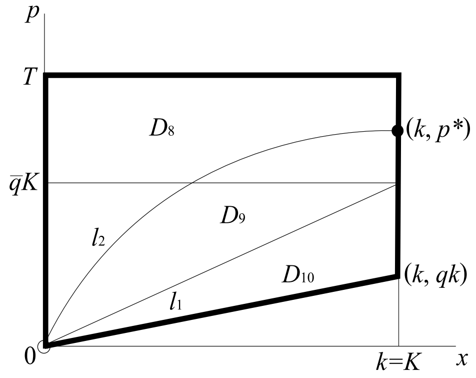


FIGURE 5. The nullclines and notations for case 5.

Recall that the C-nullcline is $l_1 : p = p_1(x) = \bar{q}x$, and the P-nullcline $l_2 : p = p_2(x)$ satisfies four conditions i)-iv). Define the regions

$$\begin{aligned} D_8 &= \{(x,p) : 0 < x < K, p_2(x) < p < T\}, \\ D_9 &= \{(x,p) : 0 < x < K, p_1(x) < p < p_2(x)\}, \\ D_{10} &= \{(x,p) : 0 < x < K, qx < p < p_1(x)\}. \end{aligned}$$

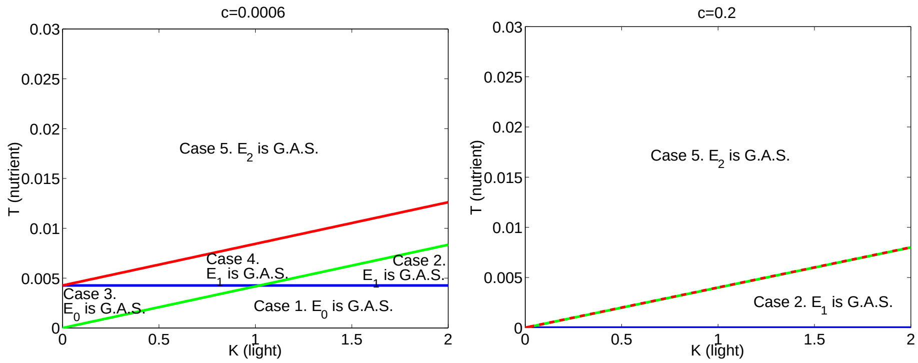
In D_8, $\frac{dx}{dt} > 0$, $\frac{dp}{dt} < 0$. In D_9, $\frac{dx}{dt} > 0$, $\frac{dp}{dt} > 0$. In D_{10}, $\frac{dx}{dt} < 0$, $\frac{dp}{dt} > 0$.

The region D_9 is positively invariant, and any solution starting from D_9 will tend to E_2. Some orbits in the region D_8 directly tend to E_2, and the others enter into D_9 first and then tend to E_2. All orbits starting in the region D_{10} enter into D_9 first, and tend to E_2 finally. □

Note that in Case 3, Case 4, and Case 5, $p^* = \alpha TK/(\alpha K + d)$, if $g(y) = \alpha y$; or $p^* = [cK + ad + Td - \sqrt{(cK + ad + Td)^2 - 4dcKT}]/2d$, if $g(y) = cy/(a + y)$. We should take these relationships into consideration when we examine how global stability conditions depend on light intensity (K) and nutrient availability (T).

4. **Discussion.**

We develop and analyze a new stoichiometric algae model. Our global stability results provide conditions on how light and nutrient availability determine algal dynamics. The numerical test (Figure 6(a)) plots separated regions for all five cases to graphically illustrate these mathematical conditions. Algae go extinct if the nutrient is severely limiting. Algae always survive with sufficient nutrient supply and any nonzero light intensity, which means that the nutrient availability is more crucial for algal survival. Whenever algae can survive, the unique internal steady state is globally attracting under strong light, while the boundary steady state is globally attracting under weak light. The five cases are reduced to two cases in the numerical simulation (Figure 6(b)) with realistic parameter values (estimated in Table 1). This figure illustrates that algae always survive with two possible globally attracting states: the internal equilibrium or the boundary equilibrium. Figure 7 shows that, with fixed nutrient availability T, the algal P:C ratio at the attracting steady state is always decreasing as light intensity K increases, that is, algal quality becomes worse when light is stronger. When the nutrient availability is higher, algal quality becomes better. However, this difference is small



(a) $c = 0.0006$ (mg P)/(mg C)/day, which is an unrealistic value. It is designed mathematically to show all possible cases.

(b) $c = 0.2$ (mg P)/(mg C)/day, which is the realistic value in Table 1. We observe that Only two cases exist in reality.

FIGURE 6. The dependence of dynamics on light intensity (K) and nutrient availability (T). Here, $g(y) = cy/(a + y)$. The blue line is $cT/(a + T) = d\bar{q}$; the green line is $K = T/\bar{q}$; the red line is $K = p^*/\bar{q}$. The panel (a) illustrates that all five cases can occur when the parameter c is unrealistically small. The panel (b) illustrates that only two cases have dominant probability to occur while other three cases occur with almost zero probability when the parameter c is realistic.

TABLE 1. The parameters (P) of the system (1)-(2) and their values (V) used for numerical simulations.

P	Description	V	Unit
K	Light-dependent carrying capacity of algae	$0 - 2$	(mg C)/l
T	Total P in the system	$0 - 0.03$	(mg P)/l
μ	Maximum growth rate of algae	1.2	day^{-1}
q	Minimum P:C ratio of algae	0.004	(mg P)/(mg C)
d	P loss/recycling rate of algae	0.05	day^{-1}
c	Maximum P uptake rate of algae	0.2	(mg P)/(mg C)/day
a	P-dependent half-saturation constant of algae	0.008	(mg P)/l

Note that $g(y) = \dfrac{cy}{a + y}$. Parameter values are estimated from [1, 13, 16, 19].

when light is strong. These observations are consistent to previous empirical studies [17, 20].

A transformation generated steady state appears in our model and can be globally asymptotically stable (see Theorems 2&4). Linear stability analysis cannot be applied because the Jacobian matrix is undefined at such a steady state. We devise a transformation to prove its global stability.

We model a nutrient-closed system for algae because many microcosm experiments are closed in nutrients. The system can be open such as open-water lake ecosystems. A nutrient-open system can easily be constructed by incorporating standard chemostat in- and out-flows.

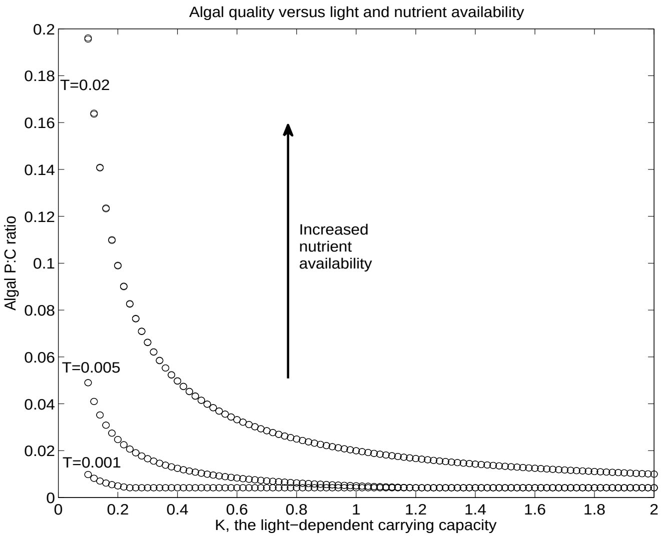


Figure 7. Algal cell quota versus light and nutrient availability. The parameter $c = 0.2$ as in Table 1.

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